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Title
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Permalink
https://escholarship.org/uc/item/2cr7n85m

Journal
International Journal of Comparative Psychology, 22(2)

ISSN
0889-3675

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Publication Date
2009

DOI
10.46867/ijcp.2009.22.02.01

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Peer reviewed

Magnitude Effects of Sexual Reinforcement in Japanese Quail (*Coturnix japonica*)

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The effect of the magnitude of sexual reinforcement on the extinction of a running response was studied in quail. In Experiment 1, a group of subjects (L) received copulatory access to eight females, whereas a second group (S) received access to a single female. Both groups acquired the running response. During extinction, Group S showed a fast decrease in responding, whereas Group L persisted longer. In Experiment 2, males were allowed a choice between one or eight females. Preference for eight females demonstrated that males discriminated between the two reward magnitudes and that access to eight females had a larger reinforcing value than access to one female. The results are discussed within the context of the paradoxical reinforcement effects and the divergence in learning mechanisms in birds.

The origin of learning processes has been a traditional topic for comparative psychology. Thorndike (1911) assumed that learning principles were general to all species and differences between species were the result of quantitative rather than qualitative divergence, as Darwin suggested in his hypothesis of continuity of mental processes (Darwin, 1871). The question of whether learning depends on general mechanisms common to all species or on species-specific mechanisms has been approached from an evolutionary perspective. This implies that research in the area should use a comparative strategy with current species, since behavior does not leave a fossil record that would allow researchers to track its evolution (Bitterman, 1986). Thus, it is important to provide answers to questions about types of learning, the mechanisms that support such types of learning, and the origin of those mechanisms (Bitterman, 1975).

Following Thorndike, authors supporting a general-processes theory consider that differences among species in associative learning are more of degree than of type (Bitterman, 2000). According to this vision, it has been found that some basic learning processes, such as gradual and asymptotic acquisition and extinction with spontaneous recovery, as well as reversal discrimination among others, appear in different species of vertebrates. In addition, it has been observed that the same physiological properties of the neurons of cnidarians, animals that possess the simplest nervous system, also appear in the neurons of mammals and other animals (Papini, 2002a).

Despite the generality of the aforementioned processes, some phenomena related to behavioral adjustment to changes in the conditions of reward that are present only in some species. These phenomena are known as paradoxical effects of reinforcement because they contradict an assumption derived from the Law of Effect according to which a larger frequency and magnitude of reward would lead to stronger response and, therefore, a stronger persistence of performance during

extinction (Amsel, 1958, 1992). It has been observed that the paradoxical effects of reinforcement show a high degree of covariation in their occurrence across species, a fact allowing for the identification of evolutionary divergence in associative learning mechanisms across species (Papini, 2002b).

Some of the most commonly studied paradoxical effects are the magnitude of reinforcement extinction effect (MREE), successive negative contrast (SNC), and partial reinforcement extinction effect (PREE). In the MREE, a small magnitude of reward during acquisition is associated with a stronger persistence of response during extinction, in comparison with a large reward. In SNC, a sudden reduction of reinforcer magnitude generates an abrupt deterioration in performance compared to that of a group always trained with a small magnitude. In the PREE, intermittent reinforcement during acquisition leads to a stronger persistence of responding during extinction, in comparison with a continuously reinforced group (Domjan, 2003).

In studies with rats, the MREE, SNC, and PREE have been observed under different experimental conditions of training (Cándido, Maldonado, Mejías, & Catena, 1992; Flaherty, Greenwood, Martin, & Leszczuk, 1998; González & Bitterman, 1969; Pellegrini, & Mustaca, 2000). SNC has been observed in marsupials (Papini, Mustaca, & Bitterman, 1988). In humans, there is evidence of both SNCE (Kobre & Lipsitt, 1972) and PREE (Svartdal, 2000). In other taxonomic groups, including reptiles (Papini & Ishida, 1994), fish (González, Behrend, & Bitterman, 1965; González, Potts, Pitcoff, & Bitterman, 1972; Longo & Bitterman, 1960; Lowes & Bitterman, 1969; Schutz & Bitterman, 1969) and amphibians (Muzio, Segura, & Papini, 1992; Papini, Muzio, & Segura, 1995), performance is consistent with the basic assumptions of the Law of Effect.

