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How do banded mongooses locate and select anvils for cracking encased food items?

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ABSTRACT

Banded mongooses (*Mungos mungo*) extract encased food items by throwing them against anvils. Observations indicate that their chosen anvils are generally hard enough to crack open casings, suggesting an understanding of the physical properties that render an anvil suitable for cracking. We report results from two field experiments investigating spatial and physical aspects of anvil selection in a wild group of banded mongooses. Mongooses rapidly carried prey items to nearby anvils in their environment, without simply returning to the last anvil they passed, suggesting a detailed knowledge of anvil locations. Moreover, in choice experiments with hard or soft anvils, they always chose the appropriate anvil when both anvils were natural but chose indiscriminately when they were synthetic. These results support a recent suggestion that mongooses lack a generalized understanding of the functional properties of anvils but also indicate that they may mediate their decisions on the basis of familiarity. Together, our experiments suggest that mongooses employ simple rules of thumb that, in most cases, result in the selection of appropriate anvils. Where environmental problems are limited and predictable, selection will favor the evolution of such rules of thumb rather than a more generalized understanding of functional properties.
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1. Introduction

If individuals encounter recurrent problems in their environment, natural selection may favor the evolution of cognitive mechanisms allowing them to respond appropriately and efficiently. The generality and flexibility of such mechanisms is likely to depend on the degree of environmental variability and the range of problems encountered. This is clearly illustrated by the variability of mechanisms underpinning tool use in animals. Tool use may be defined as "the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment" (St Amant and Horton, 2008). Where problems are limited and predictable, reflexive actions or rules of thumb, honed through simple learning processes, may suffice to enable individuals to manipulate objects to achieve a goal. For example, larval antlions (*Myrmeleon spp.*) build a pit-trap and, in response to vibrational cues, flick grains of sand to knock passing prey into the pit. Antlion tool-use occurs in this context alone and hinges on stereotyped actions refined through learned associations to better anticipate the arrival of prey (Guillette et al., 2009). In contrast, where problems are variable and unpredictable, selection may favor more flexible, generalizable cognitive mechanisms. Human tool use, for instance, is thought to be underpinned by the capacity to reason about abstract cause-and-effect relations and to generalize about the functional properties of novel objects from past experience (Hauser and Santos, 2007; Povinelli, 2000).

Experiments investigating the cognitive mechanisms underpinning non-human tool use have been conducted on a number of species, particularly primates and corvids. These have generated at best limited evidence for an understanding of abstract cause-and-effect relations (Emery and Clayton, 2009; Penn and Povinelli, 2007). For instance, in a two-trap version of the classic trap-tube paradigm (Visalberghi and Limongelli, 1994), six out of seven rooks (*Corvus frugilegus*) quickly learned to solve the problem and successfully transferred their solutions to a novel but visually similar version of the task (Seed et al., 2006). However, only one individual was able to solve two further versions of the task with no visual cues in common. Similar experiments on chimpanzees (*Pan troglodytes*) produced comparable results, with only two out of eight individuals solving equivalent transfer tests (Seed et al., 2009). Indeed, the equivocal evidence from experiments on non-human animals has led some authors to suggest that humans alone are capable of causal reasoning about unobservable physical forces (Penn and Povinelli, 2007; Penn et al., 2008).

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Stronger evidence suggests that some nonhuman animals may understand how the physical properties of objects affect their functionality as tools. For example, captive New Caledonian crows (*Corvus moneduloides*) can select sticks of appropriate length and diameter for food extraction tasks (Chappell and Kacelnik, 2002, 2004) and modify tools according to need (Weir et al., 2002). Similarly, cotton-top tamarins (*Saguinus oedipus*) trained to use a piece of cloth or a cane to retrieve food recognized that differences in shape and size affected tool functionality while color and texture did not (Hauser et al., 1999, 2002). Together, these results indicate that the use of tools by captive corvids and primates is underpinned by a basic understanding of the physical properties of objects, which may be refined and modified through generalization from previous experience. The extent to which this applies to tool use and other related behaviors in these and other species under natural conditions remains unclear.

