Anim Cogn
DOI 10.1007/s10071-009-0281-5

ORIGINAL PAPER

Do anvil-using banded mongooses understand means–end relationships? A field experiment

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Received: 29 April 2009 / Revised: 2 September 2009 / Accepted: 9 September 2009

Abstract Tool use and the associated need to choose appropriate objects for a particular task are thought to have selected for specialized cognitive abilities such as means–end comprehension. Several studies on large-brained tool-using primates and birds have demonstrated understanding of causal relationships to some extent. However, a comprehensive appraisal of this hypothesis requires testing for means–end comprehension also in non-tool-users as well as in small-brained tool users. Moreover, the results of captive studies do not answer the question whether such cognitive abilities are relevant to an animal in its natural environment. Here I presented wild banded mongooses *Mungos mungo*, small-brained carnivores that regularly use anvils to open food items with a hard shell, with a transfer test involving novel anvil objects. I found no evidence for means–end comprehension or a heuristic strategy used for anvil choice in this species. Instead, recognition of suitable anvils appears to be learned by trial and error separately for different categories of anvils. These data suggest that, at least for the anvil-choice task investigated here, the need to choose suitable objects has not selected for specialized cognitive abilities in banded mongooses, a finding that may extend to a large range of proto-tool users. Furthermore, this study adds to growing evidence that animals subjected to the selection pressures and trade-offs of their natural environment may get by with cognitively more simple strategies than sometimes suggested by captive studies or plausibility arguments.

Keywords Technical intelligence · Tool use · Means–end comprehension · Physical knowledge · *Mungos mungo* · Herpestidae

Introduction

Extractive foraging and tool use are thought to be one of the major driving forces in the evolution of intelligence (Byrne 1997, technical intelligence hypothesis), together with a complex social environment. Tool use in particular has been linked to simple forms of causal knowledge such as means–end comprehension (Visalberghi and Tomasello 1998), namely the ability to predict the consequence of interactions between objects, as well as, more controversially, to future planning (Mulcahy and Call 2006; Dufour and Sterck 2008; Osvath and Osvath 2008). A range of species, both mammals and birds, have been tested in captivity for their ability to understand physical relations and to perform novel tasks or novel variations of pre-experienced tasks at the first attempt, without associative learning. Several studies have found evidence suggesting means–end comprehension in captive animals (e.g. great apes: Visalberghi et al. 1995; O'Connell and Dunbar 2005; Herrmann et al. 2008; rhesus monkeys: Hauser and Spaulding 2006; corvids: Heinrich and Bugnyar 2005; Taylor et al. 2009), though its extent and distribution remain controversial (see Penn and Povinelli 2007 for a critical review).

To test the technical intelligence hypothesis, however, it is not sufficient to demonstrate means–end comprehension in highly intelligent tool users with comparably large

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Electronic supplementary material The online version of this article (doi:10.1007/s10071-009-0281-5) contains supplementary material, which is available to authorized users.

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brains, such as primates or corvids. A comprehensive appraisal also requires testing for means–end comprehension in non-tool-users as well as in comparatively small-brained tool users. Furthermore, the applicability of captive studies to wild animals is questionable and it remains uncertain whether means–end comprehension plays a relevant part in the lives of animals subjected to the trade-offs and selection pressures of their natural environment. Indeed, several studies that have tested free-ranging animals in cognitive tasks have found that wild animals perform more poorly (Gajdon et al. 2004; Halsey et al. 2006) or use different strategies (Hunt et al. 2006) than their captive counterparts. Captive studies on the other hand are necessarily restricted to arguing that their findings are plausibly also applicable to animals in their natural environment (e.g. Heinrich and Bugnyar 2005; Seed et al. 2006), while others ignore the ecological validity aspect altogether (e.g. Fujita et al. 2003; Blaisdell et al. 2006). These two issues can be addressed by exploring the ability to understand means–end relationships in relatively small-brained animals in their natural environment.

