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THE CALIBRATION OF THE CONTROL RANGES OF DRIVE AND INCENTIVE VARIABLES IN THE SERIAL DISCRIMINATION REVERSAL LEARNING OF TWO AVIAN SPECIES

by

Bruce A. Levine

Dissertation Committee:

Robert L. Gossette, Ph.D., Chairman
Joseph K. Andrews, Ph.D.
Philip H. Ramsey, Ph.D.

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requirements for the degree of Doctor of Philosophy
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ABSTRACT

The Calibration of the Control Ranges of Drive and Incentive Variables in the Serial Discrimination Reversal Learning of Two Avian Species

Bruce A. Levine

The goal of the present research was to determine the extent to which inter-species performance differences vary as a function of motivational and incentive variables, as an initial step in the design of a strategy for the matching of procedural variables across species.

Thirty-two pigeons and thirty-two chickens were each subdivided into four levels of drive (D) and two levels of incentive (K). Ss were trained to discriminate between two colors presented as circular shapes (red versus green). After reaching criterion, each S completed 19 successive reversals of the problem.

Results showed that D exerts a powerful influence on performance and, most importantly, that this variable has differential effects on the behavior of the species studied. The findings make clear both the possibility and the importance of determining the control ranges of such variables so that differential performances due to mismatched variables of this sort may be eliminated.

The effect of K was found to be non-significant. The implications of this finding in respect to the differential-extinction hypothesis and it's relationship to studies of K effects on resistance to extinction measures were explored.

Results were further discussed in regard to the retention-decrement hypothesis, for which they offered some difficulties, and the differential-extinction hypothesis, which they supported.

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B. A. L.

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One of the most troublesome, yet attractive, goals of the comparative analysis of behavior is the isolation of dimensions of what has been called "learning ability", or, more historically, "animal intelligence". While a number of studies dealing with the problem have been reported over the years, there has been notably little success in achieving this goal (Warren, 1965). The design of studies which attempt to examine interspecies differences present rather unique difficulties. Investigations of comparative learning ability can easily become misleading if the assumption is made that obtained differences are due solely to organismic variables (i.e. species variables). It is clear that organisms which differ taxonomically may also differ in the relative responsiveness they display to environmental and procedural variables employed in a given study. Organisms which are taxonomically similar may also differ in this respect; thus, there is no guarantee that degree of taxonomic similarity is highly correlated with any similarity in responsiveness to environmental factors. Presumed species differences on a learning task may represent some undetermined interaction of the sought-after organismic variable and the omnipresent situational variables. In a discussion of this problem, Sutherland and Mackintosh (1971) conclude that drive level (D) and reward magnitude (K) are two of the most potentially important sources of variation in comparative analyses which interact to obscure species differences.

In the present study an attempt will be made to clarify the extent and nature of drive and incentive variables as they affect performance at different taxonomic levels. Once the functional relationship of these variables is understood in comparative perspective, a more precise analysis of interspecies performance differences will be possible.

The Comparative Investigation of Learning

Most definitions of learning emphasize the ability to adapt to changing environments. Hilgard and Bower (1966) suggest that learning is the process "...by which an activity originates or is changed through reacting to an encountered situation (pg. 2)." Among the earliest attempts in the comparative study of learning were those of Thorndike. His use of the puzzle-box (Thorndike, 1898, 1911) marked the beginning of a series of attempts to devise techniques applicable in the comparative analysis of learning. Since then a host of different tasks and methodologies have been applied in a disappointingly fruitless search for a taxonomically sensitive and widely applicable measure of interspecies learning differences. The following sections provide some background into this search.

The Acquisition of Simple, Non-Discriminative Responses

Investigations of the variations in acquisition of classical responses of different species have failed to result in any consistent ordering of performance differences along taxonomic lines. Razran (1961) indicated that only inconsequential species differences emerge during acquisition. Hilgard and Marquis (1936) demonstrated that classically conditioned responses of dogs and men were more alike than those of monkeys and men. Marx (1970), summarizing much of this work suggests that the assessment of species differences is extremely hazardous. Reasons for this include the tremendous intraspecies variability, the apparent differences in difficulty of forming autonomic and skeletal conditioned responses and the great diversity in experimental designs of the investigators. Marx (1970) concludes that, based upon the available evidence, it is most difficult to support the contention that quantitative differences in the rate of acquisition of classically conditioned responses will permit any systematic ordering of species in terms of learning ability.

Simple operant response acquisition studies have also failed to provide any sensitive measure of interspecies learning differences (Clark, 1961; Kelleher & Cook, 1959). Reviewing the literature, Warren (1965) has concluded that, "the rate of conditioning varies markedly within the same species, even within the same organism, as a function of many experimental conditions." It is evident also that insignificant differences result when species are compared under various schedules of partial reinforcement (Ferster & Skinner, 1957).

Simple Discrimination Learning

Early studies with dogs (Karn & Munn, 1932) and chimpanzees (Nissen, et al., 1949) suggested that visual discrimination learning might provide a sound basis for phyletic comparisons. However, evidence began to accumulate which indicated that simple discrimination tasks were inadequate (Siegel, 1953). Discrimination learning of both the spatial (Mason & Harlow, 1958) and non-spatial (Gardner & Nissen, 1948) varieties have been examined. Summarizing the available literature, Waters, et al. (1960) conclude, "The rate of formation of simple discrimination habits does not increase regularly from the so-called lower to higher phyletic levels (p. 212)."

Probability Learning

In probability learning the stimuli presented differ in respect to the reinforcement ratios associated with each. The optimal type of behavior in this situation, known as "maximizing" (Bitterman, 1965), occurs when the organism makes only the more frequently reinforced choice and refrains from making the less frequently reinforced one. A less effective strategy, "matching", occurs when the organism produces a choice ratio that tends to match the reinforcement ratio. Numerous investigations with monkeys (Meyer, 1960; Wilson, et al., 1964), rats (Bitterman, et al., 1958), pigeons (Bullock & Bitterman, 1962) and fish (Behrend & Bitterman, 1961) point to the conclusion that monkeys and rats typically maximize, pigeons often maximize (on simplier, spatial tasks) and fish only match. There is, however, a good deal of overlap in performance across species. Since, as Warren (1965) asserts, monkeys' behavior seems "... not to differ in any important qualitative respect from that of rats", probability learning fails to meet the need for a reliably sensitive measure for interspecies comparison.

Oddity Learning

Oddity learning involves the selection of the odd member among three stimuli, two of which are alike. Most typically the odd stimulus is changed from trial to trial or session to session. In an early demonstration by Meyer and Harlow (1949), it was shown that rhesus monkeys were capable of solving such a problem. Strong and Hedges (1966) more recently demonstrated the sensitivity of this procedure to differences between raccoons and two orders of primates. However, results of studies using subprimates are usually inconsistent with presumed taxonomic status. Warren (1960) showed that cats were able to learn a set for the solution of oddity problems within the range of performance established for rhesus monkeys. Stettner and Matyniak (1968) cite work by Pastore, which shows that canaries are capable of oddity learning whereas some "more advanced" species are not. This work also indicates that rats can solve such problems only when given extensive preliminary training (Wodinsky & Bitterman, 1953). It would appear, from the present literature, that while oddity learning may show promise in the investigation of primate learning, it's usefulness can not yet be extended to lower species.

Extrapolation Reflexes

Extrapolation reflex behavior is a problem solving task outlined primarily in the Russian literature, similar in many respects to the detour problem. In it's usual form (Krushinskii, 1961) an extrapolation of simple visual information is required. Two food bowls, one of them full and one empty, are placed behind a screen with a narrow slit in it, minimally wide enough for the animal's head to reach the bowls. After the animal has tasted the food, the two dishes are moved out of sight, one to the left and one to the right. The organism must remove it's head from the slit and go to the correct side in order to reach the food. Krushinskii (1961) having studied the extrapolation reflexes of several species concludes, "From the discovery of the considerable difference in the degree of development of the extrapolation reflexes in the animals studied, it may be suggested that this form of reflex activity undergoes a significant modification in phylogenesis." In spite of this conclusion, Krushinskii reports that rabbits, hens and pigeons do poorly, while dogs and crows solve the problem immediately. Therefore, it must be concluded that this methodology too suffers from an insensitivity to relative taxonomic levels.

Procedures Showing Promise in Phyletic Comparisons of Learning Ability

The foregoing discussion suggests a general failure of a number of tasks to yield meaningful interspecies differences. Primarily, the tasks are either insensitive to taxonomic levels or result in ranges of individual or species differences so great that the organisms cannot be reliably discriminated between, with the specific technique employed. Two procedures will now be examined which appear promising in the comparative analysis of learning ability.

Learning Set

Ward (1937) was one of the first to experimentally demonstrate the effect known as learning set. He found that the number of trials required to learn a list of nonsense syllables decreased as a function of the number of lists learned. This type of cumulative positive transfer, of a non-specific nature was later established with monkeys, learning discrimination problems (Harlow, 1949). Learning set methodology requires the organism to choose the rewarded one of two objects, differing in a number of characteristics. The objects are usually presented in counterbalanced, left-right order. After a predetermined number of trials the objects are removed and a new set is introduced. Performance is evaluated in terms of the number of correct responses across trials and/or sets. Recent studies have demonstrated rather marked differences in ability to form learning sets among several species of primates. Squirrel monkeys and marmosets have been shown to improve on learning set tasks considerably less rapidly than phylogenetically more "advanced" rhesus monkeys (Miles & Meyer, 1956). Commenting on the current state of learning set literature, Denny and Ratner (1970) state, "Among primates the chimpanzee, gorilla and rhesus monkey are at the top and the marmoset at the bottom...in much the same order that phylogeny might predict...Thus learning set has been entertained as a comparative psychology measuring stick of degree of intellectual development (p. 734)." Results obtained by Kaufman and Peterson (1958) reveal that learning set formation is more rapid in either normal or mentally retarded children (IQ 50-75) than in any of the non-human primates tested. Below the primate level learning sets have been demonstrated with rats (Weaver & Michels, 1961; Wright, Kay & Sime, 1963), skunks (Doty, Jones & Doty, 1967), cats (Warren & Barron, 1956) and birds (Plotnick & Tallarico, 1966). Comparisons by Koronakos and Arnold (1957) show that rats, cats and raccoons are inferior in performance to primates.