To date, the vast majority of work on animals' understanding of the functional properties of objects has been conducted in captivity (studies of nut cracking in wild chimpanzees and capuchins are a notable exception: Sakura and Matsuzawa, 1991; Matsuzawa, 1994; Boesch and Boesch-Achermann, 2000; Visalberghi et al., 2009). While captive studies enable a great deal of experimental control, they often have little bearing on problems encountered under natural conditions, and it is not clear to what degree their results reflect the mechanisms employed by animals in the wild (Cheney and Seyfarth, 1990; Boesch, 2007; Gajdon et al., 2004; but see Tomasello and Call, 2007). If we are to understand of the evolution of cognitive mechanisms it is therefore critical to investigate how wild animals solve problems in their natural environments. In the case of object-directed behaviour such as tool use, this requires consideration of both animals' understanding of the physical properties of the objects they manipulate and mechanisms of spatial cognition allowing them to locate relevant objects in their environment. Here, we used a combination of observational and experimental data to examine elements of spatial and physical cognition underpinning object use in wild banded mongooses (*Mungos mungo*).

Banded mongooses are communally breeding carnivores that live in stable groups of 8–40 individuals in moist savannah and open woodland in eastern and southern Africa and eat a variety of invertebrate and small vertebrate prey (Rood, 1975). In common with certain other mongoose species, banded mongooses regularly pick up encased prey items such as beetles, eggs and balls of dung containing insect larvae and throw them between their legs against anvils to crack them and extract the food within (Rood, 1975). While not a form of tool use under most definitions (because individuals are manipulating a food item as opposed to the anvil; St Amant and Horton, 2008), this behavior, like tool use, requires the use of an external object (the anvil) to achieve a goal, and may therefore call on some understanding of object properties, as well as the ability to locate anvils in the environment.

Adult mongooses typically select anvils hard enough to crack open prey, and have had experience using different types of anvil (such as rocks and tree trunks) throughout their lives. Nevertheless, a recent study suggests that they may not be capable of generalizing from their previous experience of the physical attributes that render an anvil suitable for cracking (hardness) to choose appropriately if confronted with novel anvil types. Müller (2010) allowed mongooses to inspect a hard anvil suitable for cracking open encased items (a brick wrapped in a cotton sheet) or a similar anvil rendered unsuitable by wrapping it in foam. When subsequently given the choice of throwing an encased food item against either anvil, there was no preference for the suitable anvil, although there was some indication of a shift towards the suitable anvil over the course of several trials. This study suggests that while mongooses may learn about individual anvil types through trial and error, they cannot call upon a more general knowledge of functional properties. However, it may be that mongooses did not perceive a brick wrapped in a sheet or a brick wrapped in foam as differing substantially in hardness, since both would retain their shape when sat on. Thus, it remains unclear (a) how mongooses locate suitable anvils in their environment, (b) whether they can spontaneously choose anvils based on their functional properties and (c) how familiarity with anvil materials mediates their decisions.

To examine how mongooses find anvils within their territory, we presented adult individuals with an artificial food item and recorded where they took it, making note of whether they scanned their surrounding beforehand. This simple experiment allowed us to determine whether mongooses (i) visually scan their environment for the presence of anvils or (ii) simply return to the last anvil they passed. Alternatively, they may possess detailed knowledge of the locations of anvils within their territory, allowing them to go directly to a nearby anvil without the need for scanning.