Tests for causal knowledge in the context of tool use commonly investigate the choice of appropriate tools for a particular task, either tools of the correct shape (Fujita et al. 2003; Herrmann et al. 2008; Holzhaider et al. 2008), diameter (Chappell and Kacelnik 2004), length (Chappell and Kacelnik 2002; Hunt et al. 2006) or weight and friability (Visalberghi et al. 2009). A widely occurring form of tool use is cracking food items with a hard shell on an anvil, perhaps most famously found in chimpanzees (Boesch and Boesch 1990) and other primates (e.g. Visalberghi et al. 2009) but in a form of proto-tool use also in a variety of birds (see Lefebvre et al. 2002 for a review). Crows and gulls, for example, carry molluscs to the skies and drop them over rocky areas and thrushes break snail shells by smashing them against rocks. The critical property for these proto-tools is their hard surface. However, to my knowledge no experimental study has tested whether anvil users show an understanding of what properties a suitable anvil (SA) object has. I therefore explored the ability of wild banded mongooses *Mungos mungo*, relatively small-brained social carnivores (the 11 g brain of a 1.5 kg banded mongoose is less than half the size of the brain of a comparably small primate, Pérez-Barbería et al. 2007), to understand means–end relationships that are directly relevant to their natural behaviour.

Banded mongooses show behaviour similar to the bird species described above. They commonly smash food items with a hard shell, such as rhinoceros beetles, bird eggs, snail shells or pupating dung beetle larvae on hard anvil objects, typically rocks or the stem of trees or shrubs, occasionally also on the wall of a gully or against a pile of dry elephant dung (0.21 smashing events per observation hour during 594 h of ad libitum observations, own unpublished data). Such food items are sometimes carried over large distances (up to several hundred meters, pers. obs.) in search for an anvil, suggesting that the smashing individual has an idea of what makes a SA. While the described behaviour does not fulfil the widely accepted definition of tool use by Beck (1980; see also St Amant and Horton 2008) since the food item is carried to an immobile object, it nevertheless has parallels with tool use in that it requires that the animal makes a choice about which object is suitable for the purpose and in that spatial relations that do not occur by default are produced (Visalberghi and Fragaszy 2006).

The basic motor sequence of smashing, holding an item in both front paws followed by an abrupt movement underneath the body towards the animal's rear, is already performed by pups aged 2 months. However, successful smashing is typically shown only by subadult and adult individuals above 6 months of age (pers. obs.) and follows a learning process which includes raising the item above ground for smashing, avoiding hitting one's groin and choosing an appropriate anvil. As suggested by observational data (see above), the latter may involve means–end comprehension based on physical knowledge acquired during smashing events in an individual's early life (A). Alternatively, recognition of SAs may be learned by trial and error separately for different types of anvils (B), or a heuristic strategy may be employed to choose suitable over unsuitable anvils (C), similar to the two-stage strategy found recently in wild New Caledonian crows (Hunt et al. 2006). To distinguish between these three alternatives, I presented banded mongooses with a choice between novel suitable and unsuitable anvil objects, thus testing whether they could transfer knowledge about SAs acquired in prior interactions with natural anvils to these novel objects. Under scenario (A), individuals are predicted to preferentially choose SAs already in the first trials whereas under scenario (B) random choice in the first trials and a gradual shift towards using the suitable novel anvil preferentially in later trials is predicted. Finally, under scenario (C), a random choice in the first stage would be followed by a consistent shift to a more suitable anvil within trials.

Methods

The study was carried out between December 2008 and February 2009 on a population of wild banded mongooses on and around Mweya Peninsula in Queen Elizabeth National Park, Uganda (0°12′S, 29°54′E). Individuals from six groups (range 6–40 individuals) were habituated to observers at close distance (<4 m) and individually marked (see Cant 2000 for details). Individuals tested for means–end

Table 1 Individuals tested in the anvil-choice task

Individual	Group	Gender	Age (years)
BF214	B	Female	5
BM312	B	Male	2.5
BM316	B	Male	2
BM346	B	Male	1.5
BF348	B	Female	1.5
BM360	B	Male	1
VM050	V	Male	2
VF060	V	Female	1.5

comprehension included five males and three females from two different groups and aged between 1 and 5 years (Table 1).