Despite these rather encouraging findings, several investigations suggest that the learning set task may not be as sensitive within the sub-primate range as it appears to be with primates. Zeigler (1961) and Plotnick and Arnold (1957) have found that pigeons and chickens are capable of performing in a manner comparable to cats. Further evidence indicates that pigeons and chickens can outperform marmosets (Stettner & Matyniak, 1968). Therefore, while learning set studies provide one of the most nearly satisfactory sources of evidence for phyletic differences in learning ability among primates (Hinde, 1966), a markedly decreased sensitivity among sub-primate species is evident. Gossette (1970b) suggests that, "The sensitivity of LS to interspecies differences would appear to be sharply reduced among the inframammalian species... Thus, to provide a more comprehensive analysis of vertebrate learning, across broader reaches of phyletic or taxonomic separation, an alternative strategy would appear desirable."

Serial Discrimination Reversal (SDR)

Serial discrimination reversal tasks typically require the organism to make an initial spatial (left - right) or visual (color, brightness or form) discrimination. One of the two alternatives is consistently rewarded until some criterion (trials or performance) is reached. Once having attained the criterion, the reinforcement contingencies are reversed, with the previously non-reinforced stimulus now being reinforced. This new discrimination is again learned to the previous criterion. The successive reversal of contingencies is continued a predetermined number of times. Each reversal is considered a separate problem and successive decreases in errors across problems constitutes effective learning.

Since the first demonstration of reversal learning

(Yerkes & Huggins, 1903), a wide range of species have been studied; including humans (Rajalakshmi & Jeeves, 1965), monkeys (Gossette & Inman, 1966; Harlow, 1950), rats (Pubols, 1957; Warren, 1965), kangaroos (Munn, 1964), monotremes (Sanders, et al., 1971), birds (Bacon, et al., 1962; Gossette, et al., 1966) turtles (Bitterman, 1965), alligators (Gossette & Hombach, 1969), fish (Warren, 1960) and cockroaches (Longo, 1964). Results from such studies, although numerous task and environmental differences exist, indicate a "Systematic improvement in flexibility - as defined by the reversal problem - from lower to higher vertebrates (Maier & Maier, 1970, p. 304)." Not only is SDR learning acquired more slowly by infraprimates than by primates (Waters, et al., 1960), but phylogenetically meaningful differences emerge within the primate range (Gossette & Inman, 1966; Gossette & Slonim, 1969). While progressive error reduction is greatest for primates, it is successively smaller for rats, birds, reptiles and fish. As phylogeny would suggest, birds are less efficient reversal learners than rats (Sutherland & Mackintosh, 1971) and lower orders of birds, such as Galliformes are less efficient than higher orders, such as Passeriformes (Gossette, et al., 1966; Gossette & Inman, 1966; Gossette, 1967). There is evidence of discrimination reversal improvement on simplier tasks (spatial rather than brightness) for turtles (Bitterman, 1965) and alligators (Gossette & Hombach, 1969). Data on fish are equivocal, with some studies demonstrating improvement (Setterington & Bishop, 1967; Squier, 1965) and others not

(Behrend, et al., 1965). Studies with invertebrates have generally failed to show successive improvement (Thompson, 1957; Young, 1962) across reversals (for exception, see Mackintosh & Mackintosh, 1964). Such data indicate that SDR may be the one procedure yet devised which is indicative of phyletic status (Kendler, 1959).

Advantages of SDR over Learning Set Methodology

The learning set (LS) task suffers from an important methodological difficulty. The specific tasks employed are assumed to be of the same order of difficulty. However, as Rajalakshmi and Jeeves (1965) point out, "Such an assumption seems hardly warranted for species such as the rat for which tasks which appear similar on the surface prove to be otherwise." While in SDR methodology a task of fixed difficulty is repeatedly reversed, LS tasks present, with each new set of stimuli, a new and variable degree of difficulty. It has been suggested (Gossette, 1969) that variation in the magnitude of negative transfer on successive reversals is one dimension along which vertebrates may be ordered. Serial reversals tend to maximize the occurrence of negative transfer, by the complete reversal of all stimulus controls. LS tasks, on the other hand, require constantly changing degrees of reversal (or none at all). The degree of interproblem transfer therefore, is both uncontrolled and unevaluated. In this regard, the importance of negative transfer effects are clearly demonstrated in a study by Mackintosh (1969) comparing reversal (maximum negative transfer) and non-reversal shifts (minimal negative transfer). It was found that the discrimination performance of rats and doves differed when the problems were sequentially ordered to provide reversal training (reversal shifts), but not when randomly ordered (non-reversal shifts) as in a learning set series. The reversal shift provided ample opportunity for negative transfer effects, thereby resulting in differential performances, while the LS type tasks did not.

Schusterman (1964) compared SDR and LS performances of chimpanzees. His main concern was the evaluation of the transfer value of these two tasks on the learning of additional discrimination problems. The tasks yielded similar positive transfer effects on the additional problems (although the SDR training group was slightly superior), but a striking dissimilarity during initial training was noted. The SDR tasks produced abundant negative transfer from problems 2 to 7, while the LS task produced none.

Thus, SDR appears more useful in comparative analysis, when the dimension of negative transfer is considered. In addition, LS methodology fails to maintain it's sensitivity among the inframammalian species, while SDR tasks show an "Impressive correspondence with taxonomic assignments derived from anatomical-morphological factors" (Gossette, 1970). Serial discrimination reversal learning therefore provides the "more comprehensive analysis of vertebrate learning" which LS has failed to provide (Gossette, 1970a).

Theoretical Bases of SDR Performance

The premise of comparative investigations, utilizing such tasks as have been outlined above, is that variation in performance between species represents specific organismic differences. Three major theoretical arguments have been advanced to explain the organismic dimensions along which these phyletic dissimilarities are found.

Retention-Decrement Hypothesis

This position, adopted by Bitterman and his colleagues (Gonzalez, et al., 1967; Bitterman, 1968), is based on the assumption that improvement on SDR is a function of species differences in the accumulation of proactive inhibition. Based on earlier work by McGeoch (1942) and Underwood (1952), Bitterman has suggested that improvement in reversal learning is a function of decrements in retention produced by proactive inhibition. The key to successful reversal learning then, is the ability to forget the previously correct response. Higher vertebrates make fewer errors on later reversals because they are presumably capable of forgetting an increasing proportion of their prior training; whereas lower organisms have more difficulty forgetting the previously learned material.

An integral part of this theory is an assumption, known as the discontinuity view, that the reversal performance of higher vertebrates differs qualitatively from that of lower vertebrates. Upon finding little evidence of reversal improvement in fish (Bitterman, et al., 1958; Behrend, et al., 1960), Bitterman postulated that fish are unable to build up proactive inhibition; they cannot forget (Gonzalez, et al., 1967). Based on these studies a two-category scaling system was devised which classified a given organism's behavior as either "ratlike" (improvement) or "fishlike" (no improvement). The discontinuity view was slightly modified with a third category for reptiles, when it was found that they showed improvement on spatial, but not visual problems. Reptiles were then presumed to represent an intermediate step in the phylogeny of learning. Evidence for this view is quite tenuous. Gossette (1970a) has noted that most studies of reversal learning with fish employed a methodology (discontiguity of reinforcement) likely to impair performance. Typically, the fish is required to swim from the side of the tank where the response was made, to the opposite side, in order to receive reinforcement. Similar procedures have adversely affected discrimination performances of higher vertebrates (Meyer, et al., 1965). Finally, there are a number of studies which demonstrate effective reversal learning and error reduction among fish (Setterington & Bishop, 1967; Squier, 1969). A demonstration of error reduction in the octopus, by Mackintosh (1969), is also inconsistent with the discontinuity view.

The retention-decrement hypothesis also fails to account for intraproblem error reduction and one-trial error solutions, as often occur in later reversals (Gossette, 1970a). In regard to interproblem error reduction, Weiner and Huppert (1968), Gossette (1969) and Sutherland and Mackintosh (1971) have noted that if proactive inhibition were the source of improvement, the error curve would not fall below the error level on the initial problem. Since later problems may be learned more rapidly than the original problem (Weiner & Huppert, 1968), the retention-decrement hypothesis appears inadequate.

Additionally, Bitterman and his associates have recently presented evidence contrary to their original position and now suggest the possible importance of inhibitory processes in SDR (Woodward, et al., 1971). In addition, they have demonstrated progressive improvement in the SDR performance of goldfish.

Attention Hypothesis

This hypothesis is a recent formulation (Mackintosh, 1969; Sutherland and Mackintosh, 1971) which views interspecies differences on serial reversal tasks as differences in the attentional process. Specifically, this theory holds that a given stimulus input is fed into several "analyzers", each dealing with that input along a unique dimension. One analyzer might classify stimuli along the brightness dimension, another along the hue dimension, and so on. More advanced species are purported to be capable of learning to switch to the most appropriate analyzer (selective attention) more rapidly than lower organisms. The basis of the theory rests to a great extent on evidence concerning the overlearning reversal effect (ORE). In a typical ORE study, Mackintosh

(1962) trained rats in a jumping stand to discriminate a black from a white square to a criterion of 18 correct out of 20 trials. Half the subjects were then given reversal training, with the previously nonreinforced choice now being rewarded. The other half received an additional 150 trials on the initial discrimination (overtrained). The non-overtrained group required a mean of 125 trials to reach the criterion again, while the overtrained group required only a mean of 77 trials. Mackintosh suggests that this effect lends support to his position by postulating that the overtrained group was actually receiving more extensive training in selective attention - the use of the most appropriate analyzer (brightness) was being strengthened.