We also tested adult mongooses' ability to make spontaneous anvil choices after examining pairs of anvils that differed substantially in hardness. Adult mongooses have used numerous different anvil types throughout their lives, allowing ample opportunity for them to acquire a generalized understanding of the physical properties required for a functional anvil. One would therefore predict that, if they recognize that the property of hardness is crucial, they should spontaneously make the correct choice when confronted with a novel hard or soft anvil. As mongooses' anvil selection may also be mediated by their familiarity with anvil materials, we used both anvils made from natural materials commonly found in the area and anvils made from synthetic materials that were likely to be unfamiliar to the mongooses. We predicted that if mongooses are able to generalize about the functional properties of anvils, they should consistently select the hard surfaces when attempting to crack open an encased food item, irrespective of whether anvils were natural or synthetic. However, if experience with different materials mediates anvil selection, we predicted that mongooses should select hard natural anvils when paired with soft natural anvils but show no preference between hard and soft synthetic anvils. We supplemented our experiments with observations of natural throwing behavior to assess the extent to which mongooses tend to choose appropriate food items and anvils for cracking.

2. Methods

2.1. Study site and population

Data were collected from August to September 2007 on a group of 34 habituated banded mongooses in Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E; details of habitat and climate are given in Cant, 2000). The group ranged within an area including Mweya Safari Lodge and an adjacent village and so had access to refuse in addition to their normal diet (Gilchrist and Otali, 2002). The study population also had access to a number of manmade objects including wooden posts and concrete walls, many of which served as suitable surfaces for cracking open encased food items. All individuals were identifiable through unique haircuts or color-coded plastic collars (Cant, 2000).

2.2. Research design

We collected a combination of experiments and supporting observational data. During 84 h of behavioral observation, we recorded instances of mongooses throwing objects against anvils ad libitum (Altmann, 1974) noting the identity of the individual, its age (adults: >12 months; juveniles: <6 months; Furrer and Manser, 2009), the type of object thrown and the type of surface.

Table 1
Observations of individuals throwing objects against anvils. The initial letter of individual identities denotes sex (F, female; M, male).

Individual	Age	Object thrown	Anvil	Suitable?
F262	Adult	Sanitary pad (used)	Cement rubbish bin	No
M340	Juvenile	Bottle cap	Mongoose	No
F339	Juvenile	Round fruit	Tree	Yes
M340	Juvenile	Plastic yoghurt bag	Tree	No
F341	Juvenile	Hammerkop egg	Hardened earth	Yes
Unknown[a]	Adult	Beetle	Wall	Yes
M228	Adult	Fish tail	Tree	No
F339	Juvenile	Fruit	Mongooses	No
F341	Juvenile	Bottle cap	Mongoose	No
Unknown[a]	Adult	Ball of mud with larva	Hole in ground	Yes
F348	Juvenile	Lollipop	Pole	Yes (arguably)[b]
M311	Adult	Lollipop	Block of wood	Yes (arguably)[b]
M210	Adult	Small stone	Mongoose	No
M310	Adult	Beetle	Tree	Yes
F309	Adult	Beetle	Pole	Yes
M311	Adult	Beetle	Pole	Yes
M316	Adult	Beetle	Pole	Yes
M307	Adult	Beetle	Pole	Yes

[a] In two cases, we were unable to identify the individual throwing the object.
[b] We have denoted two instances in which individuals threw a hard-boiled sweet lollipop against an anvil as 'arguably' suitable because they could potentially be cracked open.

We classified objects and anvils as suitable or unsuitable for cracking depending on whether they could potentially be broken open to yield encased food (objects) or were hard and large enough to crack open a raw egg (anvils; these included rocks, trees, and walls). In addition, we conducted two experiments on a total of 19 subjects, all of which were adults. We attempted to test all subjects in both experiments but this was not possible due to different levels of habituation, so sample sizes in experiments vary. In both experiments we presented individuals with either a hollow plastic ovoid (Kinder Surprise, Ferrero UK, Watford, U.K.) or a hollow film canister with the lid taped shut (hereafter both objects are referred to as "eggs"). Eggs were filled with food rewards and had several small perforations so that the subjects could smell the food inside. Food rewards were either scrambled egg, dried fish or a thick syrup of powdered milk, sugar and water. We used different food rewards to maintain subjects' interest in the objects and their motivation to throw them. Subjects threw the eggs in all experimental presentations regardless of their reward content and in every case, indicating that they perceived them as encased food items. Throwing resulted in small quantities of food coming out of the perforations. All presentations were videotaped. Statistical analyses were conducted in GenStat 10.1 (Rothamstead Experimental Station, Harpenden, U.K.). All statistical tests are two-tailed. Test proportions for binomial tests were set at 0.5.