Experimental protocol

I introduced artificial food items, modified 'Kinderegg' plastic containers (Ferrero S.p.A., Pino Torinese, Italy; Fig. 1a), to 72 adult banded mongooses in six groups (46 males and 26 females). The plastic containers were filled with 5–7 g of boiled rice and fried fish, attractive food for the mongooses, and could be opened by smashing them against a hard surface. Individuals varied in how consistently they used the smashing technique with these items. For the experiment described below I chose eight of most reliable smashers, namely those individuals that were most likely to employ the smashing technique when presented with the food items (6–9 presentations per individual). This included the five most reliable smashers, all of which were males, plus the three most reliable female smashers, with an overall success rate of 69% when smashing the artificial food items. All of these eight individuals had also been observed smashing natural food items during ad libitum observations.

In a first stage, all eight individuals were introduced to two novel anvil objects in the absence of the food items (two separate presentations for the two anvils for each individual): a brick wrapped in green unicoloured packaging foam (B&M Latex Ltd, Weybridge, UK; thickness: 1.25 cm) and thus made unsuitable for smashing and a same-sized brick wrapped in a blue and white striped cotton sheet (Fig. 1b). The two objects were thus visually distinct also for animals with possibly limited colour vision. No signs of neophobia were observed during this introductory stage and the focal individuals readily inspected, stepped on and sometimes rested on both objects (Fig. 1b). In a second introductory stage, all eight individuals were presented with open food items next to the anvil objects (two separate presentations for the two anvils for each individual). These introductory presentations provided the mongooses with opportunities for physical contact with the anvil objects prior to the first test trial and to assess their hardness (i.e. their suitability as anvils).

In the subsequent test stage, all eight individuals were presented with the artificial food item and given a choice of the two anvil objects (see also supplementary videos). The two anvils were placed on the ground 70–100 cm from each other and at least 3 m from the nearest alternative anvil (rock, tree etc.). The food item was tied to a string and presented at equal distance between the two anvils. The string prevented the mongooses from taking the food items over large distances to an alternative suitable anvil and allowed termination of the trial where applicable. A trial started with the presentation of the food item and ended either when the focal individual successfully opened the object, when it lost interest in the object or with termination by the experimenter after 20 unsuccessful smashing attempts. Each individual received a minimum of ten trials, not counting trials before an individual smashed on either the suitable anvil (SA) or the unsuitable anvil (UA) for the first time (average 1, range 0–4 trials). For some individuals that showed promise for reaching the criterion for a significant preference of the SA and/or had used an alternative anvil at some point in the series, trials were continued beyond that as feasible (maximum: 16 trials). The arrangement of the SA and UA (left/right) was randomized between trials and trials were spaced on average by 4 days. Experiments were only performed once a foraging individual had moved

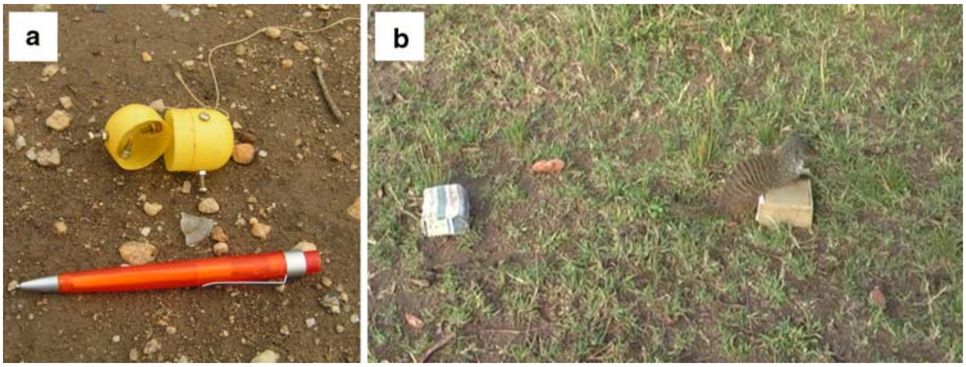


Fig. 1 Artificial food item (**a**) and anvil objects (**b**) used in the experiments