However, while overtraining effects of this nature have been demonstrated, the phenomenon is "not replicable in the general sense" (Marx, 1969, p. 344). Aside from numerous investigations which have failed to demonstrate ORE (e.g., Clayton, 1963; Erlebacher, 1963; Hill & Spear, 1963), the extent of the attention theory's application is questioned even by it's originator. Quoting from Bitterman (1969), "The hypothesis on which the entire conjectural structure rests...is characterized in the end by Mackintosh himself as "vague" and inadequate for prediction; "indeed", he writes, "it is far from clear just how attention might come to be strengthened by such training (p. 169)." In the latest description of attention theory, Sutherland and Mackintosh (1971) write, "Although selective attention may not be the whole truth, it is at least part of the truth (p. x)." Finally, Behrend, et al. (1967) have suggested that, "... the attentional interpretation is contradicted by the fact that improvement takes place concurrently in two different dimensions of stimulation which are equally often relevant and irrelevant (one relevant when the alternative is irrelevant) in a long series of problems."

Differential Extinction Hypothesis

This hypothesis, developed by Gossette (Gossette & Hood, 1968; Gossette, 1970), is based on the position that interspecies differences on SDR tasks are due to variation in the rates of successive extinctions. Gossette (1970) states, "It is not the rate with which an organism learns to respond to a stimulus but the rate with which it learns to inhibit responding, that distinguishes species of different taxonomic levels." The differential-extinction hypothesis is an extension of the Pavlovian position advanced by Voronin (1962). According to Voronin, studies of the ease with which inhibitory control can be established over behavior, "Have revealed marked distinctions in this highly important property of the nervous process on different phylogenetic levels." Reviewing his own work and that of Voronin, Krushinskii (1961) concurs by stating that the main difference between different classes of animals is revealed by the formation of variations in the extent and form of internal inhibition.

The contention that variation in the magnitude of inhibitory control underlies interspecies performance differences has received further support from studies of successive acquisition and extinction (SAE). In this direct evaluation of extinction rates, Davenport (1969) provided evidence of differences between rats and monkeys, in the predicted direction.

Coupled with the differential-extinction hypothesis, as posited by Gossette, is a view antithetical to the discontinuity position held by the retention-decrement theorists (Gonzalez, et al., 1967). This position, the continuity view, holds that interspecies differences represent quantitative, not qualitative, differences. The weaknesses of the discontinuity view have already been presented. In summarizing much of the Russian literature, Voronin (1962) concludes, "In the course of evolution of the animal world there took place only a quantitative growth or complication of higher nervous activity."

Procedural Sources of Interspecies Variability

Before an evaluation of the preceeding explainations of SDR performance can be undertaken, one must first consider those variables which appear to differentially affect SDR performance. The relationship of D and K to this performance has been evaluated in only a most general manner. The precise nature of these functions is unknown. Thus, since a given level of D or K may provide the condition for optimal performance for a given species and not for another, we cannot be certain to what extent obtained performance differences reflect true organismic variation on SDR, or merely differential responsiveness to such environmental variables.

Drive Level

Studies of the effect of D on non-discriminative tasks such as response latency (Kimble, 1951; Deese & Carpenter, 1951) and running speed (Fredenburg, 1956; Loess, 1952) generally demonstrate the facilitative function of increased D. Increases in D during extinction have at times proven effective in increasing resistance to extinction (Barry, 1967; Fredenburg, 1956; Horenstein, 1951). However, D manipulations restricted to the acquisition period have little effect on later resistance to extinction (Barry, 1967; Kimble, 1961).

In regard to simple discrimination learning, the effect of D becomes somewhat ambiguous. For example, Lachman (1961), Armus (1958) and Jensen (1960) found that D exerted little effect on discrimination performance. However, several investigators have found that increased D facilitates performance (Eisman, et al., 1956; Ramond, 1954). To further confuse matters, Birch (1955) and Brunner, et al. (1955) found that increases in D tended to impede performance on such tasks. In a recent discussion, D'Amato (1970) contends that "...the majority of studies which have manipulated drive level within a simple discrimination learning situation have found this variable ineffectual in influencing discriminative performance (p. 305)."

This complicated situation is much the same when considering single reversal studies. Carlton (1955) reported that D was of little consequence in single reversal learning. Wike, et al. (1963) indicated that heightened D improved reversal performance, while Kendler and Lachman (1958) concluded that, "High drive during reversal learning retards habit reversal."

Several studies have suggested an inverse relationship between D and SDR performance (Gossette, 1968 , 1969; Gossette & Hood, 1968, 1969; Gossette & Feldman, 1968; Gossette et al., 1970). Feldman (1968) however, reported D to have a non-significant influence on SDR performance. Unfortunately, such studies have been limited to only two levels of D, high and low, thereby making any precise evaluation of the function impossible. Gossette (1969), has considered the rather uniform superiority of the low D condition in light of the traditional suggestion that response strength is an increasing function of D. He has suggested a possible curvilinear function, with optimal performance "Possibly falling somewhere between 10% and 30% body weight reduction." Such a hypothesis finds support from the so-called Yerkes-Dodson Law (Yerkes & Dodson, 1908). This general formulation, which has received strong empirical support (Dinsmoor, 1952; Broadhurst, 1957), predicts that there exists a curvilinear relationship between performance and motivation. It further suggests that there is an optimal motivational level for learning, which tends to decrease as problem difficulty increases.

Incentive Level

Asymptotic performance on simple, non-discriminative tasks such as running speed, appear to be positively correlated with reward magnitude (Kintsch, 1962; Kraeling, 1961; Spence, 1956; Crespi, 1942; Zeaman, 1949). Measures of resistance to extinction are typically not affected by incentive level during the acquisition phase (Bolles, 1967, p. 343). Studies by Lawrence and Miller (1947), Reynolds (1950), Fehrer (1956), Metzger (1957) and Ison and Cook (1964) all point to this conclusion.

Results of studies examining K effects on simple discrimination learning are contradictory. It originally appeared that increases in K resulted in improved discrimination performance, but only when within-group designs were used (e.g. Schrier & Harlow, 1956). But, such a relationship disappeared when between-group designs were employed (e.g. McKelvey, 1956; Reynolds, 1949). The effectiveness of K when within-group designs were used was attributed to contrast effects (Schrier, 1958; Marx, 1969). However, two recent studies (Mackintosh, 1969; Waller, 1968) report that magnitude of reward facilitated discrimination learning with a between-groups design.

Using a single reversal methodology, Corey (1969) concluded, "High incentive subjects learned and reversed faster than low incentive subjects." Findings by Wike, et al. (1962) and Pubols (1961), at variance with those of Corey, indicate an inverse relationship between K and errors during both acquisition and reversal.

Learning set studies (Schrier, 1958) and SDR tasks appear to be importantly influenced by K (for exception, see Gonzalez, et al., 1966). Gossette and Hood (1968), working with birds, found that variation in K resulted in consistent effects across all problems, with high K producing superior reversal performance. Gossette, et al. (1970) reporting similar results, state, "... errors on SDR tasks are a decreasing function of K." Feldman's (1968) study with rats produced similar findings. Nevertheless, specific incentive functions for various species have not yet been determined. Sutherland and Mackintosh (1971), emphasizing the need for studies which would determine such functions state, "It is unfortunate that we do have more experimental evidence on the effects of variation in reward size, drive level, and other such variables on the behaviour of birds and fish (p. 432)."

Statement of the Problem

It is apparent that both D and K may exert important effects on SDR performance. The specific functions of these variables on SDR performance have not been extensively studied, however. In addition, these functions may be dissimilar for different species. Thus, a given D or K level for one species may result in a different performance level that the same D or K level for another species. In effect, we do not know to what extent interspecies performance differences on

SDR have represented differences in learning ability or, instead, differences due to the failure to equate D or K, or comparable variables, across species. Once the specific functions are determined, one could compare performance at comparable, preselected levels. The present study will attempt to calibrate the D function, for two species, at two levels of K.

Rationale for Species Selection

Previous investigations (Gossette & Gossette, 1967; Gossette, 1966) have indicated that different clusterings of reversal performance may be expected from species of different orders, while species of the same order show a close correspondence in SDR performance. Such studies have shown that members of the order Galliformes (chickens) perform at a level inferior to that of members of the order Columbiformes (pigeons). Therefore, the two avian orders to be examined, Galliformes and Columbiformes, would be expected to provide two distinct clusters of reversal performance which can be compared at the various levels of D and K.

Secondly, both species tested are of approximately the same size, thereby permitting use of the same test apparatus for both species.

Finally, since both species will be tested on a hue discrimination, Sturkie (1965) presents evidence that the spectral sensitivity curves for these two species are almost identical and similar to mans'.

Hypotheses

Based upon information in the preceeding sections, the following hypotheses are advanced:

1. Considering the general support for the Yerkes-Dodson type formulation, it is hypothesized that intermediate levels of D will produce superior performance for both chickens and pigeons.
2. Considering the number of studies which have found pigeon performance to be superior to that of chickens (e.g. Gossette, 1968, 1969), it is hypothesized that such previously established performance differences will persist when species are equated for D.
3. Based upon several studies by Gossette and by Feldman (1968), it is hypothesized that K will exert a significant effect on SDR performance, with increased K resulting in superior performance.

METHOD

Subjects

Representatives of two avian orders, Galliformes and Columbiformes, were selected for study. Thirty-two Seabright bantam chickens (Gallus gallus) and thirty-two White Carneaux pigeons (Columbia livia) served as subjects. While all pigeons were males, nine members of the chicken group were females. All subjects were of adult age, having reached their maximum growth potential.

Apparatus

Four BRS - Foringer Pigeon Test Chambers were used throughout the experiment. The inside dimensions of these chambers were 19½"W X 14"H X 14"D. Within each chamber were two plastic pecking keys, which could be illuminated from the rear with either red or green light. A grain magazine was located between and below the two keys. A filtered blower provided both ventilation and masking noise. Mounted on the doors were 5½" diameter one-way mirrors. The apparatus was programmed to raise the food magazine to the feeding position when the correct key (S^D) was pecked. It was possible to control the interval during which the feeder was raised and the ITI. Stepping switches automatically presented the stimuli in the following Gellerman (1933) order: 1,2,1,2,2,2,1,1,2,1,1,2,1,2,1,1,2,1,2,2

The following measures were recorded:

1. Errors per problem - This provides a measure of the total number of errors made from the first to last session of each problem. It is a general measure of improvement across successive problems and has been the most widely encountered indice of SDR performance.