When these phenomena are studied in pigeons, the results show an interesting dissociation: The PREE is observed, but the MREE and SNC are not recorded (Papini, 1997; Papini & Thomas, 1997; Papini, Thomas, & McVicar, 2002; Thomas & Papini, 2003). In general, each taxonomic group counts with more than one representative species in these studies. Nevertheless, most of the studies have been made with rats. Thus, it is important to study these phenomena in species other than mammals. Studies using birds have concentrated in pigeons, so studies with another avian model would help clarify the dissociated results found in pigeons and mentioned above. Given the apparent phenotypic similarity between birds and mammals attributable to evolutionary convergence or parallelism, it is plausible that similar behavioral effects in situations involving reinforcement downshifts could be generated by different underlying learning mechanisms (Papini, 2006).

If the focus on general-process theory is retaken, this does not only refer to the generality of learning principles in a comparative sense, but also to the application of these principles to different stimuli, responses, and reinforcements (Papini, 1998; Papini, Salas, & Muzio, 1999). However, as shown by the selective-association effect in aversive conditioning (Domjan, 1997; García & Koelling, 1966), animals in an experimental situation learn more easily certain relationships between stimuli and responses. Such discovery challenged the concept of equipotentiality, which had a wide influence in the study of learning until the

1970s (Domjan, 1997). Most of the research in this area centers on the study of paradoxical effects of reinforcement in ingestive behavior and, for that reason, they use solid food and sucrose solutions, both in varied quality and quantity. However, there is little research about paradoxical effects based on the use of sexual reinforcers or on any type of reinforcer other than food and water.

Domjan and Crawford (1998) argue that it is necessary to investigate the effects of reinforcement specifically in the sexual behavior system for two basic reasons. First, to determine empirically if the effects of sexual reinforcement are similar to the feeding reinforcers, thus avoiding generalizations based on extrapolations. Second, given that sexual reinforcement is part of a nonregulatory behavior system (not indispensable for the individual's survival) it could work in a different way from reinforcers that are part of a regulatory system, such as the consumption of water, food, or the maintenance of the temperature. In such cases, deprivation affects the metabolic process and compromises the individual's survival.

Based on the discoveries of comparative research on learning and on concerns about the reproductive behavior system (Domjan, 1994), this article presents the results of a first approach to the study of paradoxical effects of reinforcement in a sexual conditioning paradigm. The manipulated variable was the magnitude of sexual reinforcement, defined as copulatory access to different numbers of females, in male Japanese quail during a limited period of time and under widely spaced training trials (24 h). The effect of reward magnitude on performance was explored in a straight alley during the acquisition and extinction of sexual approach.

Experiment 1: Magnitude of Reinforcement Extinction Effect

Magnitude of reinforcement can affect performance in instrumental tasks (Bonem & Crossman, 1988). Despite this, there seems to be no parametric studies establishing high and low magnitudes of sexual reinforcement. For this reason, Experiment 1 involves what a priori seemed extreme values: one female for the small magnitude and 8 females for the large magnitude. The effects of this manipulation were observed in both acquisition and extinction.

Experiment 1 aimed to establish the occurrence of the effect of magnitude of reward in extinction. Studies about paradoxical effects in birds have found that these phenomena happen when the probability of reinforcement is manipulated, but not when the variable is quantity or quality of reinforcement (Papini, 1997; Papini & Thomas, 1997; Papini et al., 2002; Thomas & Papini, 2003). These discoveries have not been generalized to other response systems; thus, there is no empirical evidence about how the MREE may work in the reproductive behavior system. Male Japanese quail were used as subjects for two reasons. First, pigeons are used as subjects in most studies with birds and the results are generalized to the whole taxonomic class, which may not be appropriate. Second, Japanese quail have proved suitable as a laboratory model to study sexual conditioning.

Running in a straight alley was reinforced with copulatory access to female Japanese quail. This task was chosen because it has been used in studies

about paradoxical effects, with both birds and other species. Also, because the locomotion responses make part of the appetitive component of focal and general search, related with the consummatory component of sexual behavior (grab, mount, and cloacal contact; Domjan, 1994).

