

NUMERICAL COMPETENCE IN FERRETS (*Mustela putorius furo*)

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ABSTRACT: Ferrets were tested in a free feeding situation that required them to eat only three pieces of food from a randomly sized larger array containing between 15 - 20 items. Controls were established to preclude discrimination based on spatial or volumetric cues, or cuing by the experimenter. This demonstration represents the first evidence of numerical competence in a mustelid species, and replicates the results of pioneering research by Koehler and his associates with budgerigars (Marold, 1939), as well as more recent work with rats (Davis & Bradford, 1991). Although the performance of ferrets reached comparable levels to those reported with other species, extended training yielded a deterioration in performance. These results are discussed in terms of the role of consequences to suppress competing responses, a problem that has been reported to underlie a variety of learning situations with ferrets.

Various forms of numerical competence have been demonstrated in a host of mammalian and avian species (e.g., Boysen & Berntson, 1989; Davis, 1984; Davis, MacKenzie & Morrison, 1989; Koehler, 1950; Pastore, 1961; Pepperberg, 1987). Indeed, following a half century of research, it is no longer reasonable to treat numerical ability as a distinctly human domain (Davis & Perusse, 1988a; Honigmann, 1942).

Despite a substantial body of literature and a burgeoning research agenda (e.g. Boysen & Capaldi, 1993), there has been no attempt to demonstrate any form of numerical competence in a mustelid species. This lack of attention to mustelid learning is not altogether general. Mustelids have been tested for other forms of cognitive competence with mixed results. In 1950, Beach reported that efforts at food-rewarded maze learning in ferrets were largely unsuccessful. He observed that ferrets, unlike more conventional psychological subjects, continued to explore blind alleys.

The general impression that ferrets were a "headstrong" species was

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maintained by Pollard & Lewis (1969). Although these authors reported some degree of success in training ferrets to navigate a maze successfully, Pollard & Lewis reported that "Unless food can be obtained rapidly...large numbers of competing responses are to be expected from this species." (1969, pg 42). In contrast to these reports, Haddad, Rabe, Dumas & Lazar (1976) described ferrets as a "readily trainable animal," although they observed that this species continued to be an uncommon subject in behavioral studies.

The situation has not changed much in the ensuing 20 years, either with regard to mustelid learning studies in general, or numerical competence in particular. Arguably, mammalian species that share an ecomiche might undergo similar selection pressure to develop cognitive abilities. Although much is known about the rodent's numerical competence (e.g. Capaldi & Miller, 1988; Davis & Bradford, 1986; Koehler, 1950), the related capacities of its frequent mustelid predator remain untested.

The present study examines for the first time the ability of the common ferret, *Mustela putorius furo*, to discriminate the quantity three and use this information in a simulated foraging situation. The technique we have selected derives from pioneering work by Otto Koehler (1950) and his associates. In their original demonstration (Marold, 1939), budgerigars were trained to eat a fixed number of food items from a larger array of freely available food. More recently, Davis & Bradford (1991) successfully employed this technique with rats, marking the first time that absolute numerical cues were used to restrict foraging behavior in a mammal. The present experiment attempts to replicate this form of numerical competence with ferrets.

METHOD

Subjects

Two albino ferrets (*Mustela putorius furo*), one male and one female, served as subjects. Both animals were obtained at approximately eight months of age from a veterinary clinic which received them from a family unable to care for them. Both animals were spayed prior to experimental testing.

Subjects were housed individually, but were allowed a "social time" for approximately two hours per day. During this period, subjects were permitted to interact freely in a 10 x 12 foot room that contained cloth bedding material, plastic tunnels for shelter and various toys. Food

rations (Hills Science Diet, Feline Maintenance 200 mg pellets) were provided to maintain approximately 95% of free feeding body weights for the duration of the experiment. Water was continuously available.