2.3. Supporting observational data

We recorded 18 instances of mongooses throwing an object against an anvil. In the majority of cases (eight instances by seven adults and three cases by three juveniles) the object thrown was an encased food item and the anvil was suitably hard. However, in seven cases (three instances by different adults and four cases by three juveniles), individuals threw objects that could not be cracked or chose unsuitable anvils (Table 1).

2.4. Experiment 1: how do mongooses select anvils in their natural environment?

2.4.1. Procedure

To test whether mongooses navigate to anvils by returning to the last suitable anvil they passed, we conducted presentations on 14 subjects (9 males, 5 females; 1 trial per subject). In each presentation, we provided a mongoose with an egg when it had just walked past a suitable anvil, but was still within 10 meters (m) of it (mean ± SE = 6.8 ± 0.6 m; range = 3.3–10 m), and was also within 15 m of at least two other suitable anvils (mean ± SE to alternative anvils = 6.2 ± 0.4 m; range = 0.5–12.8 m). In each case we ensured that none of the anvils were obscured by other obstacles and that at least one of the alternative anvils was closer than the last suitable anvil they passed (Fig. 1). We recorded whether the subject returned to the last suitable anvil it passed to throw the egg or whether it went to an alternative anvil, noting whether the subject raised its head and scanned the area before picking up the egg and moving to a surface. In addition, we noted the distance to all suitable anvils within 15 m of the presentation, making note of the type of anvil (e.g. rock, post).

2.5. Experiment 2: do mongooses prefer to throw against hard anvils?

2.5.1. Procedure

To test whether mongooses preferentially choose hard over soft anvils we conducted a series of choice tests. The tests involved one hard and one soft natural anvil (a block of wood and a bunch of reeds) and one hard and one soft synthetic anvil (a piece of vulcanized rubber tire from a four-wheel drive vehicle and a pillow; Fig. 2). We judged the wood and the tire to be comparably hard as they did not compress under the weight of a human (65 kg) and could be used to crack a raw egg. The pillow and reeds, in contrast, would compress under a mongoose's weight (1.5 kg) and were useless for cracking eggs. The front surface areas of the wood, reeds, tire

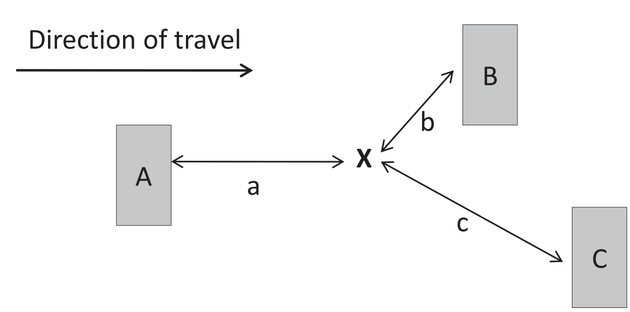

Fig. 1. Diagram of set up for Experiment 1. Rectangles represent suitable anvils for cracking. When a mongoose had just walked past anvil A, it was presented with an egg at location X. Distances are as follows: $a < 10$ m; $b < a$; $c < 15$ m.

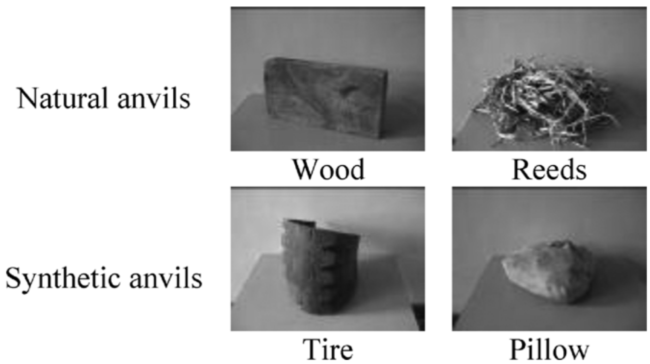

Fig. 2. Objects used in Experiment 2 where mongooses were presented with four different anvil contrasts: (1) wood versus reeds; (2) tire versus pillow; (3) wood versus tire and (4) reeds versus pillow.