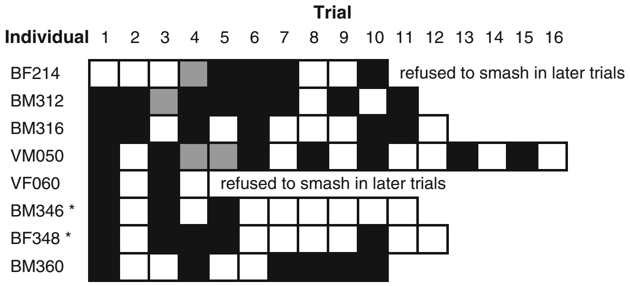
slightly away from the group to avoid interference of other individuals through foraging competition. On the few occasions when the anvil object was anal-marked during the trial, the object was washed thoroughly before being used again. Experiments were recorded with a digital video camera (Panasonic NV-GS320) for later determination of the use of the SA, UA and possible alternative anvils.

Data were analysed in R 2.8.0 (R Development Core Team 2008) using non-parametric tests and generalised linear mixed models (glmms, package lme4; Bates et al. 2008) with binomial error distribution and individual identity included as a random factor, which corrects for repeated measures of individuals.

Results

In a total of 86 trials with 8 individuals, the SA was chosen 41 times, the UA 41 times, and 4 times the focal animal smashed on an alternative anvil. The food item was opened successfully in 80% of the cases when the SA was chosen (on average after 7 smashing attempts, range 2–17), and in 12% of the cases when the UA was chosen. Only one individual (BM312) opened the food item more than once when choosing the UA which may explain his prolonged use of the UA throughout the series (Fig. 2). Another individual (VF060) lost interest in the food items after four trials and was excluded from the analysis comparing anvil use in the first and second half of the trials.

The SA was not preferably used in the first five trials. Instead, a non-significant preference for the UA was found (UA used in 21 of 35 trials, excluding trials when an alternative anvil was used, binomial test, $p = 0.16$). A shift towards using the SA more in later trials is apparent (Fisher's exact test, first half vs. second half of trials, one-sided, $p = 0.04$). However, only two individuals showed a significant preference for the SA in their last trials (Fig. 2, binomial test, $p < 0.05$). Perhaps notably, these two individuals were littermates. Inter-trial intervals were not shorter for these two than for the other individuals (linear mixed model with log-transformed data, $t_{(6)} = -0.127$, $p = 0.90$).



Individual	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
BF214	⬜	⬜	⬜	▨	⬛	⬛	⬛	⬜	⬜	⬛	refused to smash in later trials					
BM312	⬛	⬛	▨	⬛	⬛	⬛	⬛	⬜	⬛	⬜	⬛					
BM316	⬛	⬛	⬜	⬛	⬜	⬛	⬜	⬜	⬜	⬛	⬛	⬜				
VM050	⬛	⬜	⬛	▨	▨	⬛	⬜	⬛	⬜	⬛	⬜	⬜	⬛	⬜	⬛	⬜
VF060	⬛	⬜	⬛	⬜	refused to smash in later trials											
BM346 *	⬛	⬜	⬛	⬜	⬛	⬜	⬜	⬜	⬜	⬜	⬜					
BF348 *	⬛	⬜	⬛	⬛	⬛	⬜	⬜	⬜	⬜	⬛	⬜	⬜				
BM360	⬛	⬜	⬜	⬛	⬜	⬜	⬛	⬛	⬛	⬛						

