



## A new way to study teaching in animals: despite demonstrable benefits, rat dams do not teach their young what to eat

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Teaching is an altruistic act. Therefore, it is most likely to occur when pupil and teacher are closely related, costs to teachers of teaching are small, and benefits to pupils of being taught are large. Here, we determined, first, whether *Rattus norvegicus* dams would modify their food choices to teach their young which of two foods was safe to eat, and second, whether such teaching by mothers would be effective, if it occurred. We examined food choices of rat dams trained to eat one of two foods that their young could access when the dams could also access a third, more palatable food that their pups could not reach (three-bowl condition). These dams spent no more time eating the safe food available to their young than did control dams, which had access to the same three foods, but were not trained to avoid one of the two foods available to their young. Thus, dams that had learned that a food available to their offspring was toxic, failed to act to protect their young. When dams were trained to avoid one of only two foods available to them and their young (two-bowl condition), the young avoided the food that their dam had learned to avoid longer than did young of dams in the three-bowl condition. Thus, young of dams in the three-bowl condition would have been less likely to eat toxic food if their dams had behaved appropriately. The present paradigm, though providing no evidence of teaching by rat dams, should permit investigation of teaching in many vertebrate species.

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Barnett (1968, page 478) proposed two criteria differentiating teaching from other forms of social learning. First, the behaviour of the teacher must induce a change in the behaviour of the pupil, and second, teaching must be maintained and adapted to the pupil's progress until the pupil 'achieves a certain standard of performance'. However, as Ewer (1969) pointed out, Barnett's (1968) criteria do not distinguish active instruction (in which a teacher modifies its behaviour when in the presence of naïve pupils) from inadvertent provision of information (when the purported behaviour of the 'teacher' is not affected by the presence of pupils).

Several decades later, Caro & Hauser (1992) defined teaching as occurring when: (1) a teacher incurs some cost as a result of modifying its behaviour when in the presence of naïve individuals, and (2) the modified

behaviour of the teacher causes naïve individuals to acquire some behaviour more rapidly than they otherwise would. On this definition, teaching is an altruistic act that should occur only when teaching enhances the inclusive fitness of the teacher. According to Hamilton's (1964) rule, teaching would be favoured when teacher and pupil are closely related and the ratio of the teacher's cost to the pupil's benefit is exceeded by  $r$ , the coefficient of relatedness of the teacher and the pupil. For example, parents should teach offspring when the cost of teaching is less than half the benefit to each offspring ( $r = 1/2$ ). However, as Dewar (2002) has argued, the inclusive fitness benefits of teaching may be more restricted, if pupils can learn on their own at sufficiently low cost. According to this argument, not only must the parent's cost of teaching be less than half the benefit to offspring, it must also be less than half the cost offspring would pay to learn unassisted (Dewar 2002).

Although Caro & Hauser (1992) provide evidence consistent with their view that animals teach, as have others during the last decade, much of that evidence concerns the development of predatory behaviour in

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animals living in uncontrolled environments (e.g. Caro 1994; Rendell & Whitehead 2001) that some find relatively unconvincing (e.g. Galef 2001, 2004; Janik 2001; Maestripiéri & Whitham 2001). Outside the controlled environment of the laboratory, it is difficult to show that purported acts of teaching cause accelerated learning by putative pupils. For example, in a carefully conducted field study of a possible case of teaching, Caro (1994) found that maternal cheetah delay feeding and occasionally even lose prey as a result of releasing captured prey for their maturing young to stalk and kill (see also Ewer 1963, 1968, 1969). However, as Caro & Hauser (1992) note, evidence that development of independent hunting in young cheetahs is accelerated by interaction with prey released by their mother is lacking.

Evidence of an effect of teaching on development of predatory behaviour in controlled, laboratory situations is also problematic. For example, studies of development of mouse killing in young domestic cats, *Felis catus*, have both found (Caro 1980a, b) and failed to find (Baerends-van Roon & Baerends 1979) effects of interacting with adult cats that kill mice on development of predatory behaviour in kittens. Similarly, although Flandera & Novakova (1975) report accelerated development of mouse killing in rat pups whose mothers killed mice in their presence, Galef (1996) did not.