and pillow were 470 cm^2, 331 cm^2, 423 cm^2 and 247 cm^2, respectively. To ensure that all individuals had an opportunity to assess the physical properties of the anvils prior to experimental presentations, we gave each individual a pre-test assessment phase. During this phase, we presented individuals with an anvil and ensured that they had climbed on top of it. In the case of pillow, several subjects lay down and rested on it. Once individuals had an opportunity to assess both anvils that would be used in a given choice test, they were included in the test phase of the study. We conducted four choice tests in random order: wood versus reed; tire versus pillow; wood versus tire and reeds versus pillow. In each test, anvils were placed down simultaneously, 30 cm apart from each other and directly in front of a mongoose. We tapped the anvils as we placed them on the floor to draw the subject's attention towards them. Once the subject had looked up and oriented its head towards both anvils, we placed an egg between the mongoose and the two anvils, ensuring that the egg was equidistant from the two anvils and that the mongoose was not oriented towards either anvil (see Fig. 3). We noted which anvil the subject threw the egg against, whether it switched from one anvil to the other and the number of times it threw the egg against either anvil. We also recorded whether the subject looked at the anvil, then took the egg to it and began to throw (hereafter, 'active choice') or whether it backed up against the anvil without looking and began to throw (hereafter, 'passive choice'). An active choice may suggest that the subject made a decision to choose one particular anvil before moving towards it, whereas a passive choice may indicate random choice of whichever anvil the subject happened to back into first. Choice tests ended once subjects stopped throwing the egg or moved away from the anvils. Tests were conducted on 10 individuals (5 males, 5 females), although one individual only completed two of the tests. Seven of these subjects also participated in Experiment 1 (Experiment 1 preceded Experiment 2 for all subjects). The side on which anvils were presented (i.e. left or right) was counterbalanced within and between individuals. Each choice test was conducted only once per individual so as to ensure a spontaneous response and to avoid the results being confounded by learning.

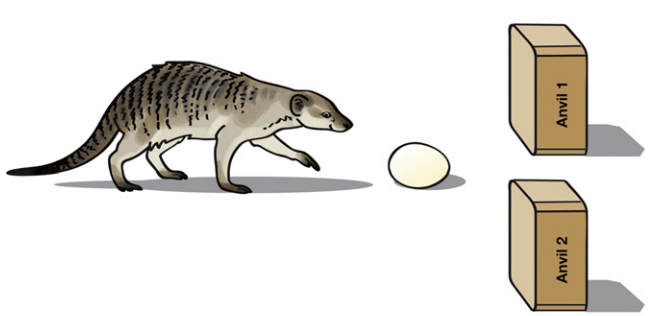

Fig. 3. Diagram of anvil and object presentation for Experiment 2. Anvils were placed 30 cm apart from each other and directly in front of a mongoose and an egg was placed, equidistant from the two anvils, between the mongoose and anvils 1 and 2 (illustration courtesy of Natalya Zahn).

Table 2
Choice of anvils by individuals in Experiment 1.

Individual	Anvil chosen	Chose last anvil passed?	Chose nearest anvil?	Looked up?
M28	Tree	No	Yes	Yes[a]
M39	Pole	No	Yes	No
F214	Conspecific	No	Yes	No
F309	Pole	No	No	No
M29	Wall	No	Yes	No
F202	Tree	No	Yes	Yes[a]
M212	Tree	No	Yes	–
M285	Fence post	No	No	–
M111	Fence post	Yes	No	No
F25	Cement block	No	Yes	No
M210	Tree	No	No	No
M310	Tree	No	Yes	No
F288	Stone block	No	Yes	No
M316	Pole	No	No	No

[a] Two individuals looked up before taking the egg to an anvil, but did not look in the direction of the anvil.