Method

Subjects

Twenty-four sexually mature and experimentally naive male Japanese quail (*Coturnix japonica*) were selected from the colony at the Animal Learning and Behavior Lab of the Universidad Nacional de Colombia, after a 5-min copulation test. Only subjects who copulated during that period were selected for the experiment. They were housed in a metallic 6-level stand. Each level had 4 compartments, each 61 cm deep, 22 cm wide, and 35 cm high, and each with an independent door.

The birds had free access to water and food, and were exposed to a photoperiod of 16 h of light and 8 h of darkness (lights on at 06:00 h). All the subjects were deprived of sexual access to females, except during the experimental sessions according to the design.

Apparatus

A wooden straight alley, divided in 3 compartments, a start box, a straight runway, and a goal box, was used. The alley was 300-cm long, 15-cm wide, and was surrounded by 15-cm high walls. Both the start box and the goal box were located on each side of the alley and they were separated from the runway by a vertical sliding door 10-cm wide and 15-cm high. The door was operated by a string and pulley system. In addition, there was another door located 15 cm before the end of the runway to retain the subject while the entrance door was opened, in order to avoid the females to escape from the goal box. The measures of the start box were 30-cm wide, 30-cm long, and 15-cm high. The goal box was 49-cm wide and 65-cm long. The alley was covered with a wire mesh, to prevent the experimental and the stimulus subjects to escape from the instrument.

Three infrared sensors were located at different points of the runway. The first sensor was located within the straight alley, at 15 cm from the start box. The second sensor was located 180 cm from the first one and the last pair was located 270 cm from the first sensors and 15 cm before the goal box. The infrared sensors were connected to a computer where a program (written in Visual Basic 6.0) registered the time that each animal took to run the different sections of the alley (in 0.01-s units).

Procedure

Subjects were randomly assigned to two different groups. The first group received a large reinforcer (Group L), that is, copulatory access to 8 females. When the male entered the goal box, it found a female. After 1 min, a new female was introduced and the previous one was taken away. The same procedure was followed until 8 females were presented.

The second group received a reinforcer of small magnitude (Group S), that is, copulatory access to a single female. Each subject of this group was kept in the goal box until it copulated with the female. If it did not achieve cloacal contact within 180 s, it was taken to its housing cage.

Experiment 1 consisted of 3 phases: pretraining (1 trial), acquisition (10 trials), and extinction (45 trials). During pretraining, subjects were exposed to the apparatus in a single 5-min trial while the doors of the runway were lifted. The subjects were free to leave the start box and move about in the runway.

During the training phase, subjects received 1 trial per day. The structure of each trial was the following: A subject was placed in the start box; 30 s later the door was opened, and the subject had 60 s to start running. If the subject did not begin running the alley in the specified time or if after having initiated, it stopped for more than 60 s, it was gently pushed to the goal box, to provide exposure to the female and facilitate acquisition. When the subject reached the end of the alley, the

front door was closed behind the subject and, simultaneously, the lateral door was opened, allowing the subject to enter the goal box.

In the following phase, subjects were exposed to an extinction procedure. Each group of 12 subjects was divided at random in two groups of 6 subjects, in order to balance the amount of time subjects remained in the goal box. This time could differentially affect extinction performance and be confounded with the effect of training with two distinct reward magnitudes, so we decided to provide and compare different intervals of permanence in the goal box during extinction.

Table 1 shows the distribution of each group during the acquisition and extinction phases. Group L was divided in two subgroups. Group LT (Large-Total), remained in the goal box the average time all 24 subjects spent in the goal box with females during the last trial of acquisition (Mean = 253 s). Group LL (Large-Large) remained in the goal box the average time spent by subjects of Group L during the last trial of acquisition (Mean = 480 s).

Table 1
Duration and Distribution of the Groups in each of the Experimental Phases

Phase and Duration (sessions)	Groups			
Acquisition (10)	Large: 8 females n: 12 males		Small: 1 female n: 12 males	
Extinction (45)	Large-Large (LL): Average time of group L in goal box during acquisition n: 6 males	Large-Total (LT): Average time of all subjects in goal box during acquisition n: 6 males	Small-Small (SS): Average time of group S in goal box during acquisition n: 6 males	Small-Total (ST): Average time of all subjects in goal box during acquisition n: 6 males

Likewise, Group S was divided in 2 subgroups. Group ST (Small-Total) remained in the goal box the average time spent by all subjects during the last trial of acquisition (Mean = 253 s). Group SS (Small-Small), remained in the goal box the average time spent time by subjects of group S during the last trial of acquisition (Mean = 26 s).