Apparatus

The experimental apparatus (illustrated in Figure 1) included a start area and test surface. The start area consisted of the seat of an upholstered chair (approximate surface 0.4 x 0.4 m). The test surface was a Melamine coated plank, approximately 0.6 m wide, which extended 2.4 m from below the edge of the start area. To prevent food pellets from being lost, 2 cm high sides were added to the edges of the test surface. A removable wooden barrier 0.6 m wide and 0.5 m high was placed on the plank next to the start area to prevent the subject from viewing the test surface or leaving the start area before the experimenter was ready to begin a trial.

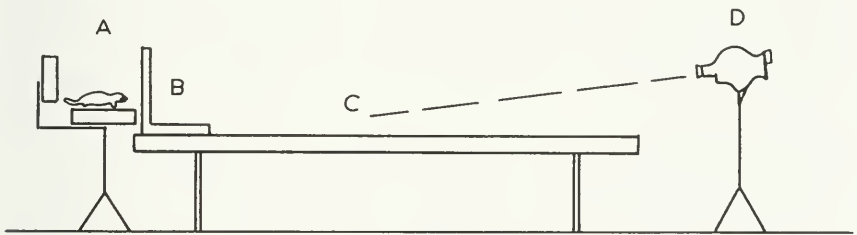


Figure 1. Representation of experimental apparatus showing location of (A) start area with subject, (B) wooden barrier, (C) test surface where food items were displayed, and (D) video recorder.

Procedure

Experimental sessions were performed once a day during each of the following stages.

Habituation. During the initial week, subjects were handled for approximately 20 minutes per day, not only to provide "gentling", but also to encourage a bond that would facilitate the use of social reinforcement during testing (Davis & Balfour, 1992; Davis & Perusse, 1988b). Handling was continued during a second week, during which food pellets (8 in 1 Ferret Diet, Pet Products Inc., Hauppauge, NY) were fed by hand. Hand-fed pellets would later be used as partial reward for successful completion of a trial. During the third week, animals were introduced to the experimental apparatus and shaped to eat several pellets off the plank, as well as from the experimenter. By the end of the

third week, subjects had learned to start a trial by jumping down approximately 10 cm from the start area of the chair (A in Figure 1) to the plank (C in Figure 1). Subjects were permitted to explore the test surface, and were rewarded with both food items and social reinforcement (petting and vocal praise) for returning to the start area after consuming food from the plank.

Training. A total of 12 training sessions were conducted. Subjects were shaped to eat exactly three pellets, their "target number," from a larger array of food on the plank. 8 in 1 Ferret Diet, a non-precision milled pellet, was specifically used in order to control for volumetric cues. These food items vary considerably in both shape and weight. A randomly drawn sample of 30 pellets used during training and testing averaged 210 mg in weight (range = 130 - 286 mg; standard deviation = 46.1 mg). Thus, it required nearly seven food items of the smallest kind to match the volume of three large ones.

Initially the array of food consisted of exactly the target number of pellets. Gradually, between one and five additional pellets were added. Initially, these additional pellets were spatially separated from the target number by between 0.1 and 0.5 m. This separation was gradually reduced to zero over the course of training. The number of pellets in the array was also increased to between 15 and 20. Array patterns were varied randomly to prevent performance based upon pattern recognition.

Five trials were run during each session. A correct trial consisted of the subject consuming its target number of pellets and returning to the start area without consuming any of the remaining pellets. Correct trials were scored as soon as the animal turned its body and began to return to the start area. Verbal praise was delivered as the animal moved back to the start area. Upon climbing up to the surface of the chair, the subject was further rewarded with petting and praise, as well as one or two extra food pellets fed by hand.

An incorrect response consisted of consuming either less or more than the target number. An error trial involving too few pellets being eaten resulted in neither positive nor negative reinforcement being delivered when the subject returned to the start area. The trial was simply recorded as an error. Attempts to consume more than the target number were immediately followed by a handclap, foot stomping and yelling the word "no!". Such negative consequences were delivered as soon as the subject made physical contact (either by paw or mouth) with a fourth piece of food. This typically caused the subject to drop the pellet and return to the start area. This form of aversive control was occasionally insufficient to control behavior of the male subject, and so it was occasionally supplemented by a light slap on the nose or posterior.

In the majority of cases, errors designated "More than" involved only a fourth pellet being consumed. Approximately 10% of such errors involved contact with a fifth pellet before consequences were effective in suppressing behavior.