3. Results

3.1. Experiment 1: how do mongooses select anvils in their natural environment?

Of the 14 individuals tested, 13 did not take the egg to the last suitable anvil they passed (binomial test: $P = 0.002$). Nine of the 14 subjects chose the nearest suitable anvil (binomial test: $P = 0.424$). All but one subject chose a suitable hard anvil (tree, wall, post or rock). The other subject picked up the egg and threw it against a sleeping conspecific despite the fact that there was a tree and some roof tiles within 5 m. In two cases we were unable to record whether the subject looked up before taking the egg to an anvil. Of the remaining 12 subjects, 10 did not look up. Neither of the two subjects that did look up looked in the direction of the anvil they ultimately chose. The responses of all subjects are summarized in Table 2.

3.2. Experiment 2: do mongooses prefer to throw against hard anvils?

In the wood versus reeds tests all nine individuals threw the egg against the wood (binomial test: $P = 0.004$). Seven out of nine individuals made an active choice and no subject ever switched from wood to reeds. In the tire versus pillow tests there was no clear preference for the hard surface, with seven subjects throwing the egg against the tire and three against the pillow (binomial test: $P = 0.344$). Of the subjects that chose the tire, five made an active choice and two made a passive choice, while all of the individuals that chose the pillow made a passive choice (Fisher's exact test: $P = 0.167$). Only one of the seven subjects that initially chose the tire switched to the pillow, while two out of the three subjects that initially chose the pillow switched to the tire (Fisher's exact test: $P = 0.367$). In the wood versus tire tests, half of the ten subjects chose the wood and half chose the tire (binomial test: $P = 1$). For both tire and wood choices, three out of five cases were passive choices (Fisher's exact test: $P = 1$). Subjects switched from wood to tire in two out of five cases and no subjects switched from tire to wood (Fisher's exact test: $P = 0.114$). Finally, in the reeds versus pillow tests six subjects chose the pillow and three chose the reeds

Table 3
Results of choice test presentations (W, wood; R, reeds; T, tire and P, pillow; '1st choice' indicates the first anvil the individual chose to throw against).

Individual[a]	W vs. R			T vs. P			W vs. T			R vs. P		
	1st choice	W	R	1st choice	T	P	1st choice	W	T	1st choice	R	P
M311	W	13	0	T	39	0	T	0	6	P	2	4
M316	W	6	0	T	8	0	T	0	25	P	0	15
F315	W	3	0	T	4	0	T	0	33	P	0	20
F025	W	35	0	P	0	64	W	36	0	R	3	0
F214	W	27	0	P	0	20	W	7	0	R	1	13
F202	W	16	0	T	59	0	T	0	21	P	0	2
F288	W	35	0	T	37	0	T	0	35	P	0	8
M029				P	25	1	W	17	15			
M312	W	17	0	T	8	4	W	32	0	R	3	15
M111	W	8	0	T	5	0	W	6	17	P	0	4

	W vs. R			T vs. P			W vs. T			R vs. P		
	P value	W	R	*P* value	T	P	*P* value	W	T	*P* value	R	P
Total times chosen first[b]	0.004	9	0	0.344	7	3	1	5	5	0.508	3	6

[a] For each individual, we report the total number of times it threw the egg against each anvil during each choice test.
[b] The total number of individuals that chose each anvil initially is reported at the bottom of the table, along with the *P* value for a two-tailed binomial test.

(binomial test: $P = 0.508$). One of the subjects that initially chose the pillow made an active choice while all other subjects made passive choices. One out of six individuals switched from pillow to reeds and two out of three switched from reeds to pillow. The results of all choice tests, including the number of times individuals threw the egg against either surface, are summarized in Table 3.