2. Percent errors on session one - This represents the percent of errors on only the first session of each problem. Since negative transfer presumably has it's most potent influence on the first reversal session, this measure should provide some insight into this influence.

3. Initial error - This is a measure of the number of consecutive errors on each session, which occur before the first correct response.

4. Reversal index (Rajalakshmi & Jeeves, 1965) - This measure is derived by dividing the number of errors on the original discrimination by the number of errors on the first reversal. It has been suggested by Rajalakshmi and Jeeves (1965) that this procedure eliminates differences due to initial discrimination performance. It is of course a much abbreviated measure.

5. Problem two errors - The number of errors on problem two can be interpreted as a rough estimate of the magnitude of negative transfer, since such effects typically have their greatest influence on the second problem. However, this measure is contaminated by acquisition effects.

6. O. D. minus peak errors - This measure represents the difference between the number of errors on the original discrimination and the number on the problem where the maximum number of errors occur (usually problem two). This too, can be viewed as a measure of negative transfer, though perhaps, somewhat more precise, since maximum errors do not always occur on the second problem.

7. Percent errors on session one of problem two - This is the purest measure of negative transfer employed. While it is truncated, it is least contaminated by acquisition effects.

Procedure

The experiment consisted of three principle phases: habituation, key-peck shaping and reversal training.

Following a two week habituation period in the laboratory, subjects were maintained on an ad libitum feeding schedule and their weights were recorded daily. This was continued until weights stabilized for three consecutive weeks. At that time pigeon groups and chicken groups were randomly assigned to one of eight conditions (see Table 1). These groups constituted four levels of D (6, 14, 22, and 30 percent weight reduction) at two levels of K (presentation of the grain magazine for either 2 or 6 seconds).

Subjects were then gradually reduced to their preassigned experimental weights. During this period the subjects were habituated to the test chambers and trained to key-peck for the opportunity to feed from the magazine.

Table 1

General Experimental Design

Species	Drive	Incentive
Chicken	6%	2
		6
	14%	2
		6
	22%	2
		6
	30%	2
		6
Pigeon	6%	2
		6
	14%	2
		6
	22%	2
		6
	30%	2
		6

Shaping was undertaken with both keys illuminated with white light. Once shaped, subjects were allowed to make 100 reinforced responses. During the last twenty trials, left-right preferences were determined.

Having reached their assigned weights, subjects began the initial discrimination training. One key was illuminated with green light, the other with red. Depending upon the left-right preference, the S^D was always presented on the non-preferred side on trial one. Pecking of the correct stimulus raised the food magazine for either two or six seconds. Following the end of either a reinforcement period or the pecking of an incorrect stimulus, an inter-trial interval (ITI) of ten seconds began. During the ITI, both the house and stimulus lights were turned off. Most studies show that short ITI's (2 to 10 seconds) provide for the best performance (North, 1959; Williams, 1971).

One daily session of twenty trials was provided for each subject. A trial was defined as the pecking of the response key with enough force to operate a microswitch located behind it. Non-correction procedures were used. Thus, subjects were not allowed to correct their errors.

The sessions of twenty trials per day were continued until the subject reached a criterion of at least 18 out of 20 correct during one session. When this criterion was achieved, reinforcement contingencies were reversed on the following test day; with responses to the previously incorrect stimulus now reinforced. Once the criterion was reached again, the contingencies were reversed, until a total of 19 reversals (20 problems) were completed.

RESULTS

The major measures selected for analysis were total errors, percent errors on session one and initial error for each problem. Additionally, data was analyzed to obtain the reversal index, a comparison of reversal and nonreversal day performance and some rough estimates of negative transfer. All of the major analyses were carried out employing a Weiner Case II type design for repeated measures (Weiner, 1971).

Total Errors

The mean number of errors per problem and the standard deviation for each group, across 20 problems, can be seen in Table 2.

The 16 groups were each designated by a letter and number combination. The letter indicates the species (C = chicken, P = pigeon). The first number refers to the K value (2 or 6 second feeder presentation), while the second number indicates the D level (6, 14, 22 or 30% weight reduction).

A 2 X 2 X 4 X 20 analysis of the data yielded both significant within and between subjects effects. The between variables were broken down into D, K, species and interaction effects. The within variables were broken down into a problems effect and all interactions with problems. These effects and their interactions are shown in Table 3.

The main effects of D ($F = 38.53$, $p < .01$), species ($F =$

Table 2

Errors per Problem

Group	Mean Errors	SD
C-2-6	33.68	9.58
C-6-6	35.56	14.07
C-2-14	27.83	8.03
C-6-14	29.73	9.45
C-2-22	24.76	7.41
C-6-22	23.19	8.51
C-2-30	28.94	9.97
C-6-30	31.26	12.82
P-2-6	30.22	8.18
P-6-6	29.46	7.60
P-2-14	17.59	9.82
P-6-14	16.03	8.95
P-2-22	26.13	11.26
P-6-22	23.78	7.62
P-2-30	26.18	6.19
P-6-30	28.44	9.73

Table 3

Four Way Analysis of Variance: Errors per Problem[a]

Source	df	Mean Square	F
Drive (D)	3	5823.85	38.53*
Incentive (K)	1	17.58	
Species	1	6928.50	45.84*
D x K	3	243.98	
D x Species	3	2343.56	15.51*
K x Species	1	236.33	
D x K x Species	3	50.88	
Subjects within Groups (Error Between)	48	151.13	
Problems	19	4085.54	18.51*
Problems x D	57	21.69	
Problems x K	19	20.74	
Problems x Species	19	61.22	
Problems x D x K	57	27.30	
Problems x D x Species	57	44.41	
Problems x K x Species	19	18.56	
Problems x D x K x Species	57	20.63	
Problems x Subjects Within Groups (Error Within)	912	22.76	

* $p < .01$

[a] Geisser-Greenhouse correction employed (Geisser & Greenhouse, 1958)

45.84, $p < .01$) and problems ($F = 18.51$, $p < .01$) were all significant. The D X Species interaction was also significant ($F = 15.51$, $p < .01$). Pigeons made fewer errors than chickens. To determine the differential effects of D, data was further analyzed using Duncan's New Multiple Range Test (Duncan, 1955). The 14% pigeons made fewer errors than any of the other groups, which did not differ significantly from one another. The 22% chicken group made significantly fewer errors than the 6% group, but none of the remaining groups differed. In no instance did a chicken group make significantly fewer errors than a pigeon group. Data for intermediate D groups (14% + 22%) were then compared to data for extreme D groups (6% + 30%). Intermediate D pigeons made fewer errors than extreme D pigeons, but no such differences emerged for the chicken groups.

In order to determine how close the D differences for chickens had come to reaching statistical significance the Duncan's Test was re-computed at the .05 level. Results showed that while the 22% and 14% groups were not significantly different, the 22% group differed significantly from both the 6% and 30% groups.

Figure 1 shows the species differences, collapsed over D and K, on blocks of three problems each, compared to performance on the original discrimination (O.D.). The superiority of pigeons is evident throughout the course of successive reversals. Figures 2 and 3 show the differential effects of D on chicken and pigeon performance, respectively. The relatively poor performance of chickens at 6% and

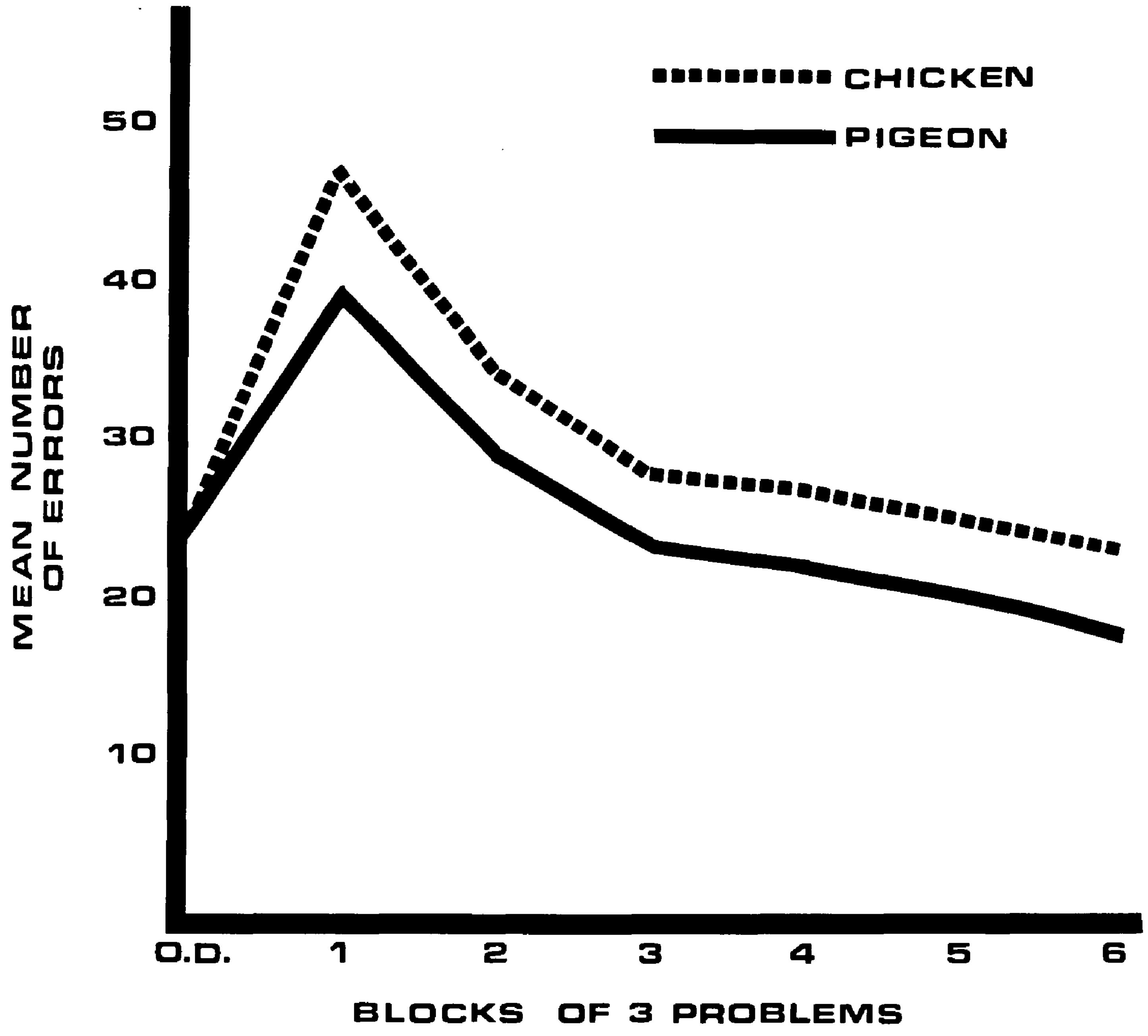

FIGURE I. MEAN ERRORS ACROSS ALL LEVELS OF D & K FOR PIGEONS & CHICKENS, OVER BLOCKS OF 3 PROBLEMS.

