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Teaching in Wild Meerkats

Alex Thornton* and Katherine McAuliffe

Despite the obvious benefits of directed mechanisms that facilitate the efficient transfer of skills, there is little critical evidence for teaching in nonhuman animals. Using observational and experimental data, we show that wild meerkats (*Suricata suricatta*) teach pups prey-handling skills by providing them with opportunities to interact with live prey. In response to changing pup begging calls, helpers alter their prey-provisioning methods as pups grow older, thus accelerating learning without the use of complex cognition. The lack of evidence for teaching in species other than humans may reflect problems in producing unequivocal support for the occurrence of teaching, rather than the absence of teaching.

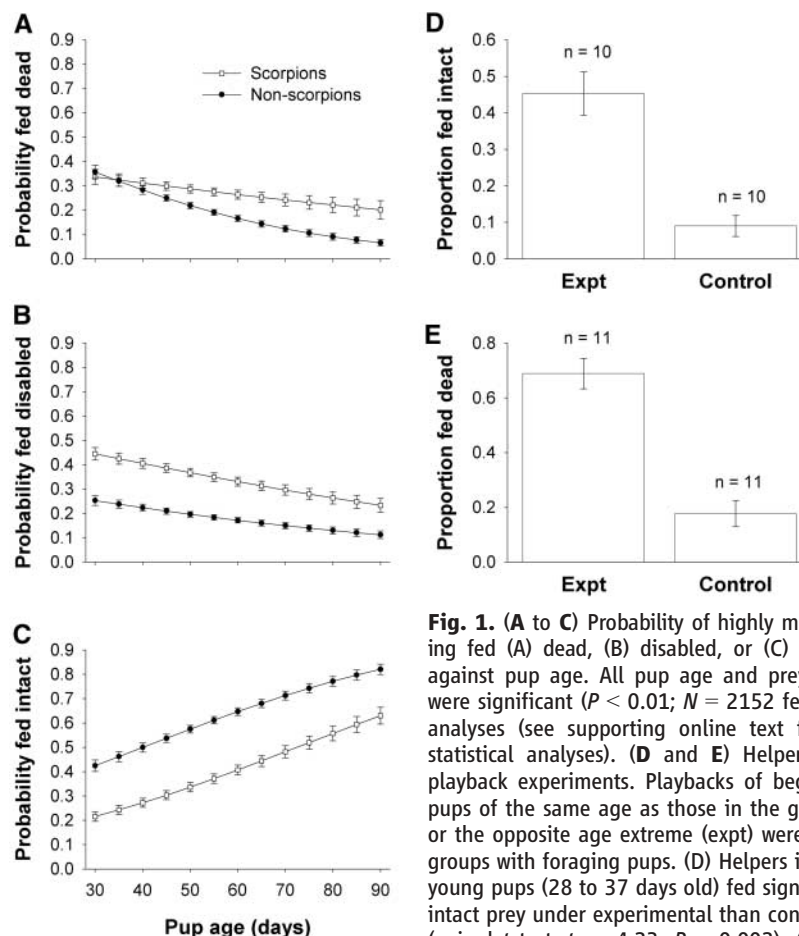
Teaching is ubiquitous in human societies, but although social learning is widespread in other species (1, 2), it is not yet clear how commonly teaching is involved. Teaching is characterized by the active involvement of experienced individuals in facilitating learning by naïve conspecifics (3, 4). The focus of definitions of teaching ranges from cognitive mechanisms (5, 6) to evolutionary function (3, 7). In this paper, we use a widely accepted (2, 4, 8–10) functional definition developed by Caro and Hauser (3). This definition comprises three criteria: (i) an individual, A, modifies its behavior only in the presence of a naïve observer, B; (ii) A incurs some cost or derives no immediate benefit; and (iii) as a result of A's behavior, B acquires knowledge or skills more rapidly or efficiently than it would otherwise, or that it would not have learned at all. Teaching is thought to allow faster and more efficient information transfer than passive forms of social learning (11), but evidence for its existence in nonhuman animals is equivocal (3, 4, 8–10, 12, 13). To date, only one study provides firm evidence for teaching (10), and its occurrence in the wild remains unconfirmed.