4. Discussion

Banded mongooses routinely crack open encased food items against by throwing them against anvils in their natural environment. To do this effectively, individuals must identify which food items require cracking and select suitable anvils. Given the demands of this task, natural selection may favor mechanisms that enable mongooses to quickly evaluate and process information about objects in their environment and discriminate between hard and soft surfaces. Initial observations suggested that individuals may have some understanding of the functional properties of objects and anvils in their environment and may know the location of suitable anvils in their habitat. These speculations were based on repeated observations of mongooses finding a food item, attempting and subsequently failing to bite it open and then taking it directly to a hard anvil that often was not in the individuals' original field of view. Here, we attempted to unpack the cognitive mechanisms underlying this behavior by investigating how mongooses select suitable anvils and whether experience with different materials mediates anvil selection.

One possible mechanism for navigation to anvils is to return to the last anvil passed (Manser and Bell, 2004). However, results from Experiment 1 suggest that individuals do not generally return to the last object they passed but rather select alternative surfaces nearby. Although in many cases the subject chose the nearest suitable anvil, this did not occur significantly more frequently than chance, so does not appear to be the common heuristic for anvil selection. The majority (83%) of individuals in Experiment 1 did not scan their surroundings before selecting a surface and those that did look up before running to an anvil ultimately chose an anvil located in a different direction from whence they had looked. It is possible that subjects had been scanning the area as they approached and retained a memory of its notable features, such that they did not need to scan again when presented with an egg. Alternatively, mongooses may possess detailed spatial knowledge of their environment, allowing them to move directly to suitable anvils without needing to scan at all. A similar suggestion has been made for meerkats (*Suricata suricatta*), a closely related species, which appear to remember the location of the thousands of underground shelters in their territory and will retreat rapidly to the nearest shelter when alarmed (Manser and Bell, 2004). The precise mechanisms by which mongooses locate suitable anvils remain unclear, but possibilities include reorientation of landmark features (Cheng and Spetch, 1998; Save et al., 1998), place recognition (Cartwright and Collett, 1983; Dyer, 1994, 1996) and spatial maps (O'Keefe and Nadel, 1978).

Although mongooses may know the location of suitable anvils in their territory, Experiment 2 showed that they are sufficiently flexible to recognize and use novel anvils that appear in their environment. Experiment 2 also allowed us to investigate whether mongooses understand that anvils must be hard and to examine whether familiarity with different materials mediates their selection of anvils. In tests with two natural anvils, wood and reeds, 100% of individuals threw the egg against wood and in the majority of cases (7/9) made an active choice. Furthermore, individuals never switched from throwing the egg against the wood to the reeds. Taken alone, this result suggests that mongooses can choose suitable anvils by discriminating between hard and soft objects, through an unlearned capacity to categorize objects according to their functional properties, and/or by generalizing from previous experience with anvils in their environment. However, the tire versus pillow test seems to contradict this suggestion. Here, there was no statistically significant preference for the hard anvil, nor was there a significant difference in the distributions of active versus passive choices. Moreover, individuals in this contrast test switched in both directions: from pillow to tire and from tire to pillow. The failure of three of the ten mongooses to make the correct choice may indicate that mongooses choose randomly, rather than acting on knowledge of critical functional properties. Given the paucity of independent replication for cognitive studies, particularly on wild populations (Tomasello and Call, 2011), this result provides some important independent support for Müller's (2010) findings. Our suggestion is further supported by the fact that some individuals switched both from tire to pillow and from pillow to tire, indicating that they perceived them as equally suitable for cracking. Observations of mongooses choosing unsuitable anvils and throwing items that cannot be cracked (Table 1) provide further indications that they may not recognize necessary functional properties. Nevertheless, given our small sample size, we must be cautious when interpreting a negative result and we cannot rule out the possibility that the failures of mongooses in contrast tests simply reflect natural individual variation.