Testing. Data collection was begun during this Phase. Four trials were run during each session. Correct responses and errors were recorded and continued to be rewarded with food and social contact and/or negative consequences following completion of a trial. In order to minimize the amount of feedback during testing, praise was no longer delivered during a trial as it had been during the training phase. Following each trial, regardless of its outcome, the animal was required to return to the start area in order to "reset the counter to zero" and signal the end of a trial.

The temporal spacing of trials was determined by both the subject and experimenter. A sequence of four correct trials could proceed without intervention by the experimenter. Following an incorrect trial, however, a Time Out (range 10 - 30 sec) was imposed. The experimenter intervened by inserting the barrier (B in Figure 1) and replenishing the food array as required. The next trial began when the barrier was removed.

Pellet arrays were located between 0.5 and 1.0 m from the start area and consisted of between 15-20 food items on the initial trial of each session. Pellets were located approximately 3 cm apart on the average, with interpellet space ranging between 8 mm and 5 cm. Because the animal progressively reduced the number of pellets remaining on each trial, it was occasionally necessary to replenish the plank between trials in a session. No systematic criteria were used for when pellets were replenished between trials, or for the number of pellets added to the array. This non-systematic approach was chosen to provide greater variability in the size of arrays confronted by the animals across both trials and sessions.

Small Pellet Control Procedure. Two control sessions were run during which broken pellets and small pieces of food were used exclusively. These sessions occurred during the final block of 80 trials illustrated in Figure 2. A sample of food items drawn from the same source as those used during "small item" probe trials revealed that their average weight (80.9 mg; range 40 - 133 mg; standard deviation = 23.9) was less than 40% of normally sized pellets. All other aspects of the test procedure were identical during these two control sessions.

The experimenter remained situated behind the start area in back of the subject during all sessions. Thus, animals moved in a direction away from the experimenter as they foraged on the plank. Test sessions were

run for approximately 480 trials, followed by a series of control sessions for the "Clever Hans" effect.

Clever Hans Control Procedure. In order to determine whether numerical discrimination depended on the presence of subtle cuing from the experimenter, four sessions were conducted during which the experimenter was removed from the room during testing. No feedback was given, regardless of performance, during these sessions. A sufficient supply of food items was provided so that four consecutive trials could be run without replenishing the array on the plank. A video tape record was made of each session for analysis. Clever Hans control sessions took place immediately following the final block of sessions reported in Figure 2. Regular test sessions were resumed immediately following the final Clever Hans control session and maintained for approximately 500 additional trials.

Data Collection. All sessions were videotaped. Randomly selected sessions were scored by independent observers in order to confirm the accuracy of data recorded by the experimenter during each session.

RESULTS

As in our previous work with rats, performance was analyzed in terms of three categories: Eating fewer than, more than, or exactly the target number of food items. During most initial training and early test sessions, both subjects attempted to eat all the food available in the arrays on every trial. Over the course of subsequent sessions, the behavior of both subjects began to come under control of the numerical contingency. The progressive shift in modal responding to the target number is illustrated in trial blocks reflecting early, middle and final stages of testing (see Figure 2).

The use of negative social consequences revealed an initial between-subject difference in the ease with which eating "more than" the target number was suppressed. As shown in Figure 2, the male ferret was relatively insensitive to the occurrence of negative consequences and continued to take food beyond the third pellet. Throughout the first block of 80 trials, eating "more than" remained the male subject's modal response.