Ten females in reproductive condition were used as reinforcers. They were maintained under the same feeding and illumination conditions as males, but they were group-housed in a cage. All females used as reinforcing stimuli during the acquisition phase were rotated at random to minimize exposure to the same female in subsequent trials.

Results

To improve the normality and allow the use of parametric statistics, the arrival latencies to the goal box were transformed to their natural logarithm. Transformed data were grouped in blocks of 5 trials and a repeated-measure analysis of variance was applied. The data of the first and second partial measures are not presented because they did not show significant differences.

The results of the acquisition phase are illustrated in Figure 1. The statistical tests reveal that there is an effect of blocks of trials, $F(3, 10) = 351.43$, $p < 0.05$, but not of group, $F = 0.44$ $(3, 10)$, $p > 0.05$, or interaction of Blocks X Group, $F = 0.09$ $(3, 10)$, $p > 0.05$. This demonstrates that subjects trained with a small reward did not differ in their rate of acquisition from those trained with a large reward. In comparison with other vertebrate species, male quail show a

quicker response acquisition to run the straight alley for reinforcement. It has been reported that the duration of acquisition ranges between 40 and 50 daily trials for fish (Lowes & Bitterman, 1967; Schutz & Bitterman, 1969) and 24 daily trials for pigeons (Thomas & Papini, 2003), using food as reinforcement. In this experiment, asymptotic responding was reached on trial 7 and remained stable until trial 10.
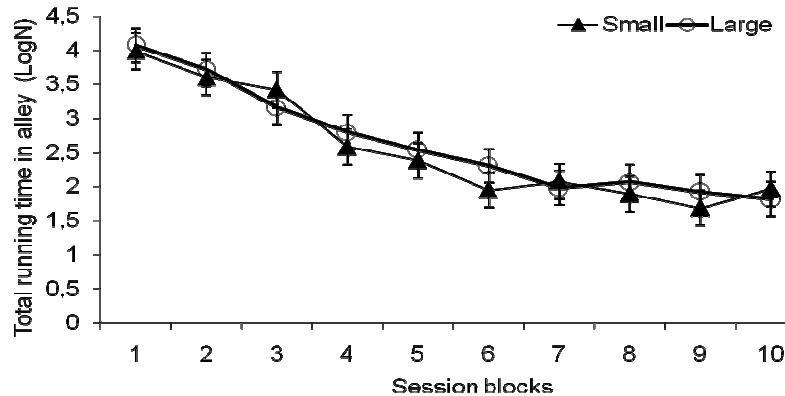

Figure 1. Total running time (and SE) in the runway during acquisition. Data were transformed to natural logarithm.

When data from Groups ST and SS were combined and compared with combined data from Groups LL and LT during extinction, a significant effect of blocks of trials was observed, $F = 7.54$ (8), $p < 0.05$. A significant Blocks X Group interaction effect in extinction was also observed, $F = 1.30$ (8), $p < 0.05$; however no group effect was identified, $F = 3.25$ (8), $p > 0.05$. The large reward magnitude groups showed stronger persistence in their running time at the alley, in comparison with the performance of the small reward magnitude groups. This is confirmed with test of contrasts in Block 7 where there is a significant difference among the groups. These results are shown in the top panel of Figure 2.