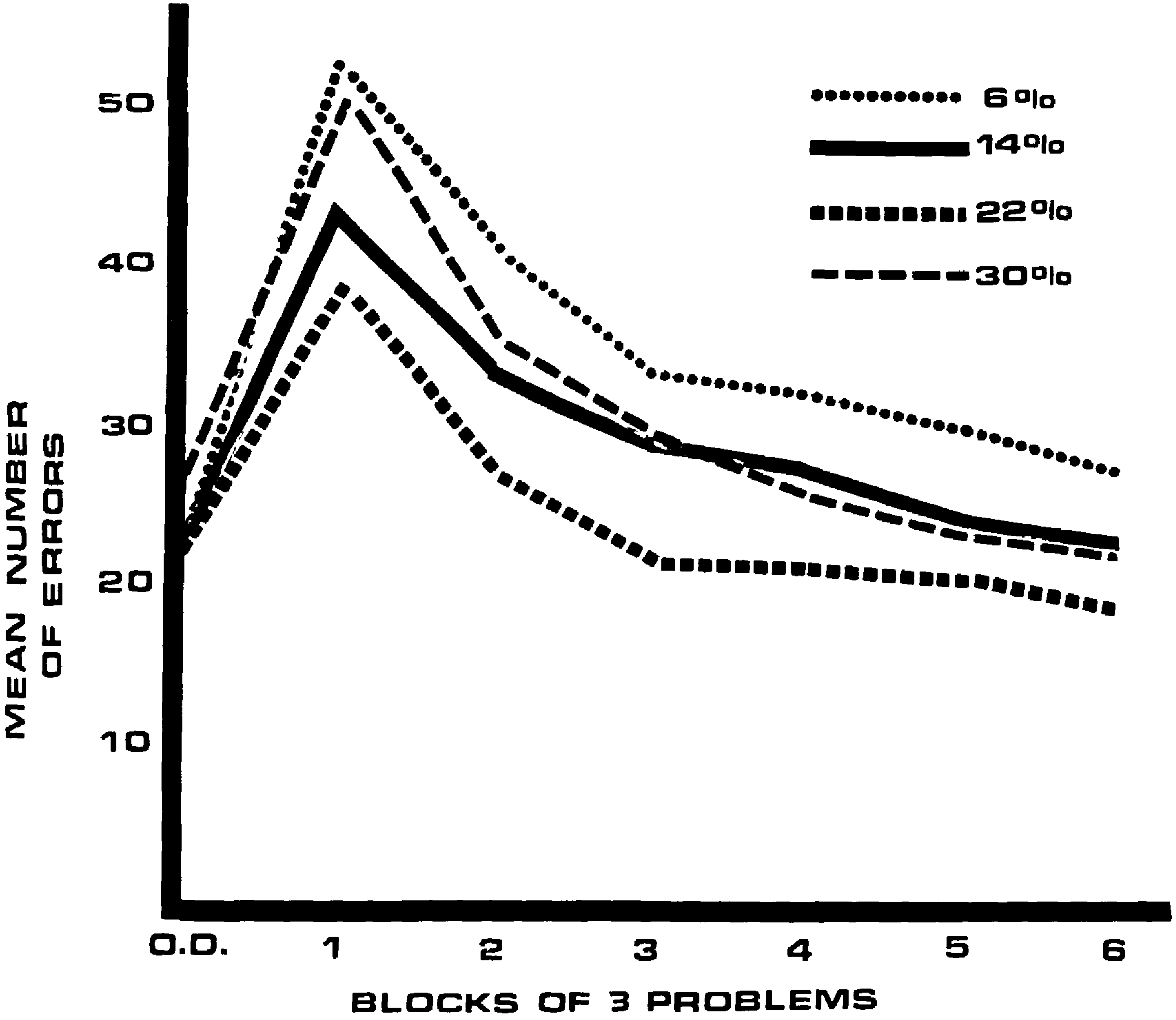

FIGURE 2. MEAN ERRORS PER PROBLEM AT 4 LEVELS OF D, FOR CHICKENS.

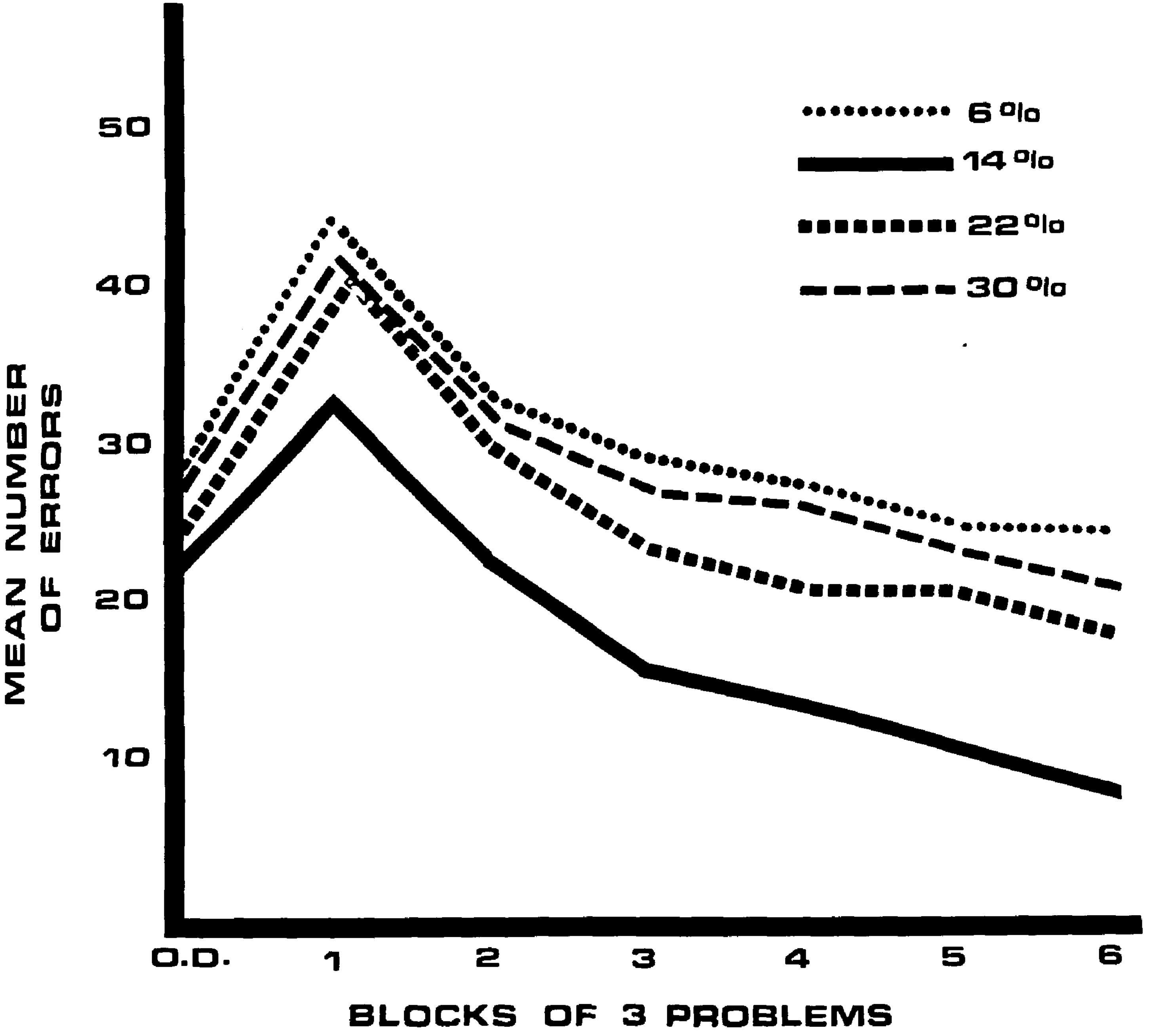

FIGURE 3. MEAN ERRORS PER PROBLEM AT 4 LEVELS OF D, FOR PIGEONS.

relatively superior performance of pigeons at 14% can be seen. Finally, Figure 4 shows pigeon and chicken performance at four levels of D, collapsed over 20 problems.

Percent Errors on Session One

The mean percent errors on session one, for 20 problems, and the standard deviations for each group are shown in Table 4. The same notation as in Table 2 is used.

A 2 X 2 X 4 X 20 analysis yielded significance for both between and within subjects effects. These were divided in the same manner as in the preceeding analysis. The main effects and interactions are shown in Table 5.