We investigated whether teaching occurs in wild meerkats (*Suricata suricatta*), a species living in demanding environments where food acquisition involves considerable skill. Meerkats are obligate cooperative breeders living in groups of 2 to 40 individuals in the arid regions of southern Africa. Groups comprise a dominant male and female, who are the parents of over 80% of the pups in the group, and a variable number of helpers of both sexes that aid in rearing the young (14). Hereafter, all individuals over 3 months old are referred to as helpers. Pups are initially incapable of finding their own prey. They begin to follow foraging groups at around 30 days of age and are provisioned by all group members in response to begging calls (15, 16) until they reach nutritional independence at around 90 days of age.

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Meerkats are opportunistic generalists, feeding on a range of vertebrate and invertebrate prey (15), many of which are difficult to handle and potentially dangerous to young pups. Scorpions of the genera *Parabuthus* and *Opisthophthalmus*, which form up to 4.5% of total prey biomass for meerkats (15), may be particularly dangerous; the former possess neurotoxins potent enough to kill a human, whereas the latter have milder toxins but are more aggressive, defending themselves with large, powerful pincers (17).



significantly more dead prey under experimental than control playbacks (paired t test, $t_{10} = 4.81$, $P = 0.001$).

Helpers typically kill or disable prey with rapid bites to the head or abdomen before provisioning pups. Scorpions are normally disabled by removing the sting. Helpers adjust the frequency with which they kill or disable mobile prey according to pup age, gradually introducing pups to live prey. The proportion of highly mobile prey fed when dead or disabled decreased with pup age (Fig. 1, A and B) while the proportion of prey fed intact increased (Fig. 1C) (controlling for characteristics of the pups, helpers, and prey) (18) (table S1). Scorpions were more likely to be provisioned dead or disabled (Fig. 1, A and B) and less likely to be provisioned intact (Fig. 1C) than were other items.

Helpers often fed pups that were out of sight (mean distance to pup = 5.4 m, range = 0 to 50 m, $N = 1399$ feeds), but pup begging calls can generally be heard by all individuals in the group (16). The acoustic parameters of begging calls are known to change with age (19). To investigate whether helpers modify prey in response to begging calls, we conducted playback experiments in which we broadcast begging calls of old pups (71 to 86

Fig. 1. (A to C) Probability of highly mobile prey being fed (A) dead, (B) disabled, or (C) intact plotted against pup age. All pup age and prey type effects were significant ($P < 0.01$; $N = 2152$ feeds) in GLMM analyses (see supporting online text for details of statistical analyses). (D and E) Helper response to playback experiments. Playbacks of begging calls of pups of the same age as those in the group (control) or the opposite age extreme (expt) were broadcast to groups with foraging pups. (D) Helpers in groups with young pups (28 to 37 days old) fed significantly more intact prey under experimental than control playbacks (paired t test, $t_9 = 4.23$, $P = 0.002$). (E) Helpers in groups with old pups (71 to 86 days old) fed significantly more dead prey under experimental than control playbacks (paired t test, $t_{10} = 4.81$, $P = 0.001$).

days old) to groups with young pups (28 to 37 days old) or vice versa (18). Begging calls of pups of the same age as those in the group were broadcast as controls. Helpers in groups with young pups fed significantly more intact prey when calls of older pups were broadcast than in control playbacks, and helpers in groups with old pups fed significantly more dead prey under experimental than control playbacks (Fig. 1, D and E).

After a helper gave a pup a food item, it normally remained with the pup and monitored its handling of the prey (87.5% of recorded feeds; $N = 10,479$ feeds). If pups did not attempt to handle a prey item, helpers sometimes nudged the item repeatedly with their nose or paws (8.3% of occasions; $N = 5343$ feeds). After nudging occurred, pups normally consumed the prey successfully (99% of occasions; $N = 446$ feeds). The duration of monitoring and the probability of nudging both declined with pup age [monitoring, analyzed with a generalized linear mixed model (GLMM), gave the following results: $\chi^2 = 142.04$, $df = 1$, $P < 0.001$ (Fig. 2A and table S2); nudging (GLMM): $\chi^2 = 80.23$, $df = 1$, $P < 0.001$ (table S3)], suggesting that helpers modify their behavior in response to improvements in pup competence. Nudging was more common when rare prey types were presented to pups [prey abundance (GLMM): $\chi^2 = 13.65$, $df = 1$, $P < 0.001$ (Fig. 2B and table S4)], suggesting that it may direct pups' attention toward unfamiliar food.