Questions concerning the ethics of staged predatory encounters make further laboratory investigations to resolve conflicting results of experiments concerned with the role of teaching in the development of predatory behaviour unlikely. Consequently, new paradigms are required if investigation of teaching in vertebrates is to proceed.

Laboratory studies have revealed several behavioural processes that result in young animals learning enhanced preferences for the foods eaten by adults with whom the young have interacted (for review, see Galef 1977, 1996, 2003). However, each of these processes involved naïve individuals extracting information about where, when or what to eat (Galef & Giraldeau 2001) from essentially passive conspecifics that were indifferent to the presence of potential 'pupils' (King 1994).

The absence of evidence of active teaching by rats participating in previous experiments on social influences on food choice may reflect experimental designs that failed to maximize the probability that knowledgeable individuals would teach the naïve. Knowledgeable and naïve subjects were often not closely related, and nothing was done to assure that the relationship between the potential costs and benefits of teaching were appropriate.

The present experiment was undertaken to determine whether a rat dam living in an environment that she had learned contained both safe and toxic foods would alter her feeding behaviour to increase the probability that her young would wean to safe food. To establish experimental conditions favourable to teaching, we made the cost of teaching low relative to both the benefits to offspring if they were taught and the costs to offspring who were not taught. Evidence of a systematic change in dams' behaviour that increased the probability that their offspring would ingest safe food, and consequently avoid ingesting

a toxic substance (Galef 1985), would provide experimental evidence of teaching.

## METHODS

### Subjects

Seventeen, adult, female, Long-Evans rats, *Rattus norvegicus*, obtained from Charles River Canada (St Constant, Quebec) together with their first-born litters (culled to three males and three females within 1 week of birth) served as subjects in one of two experimental groups. An additional six dams and their culled litters served in a control group. We randomly assigned dams to control and experimental conditions. Dams in all groups served as 'teachers' for their own young.

### Apparatus

Throughout most of the experiment, adult females lived in individual, shoebox cages, measuring  $22 \times 22 \times 46$  cm, with ad libitum access to tap water and rodent chow (Teklad Rodent Diet (W) 8640; Harlan-Teklad, Madison, Wisconsin, U.S.A.). All cages resided in a temperature- and humidity-controlled colony room that was illuminated for 12 h/day.

During training and testing (see Procedure), each adult female was housed in an enclosure measuring  $62 \times 62 \times 90$  cm and constructed of transparent Plexiglas (Fig. 1). Each enclosure rested on a galvanized sheet-metal tray ( $63 \times 92$  cm) that was covered to a depth of 1–2 cm with wood shavings and contained: (1) a painted, wooden nestbox providing harborage for a mother and litter, (2) a feeding platform ( $30 \times 40 \times 2$  cm high) free of wood shavings and (3) a feeding shelf ( $20 \times 62$  cm) mounted 20 cm above the feeding platform. Although adult female rats could easily climb onto the feeding shelf, it was too high above the cage floor for weanling pups to reach.

We presented food in the enclosure in 10-cm-diameter, Pyrex bowls, placed either 20 cm apart (centre to centre) on the feeding platform or at the midpoint of the feeding shelf. Water was available ad libitum to both mother and pups.

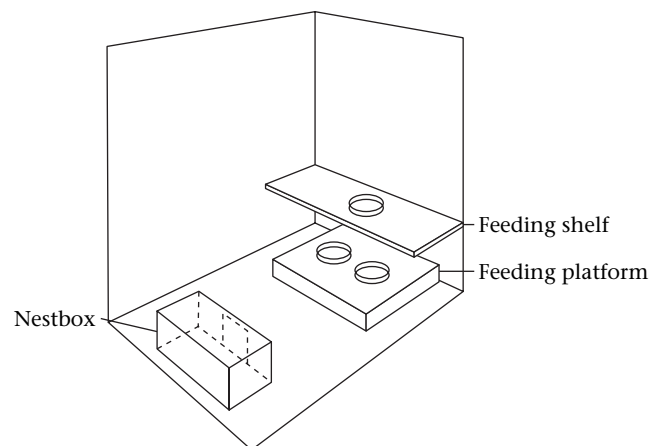


Figure 1. An enclosure in which training and testing took place.