The main effects of D ($F = 44.41$, $p < .01$), species ($F = 59.62$, $p < .01$) and problems ($F = 92.96$, $p < .01$) were significant. The D X Species interaction was also significant ($F = 21.01$, $p < .01$). Pigeons made fewer errors than chickens. The differential effects of D were analyzed using Duncan's test (see appendix 2). For pigeons, the 14% group made fewer percent errors on session one than the 6%, 22% or 30% groups, which did not differ from one another. For chickens, no significant D effects occurred. When the intermediate D groups (14% + 22%) were compared with the extreme D groups (6% + 30%), the differences were not significant.

Figure 5 shows the percent errors on session one for pigeons, across the four levels of D. The superiority of the 14% pigeon group can be seen. In Figure 6, a comparison of chickens and pigeons, across blocks of three problems is

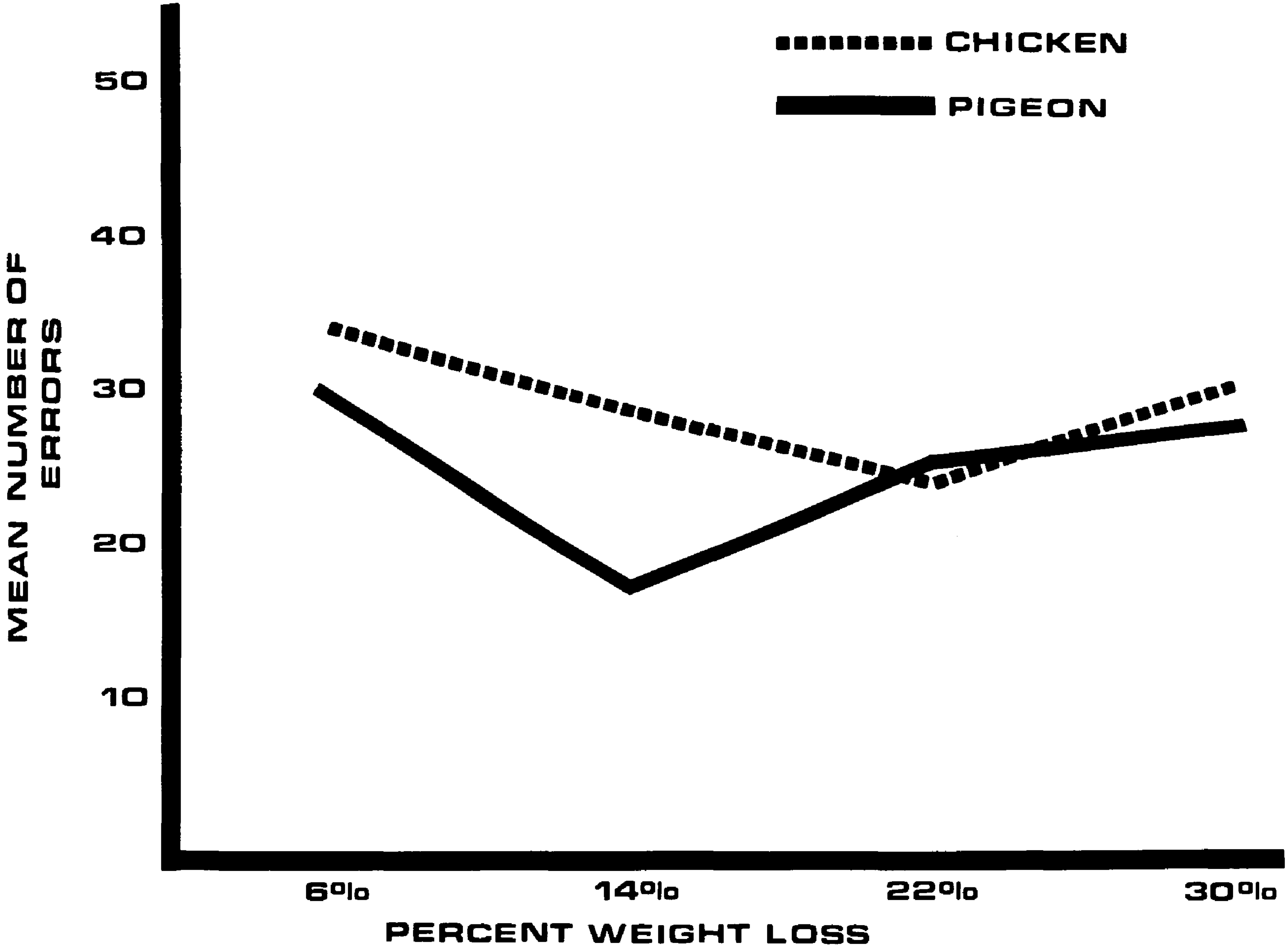

FIGURE 4. MEAN ERRORS PER PROBLEM ACROSS 20 PROBLEMS, AT 4 LEVELS OF D, FOR PIGEONS AND CHICKENS.

Table 4

Percent Errors on Session One

Group	Mean Percent Errors	SD
C-2-6	63.94	14.77
C-6-6	62.69	12.47
C-2-14	57.62	13.19
C-6-14	58.50	12.02
C-2-22	53.94	14.36
C-6-22	52.00	15.02
C-2-30	58.94	13.28
C-6-30	60.56	14.63
P-2-6	58.75	10.33
P-6-6	58.37	10.43
P-2-14	46.37	14.67
P-6-14	42.56	15.34
P-2-22	54.19	12.84
P-6-22	53.25	11.53
P-2-30	56.37	12.80
P-6-30	57.37	11.88

Table 5

Four Way Analysis: Percent Errors on Session One[a]

Source	df	Mean Square	F
Drive (D)	3	6280.70	44.41*
Incentive (K)	1	109.86	
Species	1	8430.64	59.62*
D x K	3	133.20	
D x Species	3	2970.54	21.01*
K x Species	1	54.86	
D x K x Species	3	144.97	
Subjects Within Groups (Error Between)	48	141.41	
Problems	19	6610.76	92.96*
Problems x D	57	97.17	
Problems x K	19	75.24	
Problems x Species	19	100.22	
Problems x D x K	57	51.42	
Problems x D x Species	57	114.56	
Problems x K x Species	19	56.01	
Problems x D x K x Species	57	58.29	
Problems x Subjects Within Groups (Error Within)	912	71.11	

*$p < .01$

[a] Geisser-Greenhouse correction employed (Geisser & Greenhouse, 1958)

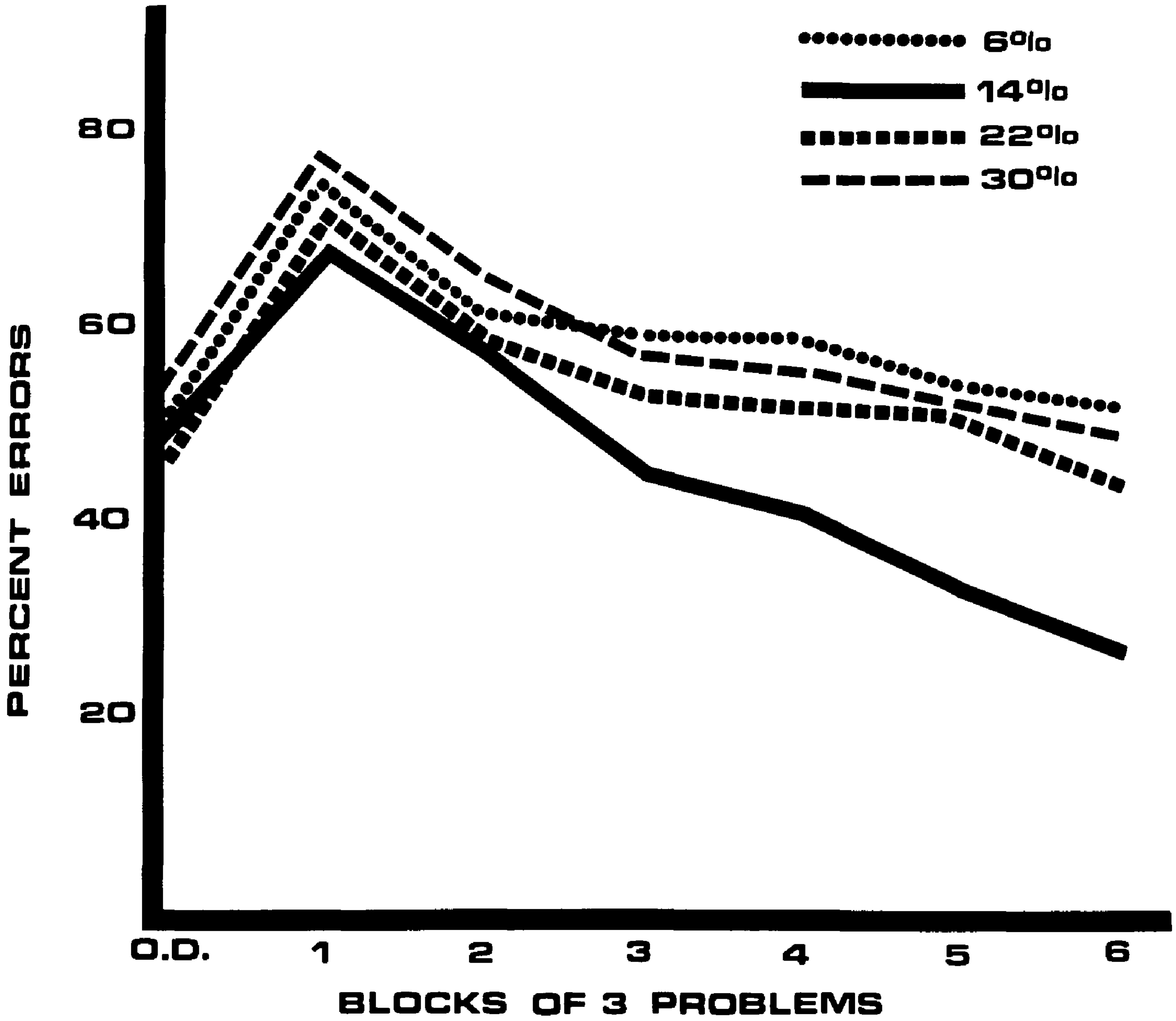

FIGURE 5. MEAN % ERRORS AT FOUR LEVELS OF D, ACROSS BLOCKS OF 3 PROBLEMS, FOR PIGEONS.