Helpers' killing or disabling prey before feeding a pup probably has few costs to helpers as compared to the post-provisioning costs of feeding live prey. Controlling for prey type and size (18), there was no significant difference between pre-provisioning handling times for prey provisioned dead, intact, or disabled [generalized linear model (GLM): $F_{2,93} = 1.67$, $P = 0.195$], suggesting that the time costs of modifying prey rather than feeding it intact are low. In contrast, there were clear post-provisioning costs involved in feeding pups live prey. These included longer times spent monitoring pups handling prey (Fig. 2A), the risk of pups losing prey (Fig. 2C and table S5), and the investment in retrieving and further modifying items lost by pups. Among 731 feeds where pups lost the prey initially, helpers retrieved prey and returned it to pups on 192 occasions (26.3%). On around 7% of occasions, helpers further modified the prey before returning it.

Helpers appear to facilitate pup skill acquisition by creating opportunities for pups to handle live prey. Young pups encounter live, highly mobile prey almost exclusively when provisioned by helpers. As pups grow older, they increasingly find such items themselves, but the mean number of items found remained below 50% of the total encountered (found by pups and fed by helpers), even for pups approaching

nutritional independence (Fig. 2D). The presence of a helper after provisioning appears to have an important effect on the likelihood that pups will attempt to handle live prey. When we presented live scorpions to helpers, they removed the sting and fed the scorpion to a pup on 13 occasions. In all cases, the pup then bit the scorpion. In contrast, when we presented stingless scorpions directly to 13 littermates when no helpers were within 2 m (18), 7 did not bite the prey (Fisher's test: $P = 0.005$).

As pups grew older, they were less likely to lose live prey (Fig. 2C) and time taken to handle scorpions declined (Fig. 2E). To examine the effect of experience with live prey on pup handling skills, rather than age per se, we trained three littermates on 3 consecutive days by directly provisioning them each day with (i) four dead scorpions; (ii) four live, stingless scorpions; or (iii) an equivalent mass of hard-boiled egg, as a control. On the fourth day, we tested the handling abilities of all three pups by provisioning each with one live, stingless scorpion (18). We conducted the experiment on six litters in four groups. All pups trained on live

scorpions successfully handled the scorpion on the fourth day, whereas those trained on dead scorpions lost the scorpion in two out of six tests and control pups lost their scorpions on four occasions. In all six trials, the pup trained on live scorpions was either the only pup to handle the scorpion successfully or had the fastest handling time (18) (Friedman test: $S = 10.38$, $df = 5$, $P = 0.006$). Moreover, all control pups and all pups trained on dead scorpions were pincered or pseudo-stung (struck by the stingless tail) by the scorpion during the test with a live scorpion, whereas this occurred only once in tests with pups trained on live scorpions (Fisher's test: $P < 0.001$).

The results of this study provide strong evidence that the provisioning behavior of meerkat helpers constitutes a form of "opportunity teaching," in which teachers provide pupils with opportunities to practice skills, thus facilitating learning (3, 7). Helpers modified their behavior in the presence of pups, gradually introducing them to live prey, monitoring their handling behavior, nudging prey, and retrieving and further modifying prey if necessary. Dan-