In contrast, the female ferret, who was generally more submissive in social interactions, was highly sensitive to the negative consequences of eating "more than" the target number. This sensitivity was so

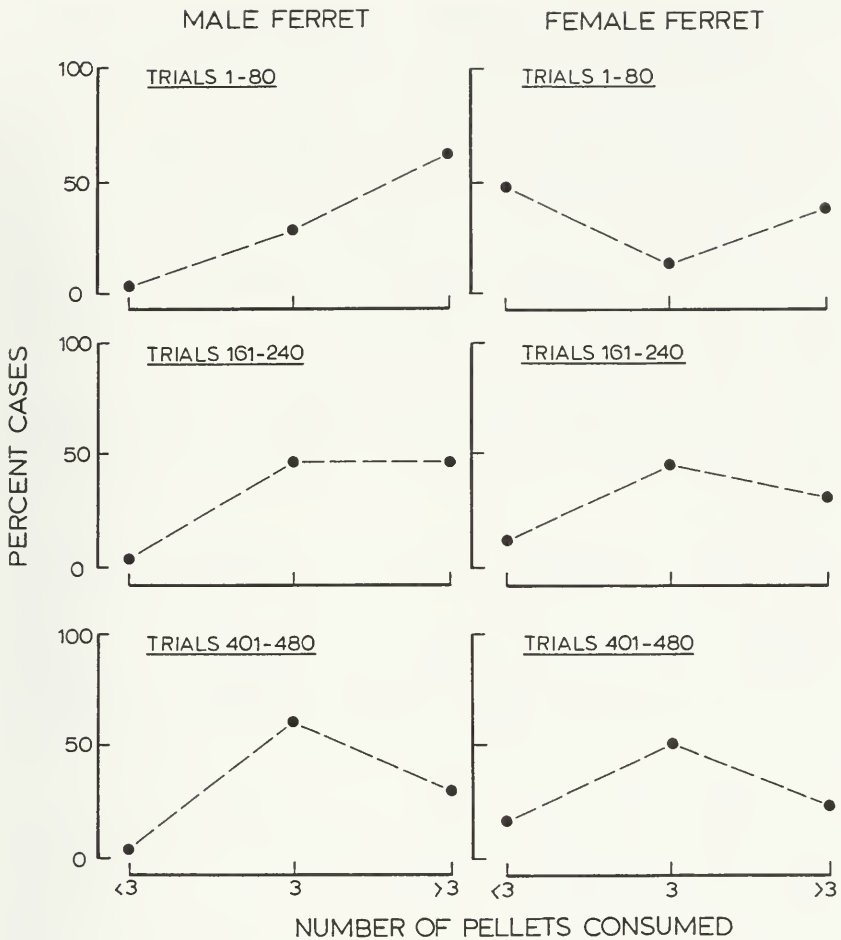


Figure 2. The percent of cases on which the male and female ferrets ate more than, less than, or exactly the target number of food pellets. Data are grouped into three trial blocks, recorded over the course of testing.

pronounced during early stages of testing that eating "fewer than" the target number was the female's most frequent response during the initial block of trials.

This difference between subjects was erased during the remaining stages of data collection shown in Figure 2. In general there was a sharpening of numerical control in both animals as the frequency of both "fewer than" (in the case of the female) and "more than" categories were substantially reduced. As illustrated in the figure, eating exactly the target number became the modal response for both subjects. Use of the binomial probability table to evaluate results of the final trial block

reveals significant performance ($p < .01$) for both subjects.¹

The time taken to consume three pellets was examined in order to evaluate the possibility that performance was based upon a "rhythmic" pattern of eating, rather than a numerical discrimination. Rhythmic patterns require regularity in inter-pellet intervals, which result in relatively stable trial durations. Such was not the case for either animal. The distribution of successful trial durations for the data reported in Figure 2 (timed from initial contact with the first pellet to the third) showed sufficient variability to preclude a case for the use of "rhythm." (Male: mean trial duration = 37.6 sec; range 24-58 sec; $sd = 9$; Female: mean trial duration 38.6 sec; range = 22-72 sec; $sd = 12.6$ sec.)

These data were further analyzed to determine whether the duration of correct trials differed from those on which fewer or more than the target number of pellets were consumed. If successful performance were based upon "rhythm," the consumption of pellets at a stable rate would yield differences in the durations associated with "fewer than," target number, and "more than" trials. However, a comparison of these three distributions for both the male and female subjects revealed no significant difference in the durations associated with these three outcomes. For the male ferret, trial durations averaged 35.4, 37.6 and 32 sec for "fewer than," target, and "more than" outcomes ($F = 1.78$; $p = .182$). For the female, trial durations averaged 35.3, 38.6 and 34.6 sec for the three outcomes ($F = .43$; $p = .656$).