## Diets

We made two diets by mixing, respectively, 1.0 g of McCormick's Ground Cinnamon (diet Cin; McCormick Canada Inc., London, Ontario) or 2.0 g of Hershey's Cocoa (diet Coc: Hershey Canada Inc., Mississauga, Ontario) with 100 g of powdered Normal Protein Test Diet (diet NPT; Harlan-Teklad, Madison, Wisconsin: catalogue number TD 170590). Diet NPT is a nutritionally adequate diet composed principally of casein and cornstarch with an energetic density of approximately 18.92 J/g.

We prepared a third diet (diet MP), more palatable than diets Cin and Coc, by adding 5.0 g of vegetable oil (Crisco, J. M. Smucker Inc., Toronto, Ontario) and 6.0 g of granulated sugar to 100.0 g of diet NPT. Diet MP had an energetic density of approximately 19.51 J/g, roughly 3% greater than the energetic density of either diet Cin or diet Coc. In a pilot experiment, six adult female Long-Evans rats offered a choice for 24 h between diets MP, Cin and Coc, ate an average  $\pm$  SE of  $65.8 \pm 6.1\%$  diet MP.

## Procedure

### *Training females assigned to experimental groups*

Experimental females ( $N = 17$ ) were trained to avoid either diet Cin ( $N = 9$ ) or diet Coc ( $N = 8$ ) and, consequently, to eat the alternative diet. To train a subject to avoid a diet, we moved her from her home cage to a separate enclosure (Fig. 1) and placed her on a schedule of food deprivation, providing a bowl of diet MP on the feeding platform for 1 h/day for 2 consecutive days. On the third day of scheduled feeding, we weighed the subject, then offered her a weighed food bowl containing either diet Cin or diet Coc on the feeding platform for 1 h. Immediately after the 1-h feeding period ended, we injected the subject intraperitoneally with a mild toxin (1% of body weight of 0.13 M lithium-chloride (LiCl) solution). The injection caused diarrhea and lethargy in subjects that lasted 1 h or less.

Next, to accustom the females to eating the diets to be used during testing, we provided subjects with 3 days of ad libitum access to either diets Cin and Coc on the feeding platform and diet MP on the feeding shelf (three-bowl condition,  $N = 10$  females), or diets Cin and Coc on the feeding platform (two-bowl condition,  $N = 7$  females). During the 3 days of habituation, none of the females used in the experiment ate any of the diet that they had been trained to avoid.

### *Training females assigned to the control condition*

Control females ( $N = 6$ ) were treated exactly as those assigned to the three-bowl experimental condition except that control females were injected with a benign saline solution instead of the LiCl solution.

### *Breeding adult females*

After each female had completed training, we placed her in the cage of a sexually proven adult male from our colony for 1 week. We then moved her to an individual cage that we subsequently monitored until birth of the

litter, which was expected to occur 3–4 weeks after the female was first placed with a male.

## Testing

For ethical reasons, we did not want to inject dams with toxin while they were pregnant or nursing. Consequently, a minimum of 6 weeks (1 week mating, 3 weeks gestation, 2 weeks lactation) passed between the end of training and the beginning of testing.

When the litter of pups born to a female was 14 days old, we placed the litter together with its dam in the nestbox of the testing enclosure (Fig. 1). As during the last phase of training, food bowls containing diets Cin and Coc were continuously available on the feeding platform and a bowl of diet MP continuously available on the feeding shelf for the 16 females and their litters assigned to the three-bowl experimental ( $N = 10$ ) and control ( $N = 6$ ) conditions. During testing, we continuously offered the females and litters ( $N = 7$ ) assigned to the two-bowl experimental condition only diets Cin and Coc on the feeding platform.

From the time that we placed mothers and litters in their enclosures until 72 h after we first observed a pup feeding from one of the food bowls on the feeding platform, we used closed-circuit television and time-lapse video recorders (set to record at 1/36 normal speed) to continuously monitor feeding by dams and pups. We subsequently scored the time that each dam spent eating from each food bowl in its enclosure for the 2 days before pups began feeding on solid food and on the 3 days immediately thereafter. We also recorded the diet eaten by the pups in each litter during their first 20 instances of feeding on solid food and during the first 20 instances of feeding beginning 24 and 48 h following the 20th instance of feeding on solid food.