Rather than discriminating on the basis of anvils' functional properties, it may be that mongooses' choices are based on their familiarity with anvil materials. That is, they learn which specific materials in their natural environment make effective anvils, and so are able to choose actively and appropriately when dealing with familiar categories of materials (e.g. wood and reeds) but cannot generalize about the properties of materials of which they have limited experience (e.g. tire and pillow). This idea is consistent with Müller's (2010) suggestion that trial and error learning plays a role in anvil selection. However, if mongooses were acting solely on the basis of experience one would expect them to prefer natural wood to synthetic tire. In fact, results from this test showed no clear preference for either material, indicating that familiarity alone cannot explain their selections. An alternative explanation is that mongooses act on the basis of the perceived solidity of anvils. That is, when the faced with a choice between two naturally occurring anvils, where one has a continuous, opaque surface (wood) and the other is rife with perforations (reeds), mongooses always select the hard, suitable object often with an active choice and never switch from one to the other. In contrast, when faced with two anvils, both of which appear solid (i.e. opaque and continuous; pillow and tire or wood and tire), mongooses choose indiscriminately.

Perceived solidity appears to provide a good explanation for mongooses' choices in wood versus reeds, tire versus pillow and wood versus tire tests, but it is inconsistent with the lack of a significant preference for the solid-looking pillow over the reeds. We tentatively suggest that this result may be explained by an interaction between perceived solidity and familiarity. That is, mongooses' lack of familiarity with the synthetic material of the pillow may reduce the probability that they choose it over the reeds, despite the pillow appearing more solid. Although further tests would be needed to confirm this hypothesis, it is consistent with both the apparent preference for solid-looking anvils (e.g. wood over reeds) and with Müller's (2010) suggestion that anvil choice is influenced by experience.

Together, our results support Müller (2010) findings and extend them in four important ways. First, we have information on how mongooses select anvils in their environment. Second, we address a potential methodical limitation of previous work on this topic by using anvils that differed substantially in the critical functional property (i.e. hardness) compared to those used in Müller (2010). Third, we show that familiarity with anvil materials may be important in mediating anvil selection. Finally, whereas Muller's study provided opportunities for learning within the task, we examine whether mongooses' spontaneous choices are based on an understanding of functional properties.

When taken together with Müller's (2010) findings, our results suggest that banded mongooses do not show a generalized understanding of the functional properties of different anvils in their environment. Instead, they may simply employ two rules of thumb: (1) if a food item does not crack or yield immediate rewards when bitten then it must be thrown and (2) it must be thrown against a solid-looking surface. These simple rules may be refined by experience, and would enable individuals to extract encased food in the majority of situations, given that mongooses typically inhabit areas where many of the food items that cannot be bitten open can be cracked and almost all solid-looking anvils are hard (e.g. rocks, trees).

When considering whether complex patterns of behavior are underpinned by particular cognitive mechanisms, it is important to consider whether such mechanisms would provide a significant fitness advantage under natural conditions. In many cases, simple rules of thumb may provide necessary and sufficient solutions to what appear to be complex problems. This argument can often be made for behavioral patterns that have been thought to be underpinned by complex mental faculties but for which the same functional outcomes can be achieved by simple means. For example, tool use was thought to be restricted to humans and to require a large brain and sophisticated cognitive faculties (Oakley, 1956). However, it is now clear that tool use occurs in a variety of taxa from insects (Pierce, 1986) to great apes (McGrew, 1992) and involves a range of different cognitive mechanism and varying degrees of causal understanding. Similarly, recent reports of teaching in ants (*Temnothorax albipennis*; Franks and Richardson, 2006), meerkats (Thornton and McAuliffe, 2006) and pied babblers (*Turdoides bicolor*; Raihani and Ridley, 2008) show that behavior that functions to promote learning in others can be achieved without the use of complex cognitive mechanisms such as higher order intentionality and mental state attribution (c.f. Pearson, 1989; Premack and Premack, 1996; Tomasello et al., 1993).

In the case of object cracking in banded mongooses, mongooses may have a detailed knowledge of the location of suitable anvils in their territory. However, our results suggest that the selection of objects and anvils is governed by simple rules of thumb and mediated by experience with specific anvil types rather than a generalized understanding of the properties of objects. Under natural conditions, these simple rules would almost invariably produce desired results (i.e. food extraction), negating the need for a more generalized understanding of the functional properties of different anvils and objects.

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