The numerical nature of this discrimination was further underscored by the fact that individual food items varied in both shape and weight (range 130 to 286 mg), thus minimizing the potential contribution of volumetric cues. In addition, data from the "small pellet" control sessions revealed that performance was not affected, thus further minimizing the role of volumetric cues. Both subjects performed normally during these probe trials (3/4 correct on two consecutive sessions for the male subject; 3/4 and 2/4 correct for the female subject). Moreover, both subjects correctly consumed the target number during the initial two trials of the first control session.

In general, subjects followed no reliable foraging pattern either between trials or sessions. Food items were consumed opportunistically; i.e., subjects ate as they walked. Movement within the array showed

¹ Calculation of the binomial probability was based upon the conservative assumption that the three outcomes (eating more than, less than, and exactly the target number) were equally likely. Using this analysis, the binomial probability associated with the male's 61% correct responses (49/80 trials) when $p/\text{success} = .33$ equals less than 0.0001. The binomial probability associated with the female's performance equals 0.0007.

considerable variability, both in terms of the location of the first pellet consumed as well as the pattern followed once consumption began.

In order to examine whether numerical performance depended upon cuing by the experimenter, four Clever Hans control sessions were run. These data are summarized in Table 1. The important results of these sessions are that (1) performance did not depend on such cuing; i.e. correct responses were recorded even with the experimenter removed from the test enclosure. However, (2) the maintenance of correct performance did depend upon the threat of negative reinforcement.

During the critical first control session, both subjects ate the target number of food items on each of the first three trials. For both subjects, however, overall trial duration increased during the session, reaching unusually high values by the third trial (65 sec for the male; 72 sec for the female). Both animals engaged in extensive exploration (e.g. sniffing

Table 1. Performance of male and female ferrets during Clever Hans control sessions in which subjects were tested in the absence of feedback with the experimenter removed from the room. C indicates a Correct response. > indicates more than the target number of pellets was consumed. -- indicates that further testing was precluded because all remaining food items were consumed on the previous trial.

Control Session	Trial	Male	Female
1	1	C	C
	2	C	C
	3	C	C
	4	>	>
2	1	C	C
	2	C	C
	3	>	>
	4	>	>
3	1	>	C
	2	--	>
	3	--	--
	4	--	--
4	1	>	>
	2	--	--
	3	--	--
	4	--	--

the air) beginning late in the second trial and continuing throughout the third trial. The fourth trial consisted of a "more than" error by both animals.

During the second control session, both animals began with two correct trials, although the duration of trial # 2 was again extended by exploratory behavior. "More than" errors were recorded during each of the remaining trials in session 2.

During session 3, the female began with a correct trial. On the second trial there was considerable exploration prior to consuming the first pellet. The trial ended in a "more than" error. On the third trial, all remaining food items were eaten by the female. The male ferret began session 3 by slowly eating three pellets and pausing. Without returning to the start area, a fourth pellet was taken. The subject then paused, and consumed all remaining pellets on the plank, periodically rearing up and sniffing.

By the final Clever Hans control session, the performance of both animals reverted to its original pretraining level; i.e. all pellets were consumed on the first trial. Evidence from the sessions that immediately followed strongly suggests that this deficit in performance was motivational. When normal testing conditions (including the use of negative consequences) were resumed, discriminative performance was reestablished to pre-control levels by the end of the third post-Clever Hans session.

Although performance stabilized during the final trial block reported in Figure 2, additional testing was undertaken for both subjects. Rather than sharpening behavioral control, these additional sessions revealed a progressive deterioration in performance. It was clear at this point that the negative consequences had ceased to be an effective controlling stimulus. When testing was terminated following approximately 1000 trials, eating "more than" had become the dominant response for both subjects (66% for the male; 45% for the female during the final block of trials). Overall accuracy levels fell to 26% and 39% for the male and female ferret, respectively.