We weighed each food bowl once every 24 h and determined how much food had been consumed from it. Because data concerning the amount of food eaten from each food bowl provided no information in addition to that provided by observation of feeding behaviour, we present here and discuss only data based on observations.

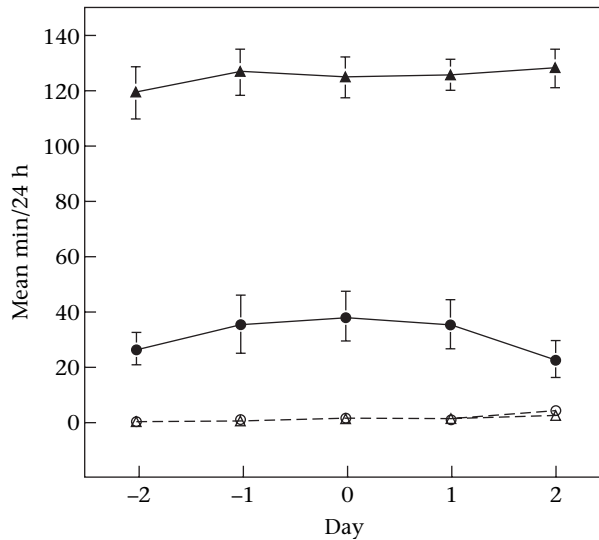
## RESULTS AND DISCUSSION

To compare the feeding behaviour of adults and pups assigned to the three conditions, we have reported data with respect to the day on which pups were first seen eating solid food (day 0) from either of the two food bowls available to them on the feeding platform.

### **Did Experimental Dams Learn to Avoid the 'Toxic' Diet?**

During testing, dams assigned to the three-bowl and two-bowl experimental conditions avoided eating whichever food they had eaten immediately before we injected them with LiCl during training (Fig. 2).

We found no difference in the time that dams assigned to the three-bowl and two-bowl experimental conditions



**Figure 2.** Mean  $\pm$  SE min/24 h that dams assigned to the three-bowl experimental condition (circles) and the two-bowl experimental condition (triangles) spent eating the food that they had been trained to avoid (open symbols, dashed lines) and the food they had learned to eat (closed symbols, solid lines). Day 0 is the day on which the pups in each litter first fed on solid food. The presence of only one broken line results from total overlap in the time spent eating the averted food by dams assigned to two-bowl and three-bowl experimental conditions. No standard errors are associated with the data of these two groups because the printed standard errors were smaller than the printed data points.

spent eating the diet that they had been trained to avoid (Fig. 2). However, as expected, dams assigned to the two-bowl experimental condition (that had access only to diets Cin and Coc during testing), spent more time eating the 'safe' food on the feeding platform than dams assigned to the three-bowl experimental condition (that had access to diets Cin, Coc and MP during testing; Fig. 2). In particular, dams assigned to the three-bowl experimental condition ate the food that they had been trained to avoid at an average  $\pm$  SE rate of only  $57.3 \pm 25.2$  s/day during the first 24 h after their pups first ate solid food and at a rate of only  $41 \pm 17.2$  s/day during the next 2 days. Similarly, dams assigned to the two-bowl experimental condition ate whichever diet they had been trained to avoid at a rate of only  $29.9 \pm 22.4$  s/day during the first 24 h after their pups first ate solid food and at a rate of  $51.9 \pm 26.7$  s/day for the next 2 days. There was no difference in the amount of time that dams assigned to the two experimental groups spent eating the diet that they had been trained to avoid either on the day their young first ate solid food (Student's  $t$  test:  $t_{15} = 0.77$ ,  $P = 0.45$ ) or during the next 2 days ( $t_{15} = 0.36$ ,  $P = 0.72$ ).