When the performance of all groups during extinction was compared, there was an effect of blocks, $F = 13.29$ (11), $p < 0.05$, and of blocks X group interaction, $F = 1.75$ (33), $p < 0.05$, but not of group, $F = 2.06$ (3), $p > 0.05$. Post hoc tests (LSD) reveal significant differences between Group SS and Group ST in blocks 2 to 4, and between Group SS and Group LL in blocks 2 to 5. No significant differences were found between SS and LT groups, LT and ST groups or LT and LL groups during extinction. This indicates a reversed MREE; that is, a performance according to the law of effect. As shown in the bottom panel of Figure 2, Group SS showed a faster extinction than the other groups; Group ST also showed an increase in arrival latencies but this process is slower. On the other hand, Group LT showed a slight increase in latencies during the initial sessions, which would indicate the beginning of extinction; later, however, its performance overlapped with group LL; this last group did not show a decrease in the running response to the goal box.
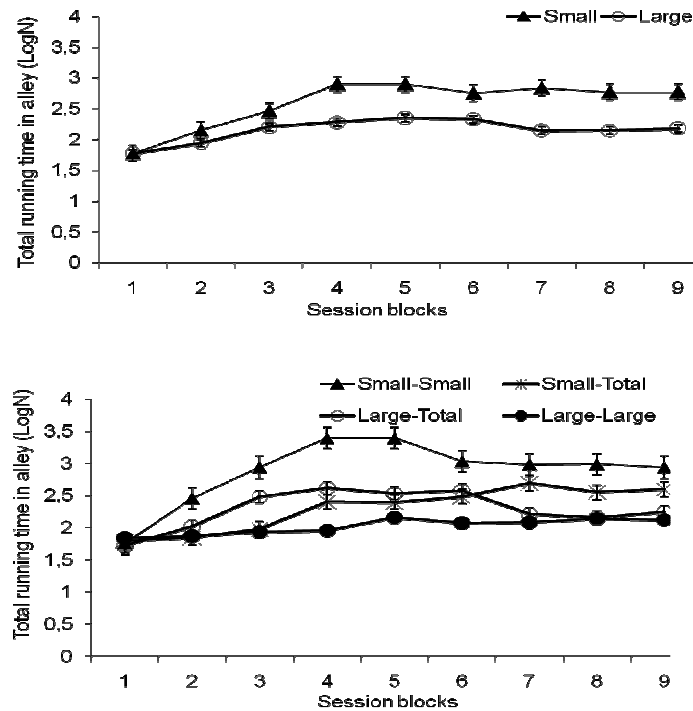
Figure 2. **Top:** Total running time (and SE) in the runway during extinction grouping data according to acquisition groups. **Bottom:** Total running time (and SE) in the runway during extinction. SS: Small reward during acquisition/Small reward (time) during extinction; ST: Small reward during acquisition/Mean time of extinction; LT: Large reward during acquisition/ Mean time of extinction; and LL: Large Reward in acquisition/Large Time in extinction. Data were transformed to natural logarithm. Each session block includes five individual sessions.

Discussion

The obtained results show that the manipulation of magnitude of sexual reinforcement did not affect the running response of quail during acquisition. This discovery is interesting because studies with other species, including pigeons, have shown that a larger reward magnitude yields a quicker acquisition in comparison with a smaller reward magnitude. Although the reported studies with pigeons use food as reinforcement, the magnitude effect persists when reinforcers associated with other behavior systems are used (e.g., defense behavior). In this vein, Cándido, Catena, and Maldonado (1984) varied the duration of safety signals in an avoidance learning experiment with rats and found that acquisition rate was directly related to the quantity of reward (safety time).

During the extinction phase, a reversed MREE was observed, that is, resistance to extinction was directly related to reinforcer magnitude during acquisition. The small magnitude groups exhibited considerable extinction, whereas the large magnitude groups continue persisting in their responses during extinction trials. These results are attributable to training with different magnitudes of reward. The persistence observed in the large magnitude groups demonstrates a strong biological predisposition of animals of this species to approach contextual cues that signal copulatory access to a female even after considerable exposure to extinction (Domjan, Lyons, North, & Bruell, 1986; Krause, Cusato, & Domjan, 2003).

When we separate the possible effects of confinement time in the goal box during extinction, no differences were observed in extinction between groups with the same retention time in the goal box (ST vs LT). Despite a graphic suggestion of an actual MREE effect in the first 4 blocks of extinction of groups ST and LT, followed by a reversed MREE, these suggestions are not supported statistically.

Significant differences were observed in extinction between two groups with the same retention time in the goal box during the acquisition phase, (SS vs. ST). Group ST was confined in the goal box longer than Group SS. It is possible that goal box cues served as conditioned reinforcers, maintaining the performance of subjects in Group ST during extinction for a longer period (blocks 2 to 4; see Williams, 1994).