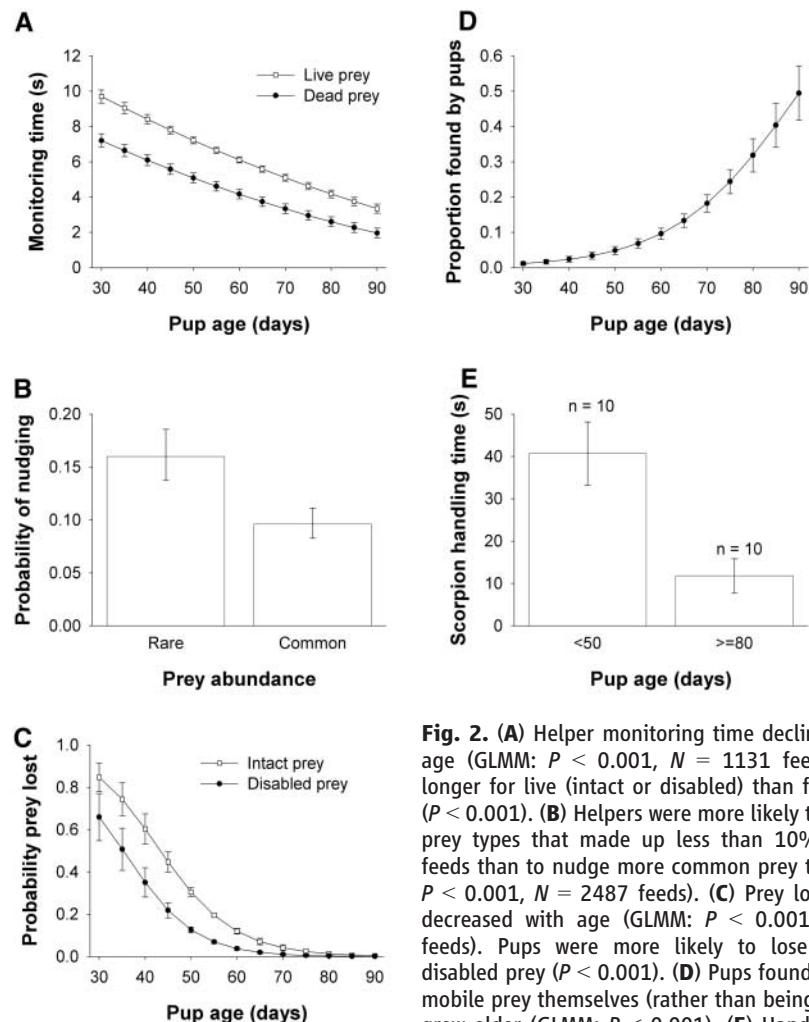


Fig. 2. (A) Helper monitoring time declined with pup age (GLMM: $P < 0.001$, $N = 1131$ feeds) and was longer for live (intact or disabled) than for dead prey ($P < 0.001$). (B) Helpers were more likely to nudge rare prey types that made up less than 10% of all pup feeds than to nudge more common prey types (GLMM: $P < 0.001$, $N = 2487$ feeds). (C) Prey losses by pups decreased with age (GLMM: $P < 0.001$, $N = 3046$ feeds). Pups were more likely to lose intact than disabled prey ($P < 0.001$). (D) Pups found more highly mobile prey themselves (rather than being fed) as they grew older (GLMM: $P < 0.001$). (E) Handling time for pups experimentally provisioned with stingless scorpions was higher for pups <50 days old than for pups ≥ 80 days old (paired t test: $t_9 = 3.98$, $P = 0.003$).

gerous items were more likely to be killed or disabled than other mobile prey. Helpers gained no direct benefits from their provisioning behavior and incurred costs through giving pups prey that was difficult to handle and might escape. Finally, there was strong evidence that helper provisioning behavior plays an important role in promoting the development of pup handling skills.

It is often assumed that teaching requires awareness of the ignorance of pupils and a deliberate attempt to correct that ignorance (5, 6, 20), but viewed from a functional perspective (3), teaching can be based on simple mechanisms without the need for intentionality and the attribution of mental states. By differentially responding to the calls of pups of different ages, helpers may accelerate pups' learning of handling skills without the need for complex cognitive processes. Additional post-provisioning behavior, such as nudging and retrieving prey, may then further enhance skill acquisition.

Evidence from ants (10) and meerkats suggests that teaching, as defined by Caro and Hauser (3), may have evolved independently in many unrelated taxa. Where individuals must acquire critical skills or information but individual learning is costly or opportunities to practice are lacking, selection may favor mech-

anisms whereby experienced individuals actively facilitate learning by naïve conspecifics. The paucity of evidence for teaching is likely to reflect difficulties in producing unequivocal support for strict criteria rather than an absence of teaching per se. As evidence for teaching in nonhuman animals emerges, research will be in a position to look in more detail at the conditions under which teaching is likely to evolve and to relate forms of teaching found in humans and other animals in a broad framework.