### Did Dams Teach Their Young?

If rat dams taught their young to eat safe food or to avoid poisoned food, then when young started to wean to solid food, dams assigned to the three-bowl experimental condition (that had learned that one food available on the feeding platform was toxic) would be expected to spend

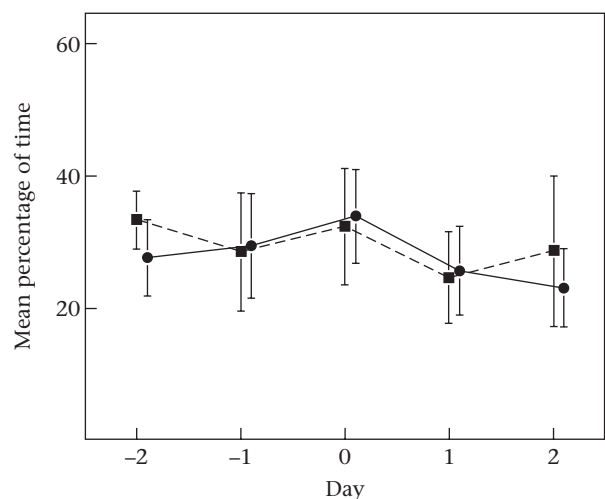
more time eating on the feeding platform than dams assigned to the control condition (that had no concerns about the safety of the foods available to their offspring). To the contrary, we found no difference in the mean percentage of time that dams assigned to three-bowl experimental and control conditions spent feeding on the feeding platform on either the first day that their young ate solid food (Student's  $t$  test:  $t_{14} = 0.13$ ,  $P = 0.90$ ; Fig. 3) or the next 2 days ( $t_{14} = 0.22$ ,  $P = 0.82$ ; Fig. 3).

Across the 5 days of testing, dams assigned to the control condition actually spent a greater percentage of time eating on the feeding platform ( $29.3 \pm 5.4\%$ ) than did dams assigned to the three-bowl experimental condition ( $28.7 \pm 6.3\%$ ). It was, therefore, impossible to calculate power statistics for the probability that dams assigned to the three-bowl experimental group spent more time on the feeding platform than dams assigned to the control condition.

If rat dams taught their young, then dams assigned to the three-bowl experimental condition might have been expected to spend more time eating from the feeding platform after their young started to eat solid food than before their young started to wean. In fact, the mean percentage of time that dams in the three-bowl condition spent feeding from the feeding platform did not differ before (days -1, -2;  $27.4 \pm 6.1\%$ ) and after (days 0, 1 and 2;  $28.4 \pm 6.7\%$ ) their young had started to eat solid food (matched-pairs  $t$  test:  $t_9 = 0.21$ ,  $P = 0.84$ ; Fig. 3). There was no evidence that dams were willing to eat a slightly less palatable, less energetically dense food in order to teach their young to avoid a potential toxin.

### Would Pups Have Learned If Their Dams Had Taught Them?

It might be argued that pups wean to solid food only after observing their dam eating (Galef & Clark 1971a),



**Figure 3.** Mean  $\pm$  SE percentage of total feeding time that dams assigned to the three-bowl experimental condition (—●—) and control condition (---■---) spent eating from the two food bowls on the feeding platform. Data points are slightly offset to facilitate reading the data. Day 0 is the day on which the pups in each litter first fed on solid food.

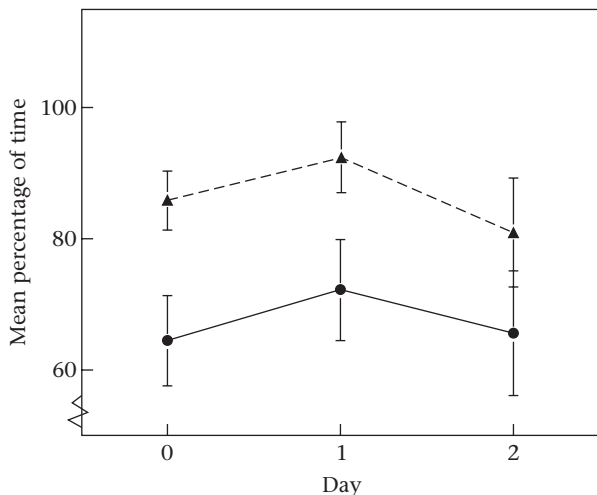


and thus, might require only brief periods of feeding with their dam to learn what foods to eat. If so, the time that a dam spent eating safe food would not affect the likelihood that her young would learn to eat that food.