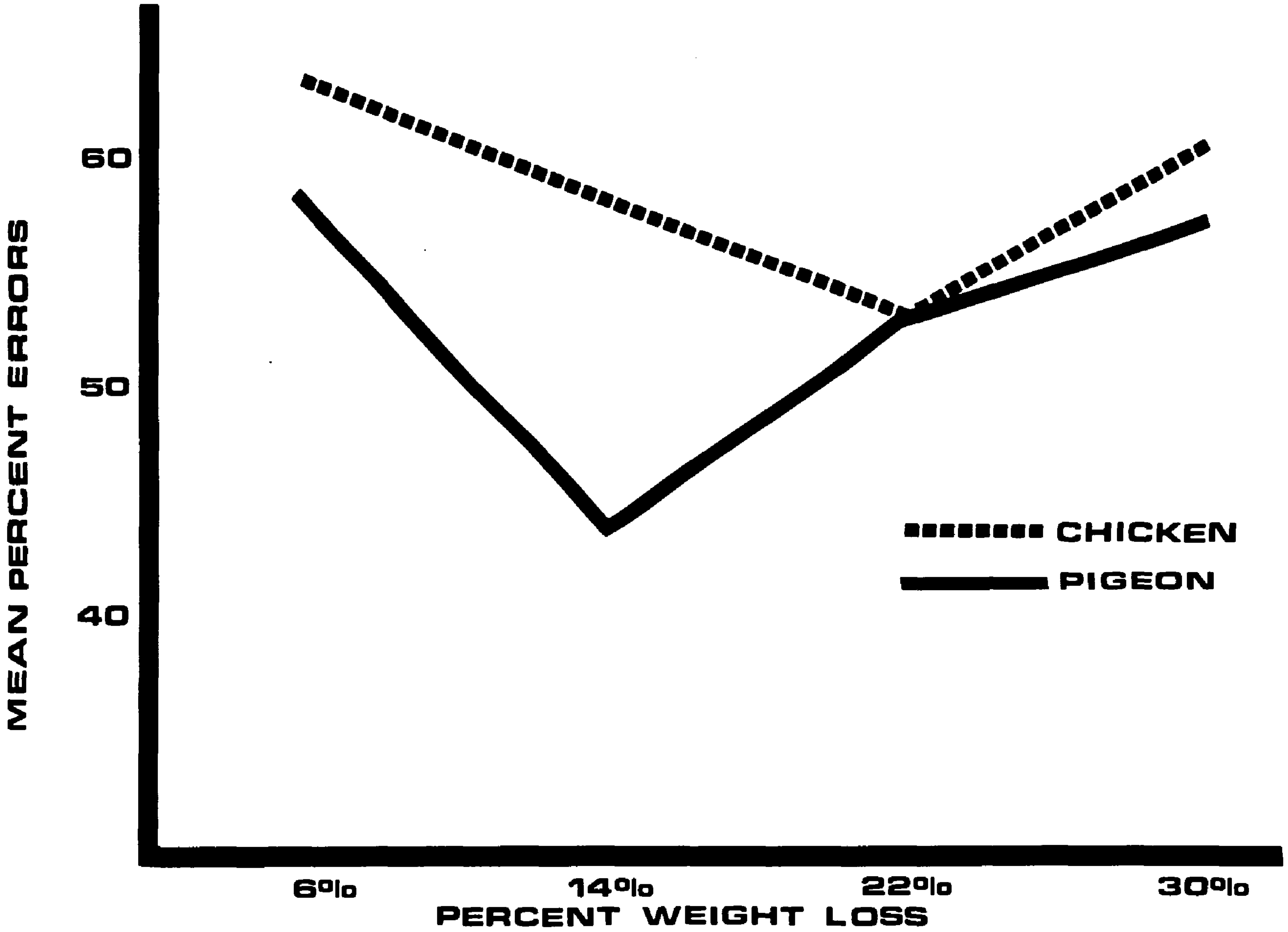

FIGURE 6. MEAN % ERRORS ACROSS 20 PROBLEMS, AT 4 LEVELS OF D, FOR CHICKENS & PIGEONS.

shown. The data is collapsed over levels of D. The performance on this measure is compared to that on the original discrimination. The superior pigeon performance is evident.

Initial Error

The mean initial error per problem and the standard deviation for each group is shown in Table 6. The same notation as in Table 2 is used.

A 2 X 2 X 4 X 20 analysis of the data yielded significant between and within subjects effects. The main effects of D ($F = 7.25$, $p < .01$) and species ($F = 75.54$, $p < .01$) were both significant, but the D x species interaction was not. The within subject variable of problems was also significant ($F = 26.40$, $p < .01$). Table 7 shows this analysis.

As can be seen in Figure 7 the mean initial error across blocks of three problems was greatest for chickens. Since no significant D X species interaction was found, the main effect of D was not analyzed further.

Measures of Negative Transfer

As mentioned earlier, Gossette (1969), has suggested an important dimension along which species differences on SDR tasks may be ordered. It is the magnitude of negative transfer that has been proposed as one major source of differential species performance.

A rough estimate of the degree of negative transfer may be derived from the number of errors on problem two.

Table 6

Mean Initial Error

Group	Mean Initial Error	SD
C-2-6	6.96	5.10
C-6-6	6.84	4.77
C-2-14	5.80	3.62
C-6-14	5.65	4.61
C-2-22	5.21	4.61
C-6-22	5.41	5.11
C-2-30	6.00	3.82
C-6-30	6.94	8.48
P-2-6	4.60	4.30
P-6-6	4.16	2.97
P-2-14	2.85	2.66
P-6-14	2.66	2.31
P-2-22	4.74	4.85
P-6-22	3.63	2.64
P-2-30	4.58	4.55
P-6-30	4.70	4.07

Table 7

Four Way Analysis: Initial Error[a]

Source	df	Mean Square	F
Drive (D)	3	137.82	7.25*
Incentive (K)	1	2.81	
Species	1	1436.51	75.54*
D x K	3	11.21	
D x Species	3	53.47	
K x Species	1	33.15	
D x K x Species	3	5.92	
Subjects Within Groups (Error Between)	48	19.02	
Problems	19	334.37	26.40*
Problems x D	57	19.35	
Problems x K	19	45.57	
Problems x Species	19	36.08	
Problems x D x K	57	24.21	
Problems x D x Species	57	21.73	
Problems x K x Species	19	42.80	
Problems x D x K x Species	57	15.36	
Problems x Subjects Within Groups (Error Within)	912	12.66	

* $p < .01$

[a] Geisser-Greenhouse correction employed (Geisser & Greenhouse, 1958).

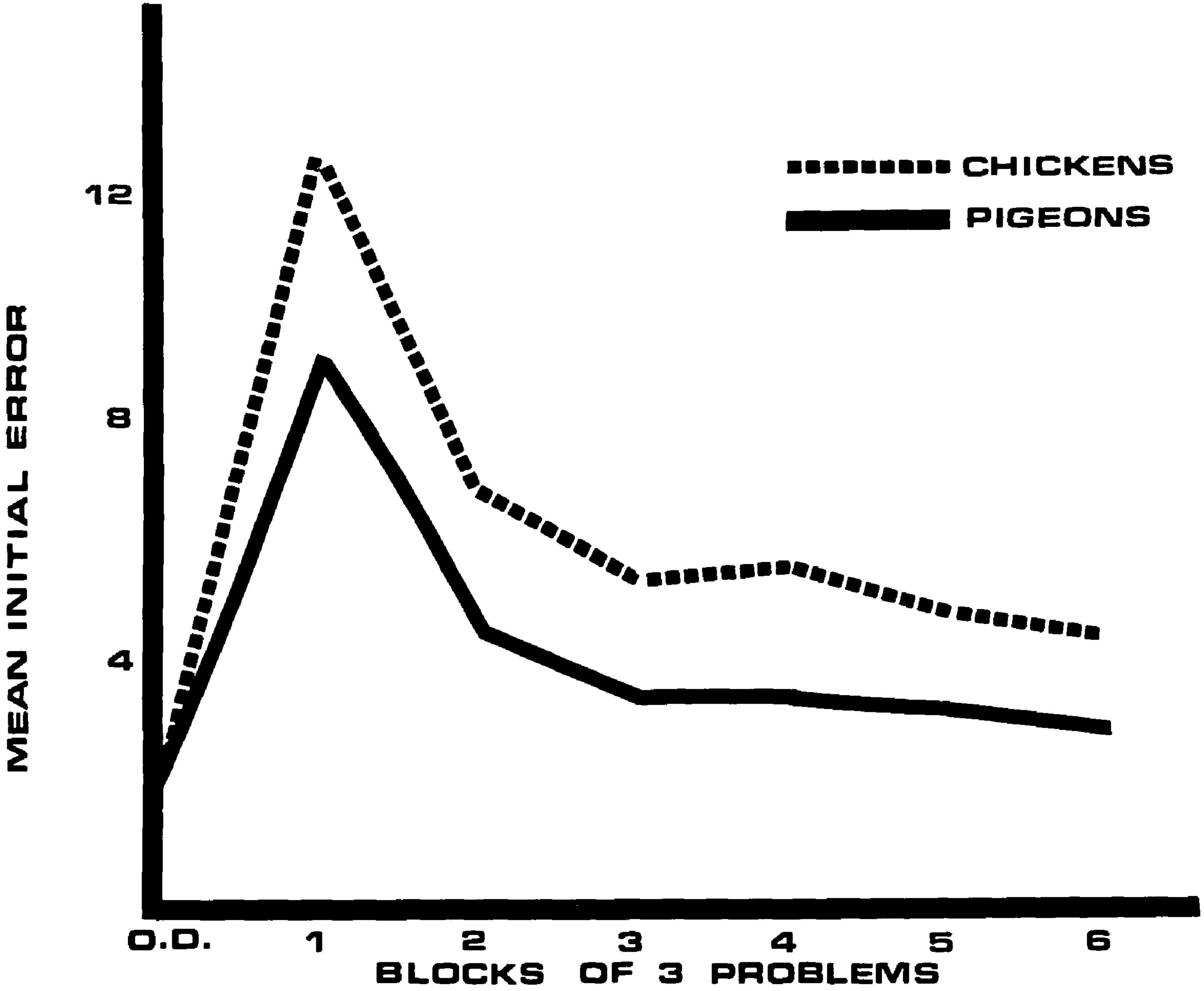

FIGURE 7. MEAN INITIAL ERROR ACROSS D LEVELS, OVER BLOCKS OF 3 PROBLEMS, FOR CHICKENS & PIGEONS.