DISCUSSION

There are three important aspects of these data. Firstly, the progressive shift in modal frequency to the target number shown in Figure 2 and, in particular, performance levels reported in the third trial block. These data confirm that ferrets are capable of numerically restricting their food intake. The results are essentially similar to those

previously demonstrated with this procedure using rat subjects (Davis & Bradford, 1991), as well as those originally reported with budgerigars by Marold (1939). It should be stressed, however, that ferrets required more than twice as many trials as rats to suppress competing responses and yield modal levels of correct responding.

Secondly, as in our previous report with rats, the various control procedures suggest that performance was essentially numerical in nature and did not depend upon pellet size, volume, foraging pattern, or rhythmic cues. The data from the "Clever Hans" control sessions are of particular importance. There is a clear similarity between the present results with ferrets and those previously reported with rats (Davis, 1989; Davis & Bradford, 1991). The results of the first "Clever Hans" control session merit special attention. The maintenance of correct responding by both subjects during the initial trials confirms that performance does not depend upon cuing by the experimenter.

The deterioration of performance that occurred during subsequent control sessions does suggest, as it did in the case of rat subjects, that the threat of negative consequences rather than cuing was essential to maintaining performance. With rats and ferrets alike (no such controls were run in the study with budgerigars), the change in experimental conditions prompted considerable investigation by the animals (e.g., rearing up, sniffing). Once subjects detected that the aversive reinforcement contingency had been suspended, performance reverted to pre-training levels. The ease with which correct performance was reintroduced in both species when negative consequences were reinstated suggests that the transient failure observed during control sessions was essentially motivational in nature.

The necessity of aversive control to maintain discriminative control also bears upon the third important aspect of these data: the ultimate deterioration of performance after stability was attained. Because neither rats nor budgerigars were subjected to such additional testing (c.f., Davis & Bradford, 1991; Marold, 1939), we do not know whether their performance would have shown similar deterioration. In the present case, observation of experimenter-subject interactions during this period suggests that neither animal was as intimidated by the delivery of negative consequences as it had been earlier in testing (Davis & Balfour, 1992). Whereas "threats" (e.g., shouting, handclapping) had previously suppressed undesirable behavior, these consequences had virtually no effect on either subject during the final stages of testing. Only direct physical contact with the animal appeared to alter its behavior, and the effectiveness of this approach, itself, was inconsistent. Thus the ethically appropriate low levels of aversive consequences that we used were

insufficient to consistently suppress behavior. There are similar reports by a number of Koehler's (1950) colleagues (Wesley, 1961). In any case, when the efficacy of punishment declined in the present situation, performance of both ferrets deteriorated dramatically.

Although this account places a large emphasis on the suppression of competing responses, it should be stressed that aversive control alone could not have resulted in successful performance. In short, negative consequences are a necessary, but not sufficient ingredient for successful performance. Without the underlying ability to discriminate the quantity three, the threat of events alone would not yield the success reported with this procedure (see also Marold, 1939; Davis & Bradford, 1991).

Are ferrets truly "headstrong" and therefore relatively poor subjects in laboratory learning situations (e.g. Pollard & Lewis, 1969)? Such judgments should be tempered by the fact that competing responses in the present situation were essentially consummatory in nature. Their probability may have been raised by our use of food deprivation (albeit low level by conventional standards), as well as the presence of freely available food. It has been argued (e.g., Davis & Shattuck, 1980; Decosta & Ayers, 1971) that consummatory behavior may be harder to suppress than the arbitrary instrumental acts typically employed in numerical testing (e.g., Boysen & Berntson, 1989; Davis, 1984; Fernandes & Church, 1982).

In summary, ferrets, like rats, show evidence of numerically restricted food intake only as long as there is ample reason to do so. Both species clearly revert to pretraining consummatory levels when the threat of negative consequences is temporarily suspended during control sessions (Davis, 1989), or when it ceases to be a deterrent. Insofar as numerical competence, especially involving absolute quantities, has little to do with success in the natural environment, it is arguably adaptive to abandon learned behavior when the cost is low, in favor of more opportunistic foraging strategies. General statements about a species' "trainability" or its potential for numerical competence should be tempered by such considerations.

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