Everitt, Fray, Kostarczyk, Taylor, and Stacey (1987) suggest that the performance shown by rats during instrumental extinction is affected by the level of sexual deprivation during the experiment. Such effect cannot be determined in the present experiment, because all groups were exposed to the same deprivation conditions. However, it would be interesting to observe performance when extinction is prolonged using sexual reinforcers. Lastly, although it may be argued that access to 8 females in the large group produced satiation in male quail, a dissociation between appetitive and consummatory sexual responses has been observed. Hilliard et al. (1998) exposed male quail to successive presentations of conditioned stimuli followed by female conspecifics and found that although the subjects decreased their copulation responses over time, they continued exhibiting approach responses to the conditioned stimuli and females. They argued that appetitive and consummatory sexual responses might be differentially affected by motivational changes.

Experiment 2: Preference for Reinforcers of Different Magnitude

In Experiment 1, the subject's extinction performance reflected a reversed MREE. Large and small groups differed significantly in some extinction sessions, but did not differ graphically or statistically in acquisition. The acquisition results did not provide evidence that the subjects discriminated large and small reinforcers used in this study. To evaluate this possibility, an experiment comparing the response of males to two different magnitudes of reward was designed. The discovery of a significant preference for one of two reward magnitudes would imply that the subjects discriminate between the alternatives. Therefore, the results

reported in Experiment 1 would not reflect a lack of discrimination of actual reward magnitudes.

Method

Subjects

Four sexually mature, experimentally naive male Japanese quail (*Coturnix japonica*), from the colony at Universidad Nacional de Colombia were used. The subjects were maintained under the same conditions of the previous experiment.

Apparatus

A straight alley similar to that used in Experiment 1 was used. The two boxes at each end of the alley had the same dimensions (30-cm wide, 30-cm deep, and 15-cm high). In addition, two guillotine doors at the center of the runway and separated by 15 cm from each other controlled access to the two boxes. These doors formed a central compartment that served as the start box. After leaving the start box, the subjects had to walk a distance of 127.5 cm to reach anyone of the choice boxes.

Procedure

The experiment consisted of 3 phases. In the habituation phase, subjects were placed in the start box, with all the doors of the runway lifted and they were allowed to move about freely during 5 min. In this phase, no reinforcement was provided. In the forced-election phase, each subject was placed in the start compartment for 30 s; then, one of the doors was opened and the subject was gently guided to one of the goal boxes in a series of 8 trials, 4 toward each box. When the subject crossed the goal line, in one of the ends of the runway, the goal box door was raised. Reinforcement consisted of copulatory access to one female during 1 min or to 8 females, presented one per minute, as done in Experiment 1.

Males received 1 female in one of the goal boxes and 8 females in the other goal box. The assignment of the reward magnitude was counterbalanced with respect to the goal boxes to minimize possible spatial biases. The order of forced election trials was also counterbalanced.

In the election phase, the subjects were placed in central start compartment during 30 s. Then both doors of this compartment as well as the doors of the goal boxes were elevated simultaneously. The assignment of the reinforcement was the same as in the previous phase. Twenty-five election trials were administered at a rate of 4 trials per day, 90-min apart. The frequency of election of each reinforcement magnitude and goal box were registered.

Results

Subjects consistently chose 8 females over 1, in a proportion of 0.71 to 0.29. These differences are statistically supported by the results of a test of proportions differences, $z = -5.94$, $p < 0.05$. Subjects preferred the side of the alley that was always associated with the larger reward. An analysis of side preferences for the group as a whole showed that subjects were not spatially biased toward a specific goal box. The proportion of choices for each of the two goal boxes was 0.47 and 0.53, $z = 2.456$, $p > 0.05$. This means that the between-subject elections did not result from the subjects' preference for a specific place of the experimental apparatus, but from the value of reinforcement.

Discussion

The results obtained in Experiment 2 demonstrated that male quail discriminate between the two reinforcement values used in Experiment 1; sexual access to 8 females was preferred over access to a single female. Therefore, the overlapping of acquisition curves of two experimental groups and the reversed MREE in male quail's performance observed in Experiment 1 cannot be attributed to a failure to discriminate the reward magnitude.

There are different dimensions of magnitude of reinforcement such as quantity, density, or time of access to reinforcers; the manipulation of each one of these parameters could produce results different from those reported here. In addition, time exposure to the reinforcer may interact with other parameters of reinforcement to produce different results. This requires a redefinition of the concept of reward magnitude that specifies multiple effects produced by each parameter not only mentioned in the field of paradoxical reinforcement effects but in other areas such as incentive contrast (Pellegrini, Ruetti, Mustaca, & Muzio, 2004). In the case of this experiment, although males consistently chose 8 females over 1, it is not possible to isolate the effect of reinforcer magnitude from the effect of exposure time to the goal box. For example, a single female, available during 8 min, may have the same value as eight females available at a rate of one per minute.