Fig. 2 Choice of the suitable (*white*), unsuitable (*black*) or an alternative anvil (*grey*) for eight individuals with 10–16 trials each. * Individuals that showed a significant preference for the suitable anvil in later trials

Success in the preceding trial did not influence anvil choice in the subsequent trial. Focal animals were no more likely to switch anvils after an unsuccessful trial than after a trial during which they had successfully opened the food object ($N = 74$, excluding trials after an alternative anvil was used, glmm: $z = 0.25$, $p = 0.80$). That is, they chose an other anvil than in the preceding trial in 62% of the cases after a successful trial and in 59% of the cases after an unsuccessful trial. Instead, anvil choice was predicted by the direction of approach of the focal animal (via SA, via UA or through the middle): Only in 4 of 59 trials did an animal smash on the anvil other than the one it had passed on the way to the food item (glmm for anvil choice depending on direction of approach and excluding trials where the animal came through the middle: $z = 4.65$, $p < 0.0001$). Furthermore, once an animal had started to smash on one of the anvils, it generally stuck with its choice until either the food item was opened, the animal lost interest and abandoned the item, or the trial was terminated (after 20 unsuccessful smashing attempts). Switching between anvils during a trial was observed only in two of the 86 trials, once from the UA to the SA and once in the opposite direction.

Discussion

I found no evidence that banded mongooses show means–end comprehension in their choice of anvils as they showed no preference for the SA in the initial trials. Instead, at least some individuals seem to choose SAs preferentially after associative learning by trial and error. The mongooses' physical knowledge regarding suitability (hardness) of anvil objects therefore appears limited and does not reach the level of understanding that other, larger-brained tool users show when choosing appropriate objects. Capuchin monkeys, for example, appear to have a good and surprisingly detailed idea of which stones are suitable as hammers (Visalberghi et al. 2009) and chimpanzees choose sticks of the appropriate diameter to poke a food reward out of a tube without prior training (Visalberghi et al. 1995), an ability that appears to be matched by New Caledonian crows (Chappell and Kacelnik 2002, 2004). Observational data of sequential tool use and tool modification further suggest that a detailed understanding of the function of tools is also present in wild chimpanzees and is used in their natural environment (Sanz et al. 2004; Sanz et al. 2009).

The mongooses also did not show any evidence for a heuristic strategy like wild New Caledonian crows (Hunt et al. 2006), whereupon a random initial choice of anvils would be followed by consistent switching from the unsuitable to the suitable anvil within trials. Indeed, even though switching between anvils occurs regularly when natural anvils are used (18% of events, $N = 245$, own unpublished data), switching between the suitable and unsuitable anvil occurred only rarely in the experiments. This suggests that switching during natural observations may not necessarily reflect anvil choice but may be a consequence of an animal avoiding foraging competition or catching up with its group.

Nevertheless, the mongooses regularly and successfully use anvils to gain access to valuable food sources. The presented experiment suggests that trial-and-error learning is sufficient to reach a reasonable smashing prowess and that means–end comprehension is not necessary or at least does not improve the performance sufficiently to be selected for. Instead, the mongooses might use other features, such as the shape of an object or the inclination of a slope, as a basis for their choice of natural anvils, a strategy that might lead to success sufficiently often. Use of tools or proto-tools that require choosing an appropriate object for the task at hand thus does not appear to require knowledge of 'folk physics' and regular tool use per se might not select for advanced cognitive abilities. Instead, selection pressure might arise from the use of more complex tools that require manipulation or manufacture (e.g. Boesch and Boesch 1990; Hunt 1996; Bania et al. 2009) and possibly planning for the future (Mulcahy and Call 2006). This notion is supported by a comparative analysis of bird brains by Lefebvre et al. (2002) showing that true tool users have larger residual brain sizes than borderline tool users (= proto-tool users, including species that smash food items on anvils). Unfortunately, Lefebvre et al.'s study does not include non-tool-users and it is therefore not possible to judge whether proto-tool users have enlarged brains in comparison to non-tool users. Further support arises from some recent studies of non-tool-users that found evidence for causal knowledge similar or even exceeding that of tool users (rats: Blaisdell et al. 2006; keas: Huber and Gajdon 2006; monkeys: Santos et al. 2006; rooks: Seed et al. 2006), where curiosity and object exploration (Huber and Gajdon 2006) or domain-general cognitive abilities (Santos et al. 2006) have been suggested to explain the occurrence of causal knowledge.