In fact, although during the first 3 days that pups were feeding on solid food, pups assigned to the three-bowl experimental condition ate significantly more than 50% of the time from the bowl containing the food that their dam had learned was safe (mean  $\pm$  SE =  $67.2 \pm 6.1\%$ ;  $t_9 = 2.82$ ,  $P = 0.02$ ), they ate significantly less of that diet than did pups of dams assigned to the two-bowl experimental condition ( $86.3 \pm 5.8\%$ ;  $t_{15} = 2.17$ ,  $P < 0.05$ ; Fig. 4). Thus, pups of dams assigned to the three-bowl experimental condition would have learned more about the relative safety of the diets available to them if their dams had increased the time they spent eating the 'safe' diet on the feeding platform.

The finding that, even without active teaching, pups preferred a food that their mother had eaten to one that she had not eaten is consistent with results of previous experiments showing that young rodents exposed to an adult that has eaten a food show an enhanced preference for that food (e.g. Galef & Clark 1971b; Galef & Sherry 1973; Galef & Wigmore 1983; Valsecchi et al. 1996; Solomon et al. 2002).

We did not find a significant correlation between the time that dams assigned to the three-bowl experimental condition spent eating averted diets before their young started to eat and the percentage of time their young spent eating that diet (Pearson's correlation:  $r_8 = -0.19$ ,  $P = 0.73$ ). After the young started to eat, the time that they and their dam spent eating the diet that their dam had learned to avoid was highly correlated ( $r_8 = 0.74$ ,  $P = 0.02$ ). Although we could not determine whether dams were influencing the food choices of their offspring or vice versa, there is every reason to expect that both effects were occurring (Galef et al. 1984). In any case, the



**Figure 4.** Mean  $\pm$  SE percentage of total time spent eating that pups assigned to the three-bowl experimental (—●—) and the two-bowl experimental (- -▲ - -) conditions spent eating from the bowl containing the diet that their dam had learned to eat. Day 0 is the day on which the pups in each litter first fed on solid food.

evidence presented here indicates such effects did not involve active teaching by dams.

## GENERAL DISCUSSION

In the present experiment, we offered rat dams the opportunity to make a small sacrifice (eating a slightly less preferred, less energetically dense diet) to provide their own young with a potentially large benefit (reduced probability of ingesting a potentially toxic food). We showed that dams could have increased the probability that their young would wean to a safe food by eating less of the preferred diet available to them, but not to their pups, thus increasing the time that they spent eating a safe food that their young could access. Dams failed to reduce the time they spent eating the preferred food that their young could not access and thus failed to provide their offspring with information that the young might have used to select a food to which to wean.

In the present experiment, we provided all the elements that Caro & Hauser (1992) suggested are important for teaching. Potential teacher and pupils were closely related, and naïve individuals showed better learning when they could more often observe their mothers eating the 'safe' diet. The cost of teaching, the lost opportunity to eat a food of slightly greater energetic density, was surely less than half the cost pups could be expected to pay for feeding without a teacher's guidance. Indeed, given the greater susceptibility of juveniles than of adults to gastric distress, any food that caused a dam to experience transitory illness in the natural world might well prove fatal to her offspring.

Our failure to find evidence of teaching by rat dams whose young were faced with a potentially life-threatening choice of foods is, in one sense, encouraging. If we had found evidence that Norway rats 'teach' their offspring, some might have suspected that whatever the present methods revealed, it was not teaching.

Of course, absence of evidence of teaching in one experiment cannot be interpreted as showing that adult Norway rats would not modify their behaviour to aid their offspring in other circumstances. However, the fact that teaching failed to occur under conditions where many other types of social learning by rat pups takes place may be particularly informative. It is also possible, though unlikely, that we were wrong to assume that the cost to pups of learning to avoid a 'toxic' food would exceed half the minimal cost of teaching that we imposed.

Although we found no evidence of teaching by rat dams, the present report introduces an experimental paradigm permitting investigation of the hypothesis that teaching, defined as an altruistic act (Caro & Hauser 1992), occurs in any species where adults and young can be made to feed separately and adults can be taught to avoid eating a distinctively flavoured food (e.g. red-winged blackbirds, *Agelaius phoeniceus*: Mason & Redinger 1981; chickens, *Gallus domesticus*: Bartashunas & Suboski 1984; domestic cats: Wyrwicka 1981; spotted hyaenas, *Crocuta crocuta*: Yoerg 1991; cottontop tamarins, *Saguinus oedipus*: Snowdon & Boe 2003; rodent spp: reviewed in Galef, in press).

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