General Discussion

The results of Experiment 1 demonstrated a reversed MREE in the runway in sexually reinforced quail. The acquisition curves for groups L and S overlapped and did not show any effect of reward magnitude on the speed of acquisition. This was surprising because in previous studies an inferior performance level has generally been observed in the small reward group compared to the large reward group, which shows a faster response acquisition. It was not possible to determine whether this overlap was the result of differences of sexual reinforcement with regard to other types of reinforcement, or the result of a difficulty to discriminate between the two reward magnitudes. Experiment 2 provided clear evidence for the discrimination of magnitude designed to discriminate between these possibilities in terms of performance.

Taking into account the results of both experiments, acquisition in Experiment 1 may be explained in two ways. First, the observed pattern of responses may reflect some property of the straight runway. It is possible that the length of the alley was too short and it did not allow the observation of differences in acquisition rate. In several studies on incentive contrast, very long (610 cm) or inclined straight alleys were used to avoid ceiling or floor effects (Flaherty, 1996).

Second, although quail discriminated between two reinforcement magnitudes, the motivation level generated by copulatory access to a single female may have been too high and subjects may have not exhibited differential performance toward the preferred reinforcement magnitude. In fact, the high level of sexual motivation was one reason for the use of this species as a laboratory

model for sexual conditioning. It may be argued that the manipulation of other reinforcement parameters (e.g., a longer time of exposure to a single female) would produce results different from those reported here.

As several studies with sexual reinforcement suggest, some properties displayed by these reinforcers are different from those of other appetitive reinforcers. For example, Domjan (1997) pointed out that contrary to what happens with other behavior systems in which only appetitive components are modifiable by learning, in the sexual behavior system both, appetitive components and consummatory components, are susceptible to modification by conditioning procedures.

At a methodological level, opposing patterns of acquisition could result from procedures used to provide reinforcement. For example, noise generated by the manual introduction of mates may have affected the reinforcing effect from exposure to female quail. Domjan and Crawford (1998) pointed out an inherent difficulty with the delivery of sexual reinforcers, especially in nonrestricted procedures. In this sense, the development of automation of such procedures offers a challenge for researchers of sexual behavior. Nevertheless, the fact that the choice test showed a significant tendency toward a large reinforcement demonstrates that this procedural manipulation preserves the reinforcement value.

During extinction, there is an effect of magnitude of sexual reinforcement on the instrumental response. Subjects showed a nonparadoxical performance, in agreement with Thorndike's Law of Effect. These discoveries resemble results with pigeons using different magnitudes of food reinforcement. Accordingly, it could be argued that the reproductive behavior system has a similar functioning to the foraging system. Papini (1998, 2002b) pointed out a tendency to conservation in learning mechanisms, at least in vertebrates. Such a conservation or generality is related to the fact that ecological niches and problems faced by organisms that inhabit them share a variety of common dimensions. Learning mechanisms evolved so that individuals faced basic survival challenges, such as searching for and obtaining energy and nutrition sources. Behavior then would have been organized in fundamental modules of information storage and used to solve basic individual tasks. When a new basic task arises, since there is a preexistent modular organization, this tends to be coupled to previous organization and, in this way, similar mechanisms of information gathering and use will evolve. Such cooption of learning mechanisms could explain similarities among foraging and sexual behavior systems across different species and lead to predict a dissociation between MREE and PREE with sexual reinforcement analogous to that found with food reinforcement (Thomas & Papini, 2003).

It is necessary to design similar studies with two objectives. First, applying the principle of systematic variation (Bitterman, 1975), establish the role of contextual factors (variables other than reward magnitude) on performance during the acquisition and extinction of sexual behavior. Second, to determine if the dissociation between paradoxical effects is also observed in the sexual behavior system. Once the basic parameters of sexual reinforcement manipulation and the functional regularities have been established for a group of closely related species, it would be possible to design studies aimed at uncovering underlying mechanisms

at levels of analysis (Papini, 2006). In addition, generalizing research to other reinforcers in the same species would help determine the similarities and properties of different behavior systems and of their possible evolutionary history.

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