Contrary to the prediction based on means–end comprehension, the tested banded mongooses seemed to show an initial preference for the UA as seven of eight individuals chose it in their first trial (see Fig. 2). One possible but speculative explanation for this is that the initial preference might have arisen because the 'cushioned' UA was the more comfortable resting spot during introductory trials (see Fig. 1b) and animals entered the arena via the UA because of that, or because its unicoloured appearance resembles natural anvils more than the striped SA. In any case, this apparent preference disappeared after the second trial. Since the performed experiment offered no evidence for means–end comprehension, the control experiment reversing the colour patterns of the suitable and unsuitable anvil seems unnecessary here.

This first study of physical knowledge in wild banded mongooses is naturally limited in its scope. I cannot exclude that the mongooses would show evidence for means–end comprehension in a different task/paradigm, particularly since even for chimpanzees performance in physical cognition tasks depends on the experimental approach taken (e.g. Seed et al. 2009). There are several reasons why the present study might have been less likely to detect evidence than prior laboratory-based studies of physical cognition in other species. First, the latter commonly include large numbers of trials with much shorter inter-trial intervals. In the present study, the ability to do that was traded off for increased ecological validity. Second, the functionally relevant feature in anvil choice is the hardness of an object's surface, a feature that might be less easily learned than the relevant features in previous tool choice experiments, such as the length, diameter or shape of an object (but see Visalberghi et al. 2009). The latter factor might have been further aggravated since, unlike the capuchins in Visalberghi et al.'s study, the mongooses naturally smash a broad range of food items on a broad range of anvil objects (see Introduction) with some items requiring a very hard anvil such as a stone, whereas for others a less hard object, such as a pile of dry elephant dung might be sufficient, thus making affordances of SAs more difficult to learn.

In summary, keeping these caveats in mind, my study indicates that wild banded mongooses solve an ecologically relevant task, the choice of suitable anvils, apparently without complex physical cognition. Instead, the presented data suggest that anvil use in wild banded mongooses is based on a combination of instinctive skills regarding the basic motor sequence (as suggested for the use of non-modified twigs by naïve New Caledonian crows; Kenward et al. 2005) and refinement by trial-and-error learning. Unlike corvids, these proto-tool users apparently have not developed cognitive specializations to meet the challenge of choosing appropriate objects for this particular task, nor can they draw from domain-general cognitive capacities as primates might do (Santos et al. 2006; Mendes et al. 2007). My results indicate that tool use per se and the challenge of choosing appropriate objects might not have selected for advanced cognitive abilities related to physical knowledge in this case. Further studies with small-brained proto-tool users may confirm that the critical step for the development of specialized cognitive abilities lies beyond proto-tool use but with the use of more sophisticated tools that require manipulation and/or manufacture. My data further add to growing evidence that wild animals subjected to the trade-offs and selection pressures of their natural environment make do with simpler cognitive processes than what plausibility arguments after captive studies sometimes suggest.

Acknowledgments I am grateful to Uganda Wildlife Authority and Uganda National Council for Science and Technology for permission to work in Queen Elizabeth National Park. Mike Cant provided access to the study population and valuable logistical support. Kenneth Mwesige helped with data collection. I am also grateful to Mike Cant and Sarah Hodge and four anonymous reviewers for helpful comments on an earlier draft of the manuscript. During this study, the author was funded by the Swiss National Science Foundation (PBZHA-121022). Additional funding for field expenses was provided by the Janggen-Pöhn Stiftung and the Basler Stiftung für biologische Forschung, which is gratefully acknowledged.

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