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21. H. and J. Kotze kindly allowed us to work on their land, and the Northern Cape Conservation Authority granted permission to conduct the research. We are grateful for the support of the Mammal Research Institute at the University of Pretoria and for the help of N. Jordan, T. Flower, N. Tayar, and volunteers who contributed to data collection. L. Hollén allowed us the use of some begging call recordings. We thank T. Clutton-Brock for supervision and access to the meerkats and S. Hodge, J. Gilchrist, K. Iswaran, A. Radford, N. Raihani, S. English, and A. Young for discussion and advice. The work was funded by a Natural Environment Research Council studentship to A.T.

Supporting Online Material

www.sciencemag.org/cgi/content/full/313/5784/227/DC1
Materials and Methods
Tables S1 to S5
Reference

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Ca²⁺ Entry Through Plasma Membrane IP₃ Receptors

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Inositol 1,4,5-trisphosphate receptors (IP₃Rs) release calcium ions, Ca²⁺, from intracellular stores, but their roles in mediating Ca²⁺ entry are unclear. IP₃ stimulated opening of very few (1.9 ± 0.2 per cell) Ca²⁺-permeable channels in whole-cell patch-clamp recording of DT40 chicken or mouse B cells. Activation of the B cell receptor (BCR) in perforated-patch recordings evoked the same response. IP₃ failed to stimulate intracellular or plasma membrane (PM) channels in cells lacking IP₃R. Expression of IP₃R restored both responses. Mutations within the pore affected the conductances of IP₃-activated PM and intracellular channels similarly. An impermeant pore mutant abolished BCR-evoked Ca²⁺ signals, and PM IP₃Rs were undetectable. After introduction of an α -bungarotoxin binding site near the pore, PM IP₃Rs were modulated by extracellular α -bungarotoxin. IP₃Rs are unusual among endoplasmic reticulum proteins in being also functionally expressed at the PM, where very few IP₃Rs contribute substantially to the Ca²⁺ entry evoked by the BCR.

Most IP₃R in most cells are in the endoplasmic reticulum (ER) (1–3), but IP₃-evoked Ca²⁺ release also occurs from other intracellular organelles (2, 3). Receptors that evoke Ca²⁺ release from intracellular stores usually also stimulate Ca²⁺ entry across the PM (1). This is often through store-

operated Ca²⁺ entry (SOC), where depletion of intracellular stores activates a Ca²⁺-permeable channel in the PM (4–6). The SOC channel is not itself an IP₃R, although IP₃R within the ER may interact with it (4). Non-SOC pathways, often regulated by signals derived from diacylglycerol, also contribute to Ca²⁺ entry (7), but these channels are not formed from IP₃R proteins. Cell-surface labeling, immunolocalization, subcellular fractionation, and whole-cell patch-clamp recording (8) have suggested the presence of IP₃R in the PM (9). The patch-

clamp results are disputed because the most thoroughly characterized current activated by IP₃, Ca²⁺ release-activated current (CRAC) (10, 11), is also activated by store depletion, has properties distinct from IP₃R, and is probably activated when IP₃R within ER mediate loss of Ca²⁺ from intracellular stores. The only clear evidence for functional IP₃R in the PM comes from cilia of olfactory neurons, but these IP₃R differ from those in ER (12, 13). The only IP₃-gated channels detected in the PM are thus not obviously related to IP₃R in the ER.

SOC evoked by emptying intracellular Ca²⁺ stores with thapsigargin occurred in cells lacking IP₃R (Fig. 1A) (9, 14). The whole-cell current evoked by store depletion in DT40 cells (*I*_{CRAC}) is likewise independent of IP₃R (15). SOC was completely blocked by low concentrations of Gd³⁺ [half-maximal inhibitory concentration (IC₅₀), 69 ± 9 nM (Fig. 1C)] (5). Antibody to immunoglobulin M (anti-IgM) (5 µg/ml), which stimulates phospholipase C γ 2 through the B cell receptor (BCR), predictably failed to increase the intracellular Ca²⁺ concentration ([Ca²⁺]_i) in cells lacking IP₃R, but it caused release of Ca²⁺ from intracellular stores and Ca²⁺ entry in normal DT40 cells (Fig. 1B) (16). The latter was only partially inhibited (55 ± 4%) by a concentration of Gd³⁺ (300 nM) that abolished SOC (Fig. 1D). Activation of the BCR, but not SOC, stimulates Ba²⁺ entry and requires IP₃R, leading to an earlier suggestion that IP₃R might directly mediate Ca²⁺ entry

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