A simple 2 X 4 analysis of problem two errors (see Table 8, column 1) for chickens and pigeons at four levels of D was calculated. The results of this analysis may be seen in Table 9.

The effect of D was significant ($F = 4.42$, $p < .01$) as was the effect of species ($F = 18.21$, $p < .01$). The D X Species interaction was not significant. The mean number of errors on problem two was greatest for chickens. The results of this analysis can be seen in Figure 8.

While this measure provides some estimate of negative transfer, it is contaminated by the effects of acquisition.

That is, some trials of problem two include correct responses to the new contingency. Additionally, the magnitude of problem two errors will be influenced by the number of errors on the original discrimination. Accordingly, a different measure of negative transfer was derived by Gossette (1969) by obtaining the difference between errors on the original discrimination and those at the point of peak error; the problem on which the maximum number of errors occur (typically, problem two). This O.D. - peak data (see Table 8, column 2) was analyzed using a simple 2 X 2 X 4 (species, incentive and drive) design. Results of this analysis are shown in Table 10. The species variable was the only one to reach significance ($F = 12.78$, $p < .01$). With this measure, the magnitude of negative transfer was again less for pigeons.

While this measure accounts for performance on the origi-

Table 8

Measures of Negative Transfer

Species	D	1 $\bar{X}$ Problem 2 Errors	2 O.D. - Peak	3 % Errors on Session 1, Problem 2
Chicken	6%	57.9	40.2	86.3
	14%	50.1	28.5	79.4
	22%	46.8	22.6	90.6
	30%	61.8	38.0	90.0
Pigeon	6%	50.8	24.4	82.5
	14%	37.8	16.9	71.3
	22%	40.4	24.9	74.4
	30%	42.1	23.8	74.1

Table 9

Two-way analysis: Problem two errors

Source	df	Mean Square	F
Drive (D)	3	494.06	4.42*
Species	1	2036.27	18.21*
D X species	3	154.64	
Error	56	111.80	

* $p < .01$

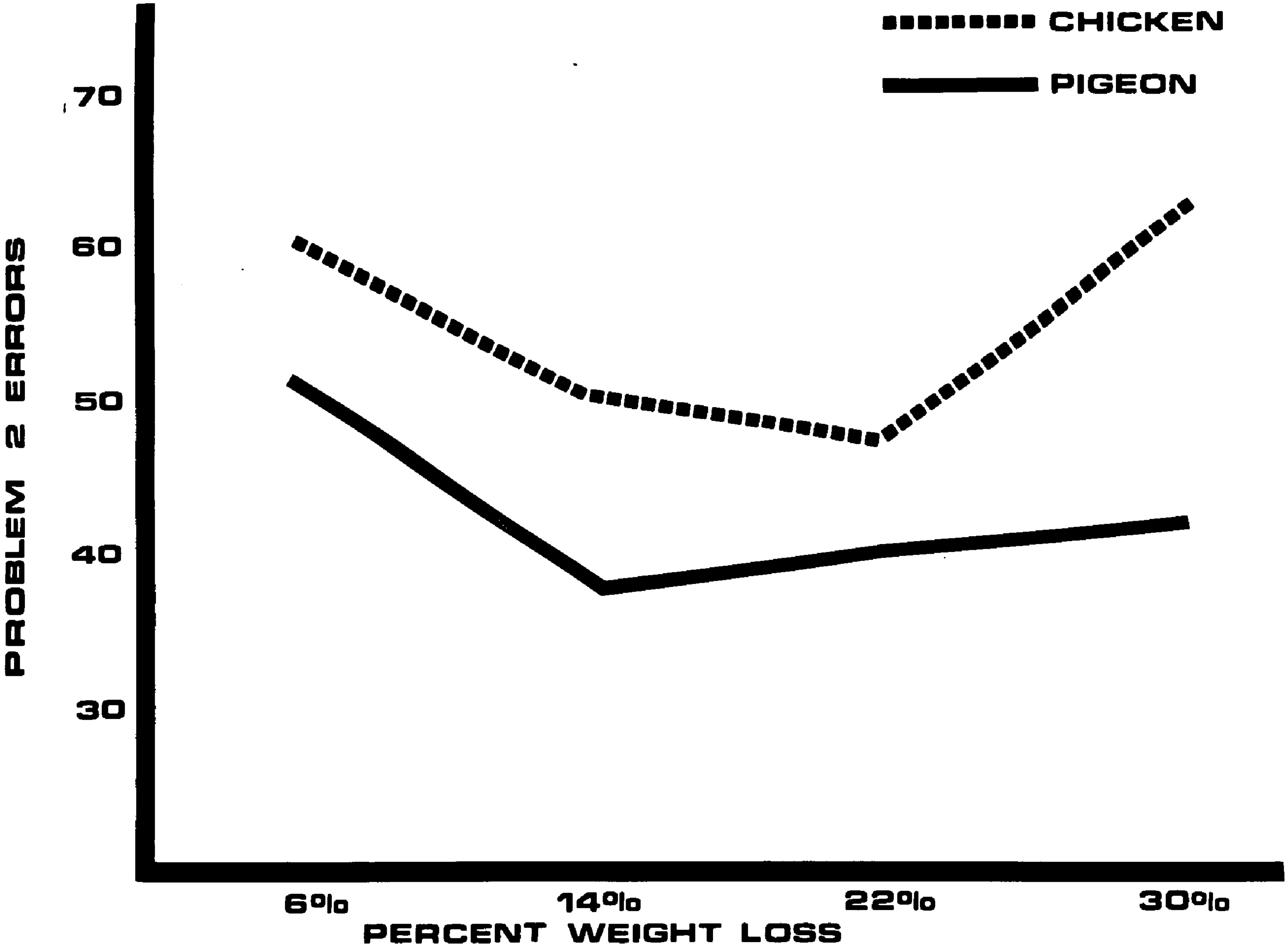

FIGURE 8. MEAN PROBLEM 2 ERRORS AT 4 LEVELS OF D, FOR CHICKENS & PIGEONS.

Table 10

Three-way analysis: O.D. - Peak

Source	df	Mean Square	F
Drive (D)	3	375.60	
Incentive (K)	1	105.06	
Species	1	1580.06	12.78*
D X K	3	122.10	
D X species	3	274.10	
K X species	1	473.06	
D X K X species	3	41.10	
Error	48	123.60	

$^*p < .01$

nal discrimination, it too is contaminated by acquisition effects. Therefore, a more refined measure of negative transfer would be the percent errors on the first session of problem two (see Table 8, column 3). This data was analyzed using a simple 2 X 4 (species by D) design. The results of this analysis may be found in Table 11. Species was the only significant effect ($F = 16.98$, $p < .01$). Pigeons obtained lower negative transfer scores than chickens.

Reversal versus Non-Reversal Day Performance

An analysis of some theoretical interest contrasts reversal (R) with non-reversal (NR) training days. Following the procedure suggested by Bitterman and his collegues (Behrend, Jennings & Bitterman, 1968), the first day of a problem is designated an R day and the second as an NR day. Table 12 shows the difference between R and NR errors for pigeons and chickens at four levels of D.

The data was analyzed by combining errors on blocks of three problems and performing a 2 X 2 X 4 X 6 analysis (species, days, drive and problem blocks). The results of this analysis can be seen in Table 13. The main effects of D ($F = 94.90$, $p < .01$), species ($F = 100.23$, $p < .01$), days ($F = 1221.54$, $p < .01$) and problem blocks ($F = 889.79$, $p < .01$) were all significant. The D X Species interaction was also significant ($F = 47.24$, $p < .01$). Pigeons made fewer errors on both reversal and non-reversal days, and errors on NR days were fewer than on R days. The differential effects of D on

Table 11

Two-way analysis: % errors on session 1 of problem 2

Source	df	Mean Square	F
Drive (D)	3	252.60	
Species	1	1914.06	16.98*
D X species	3	146.35	
Error	56	112.72	

*p < .01

Table 12

R and NR Day Errors

Species	D	R errors	NR errors
Chicken	6%	38.7	27.6
	14%	35.5	28.0
	22%	31.9	21.2
	30%	36.8	25.3
Pigeon	6%	35.5	26.5
	14%	26.9	15.5
	22%	32.8	22.5
	30%	34.7	23.7

Table 13

Four Way Analysis: R versus NR Days[a]

Source	df	Mean Square	F
Drive (D)	3	1673.20	94.90*
Species	1	1767.22	100.23*
Days	1	21537.10	1221.54*
D x Days	3	22.75	
D x Species	3	832.87	42.24*
Days x Species	1	6.94	
D x Days x Species	3	7.56	
Subjects Within Groups (Error Between)	112	17.63	
Blocks	5	4448.95	889.79*
Blocks x D	15	29.67	
Blocks x Days	5	18.36	
Blocks x Species	5	15.32	
Blocks x D x Days	15	7.28	
Blocks x Species x Days	5	21.96	
Blocks x Species x D	15	39.19	
Blocks x Species x Days x D	15	3.74	
Blocks x Subjects Within Groups (Error Within)	560	11.38	

*$p < .01$

[a] Geisser-Greenhouse correction employed (Geisser & Greenhouse, 1958)

chicken and pigeon groups was further analyzed using Duncan's test (see appendix 3). None of the groups differed significantly, except for the 14% pigeons, which made the fewest errors. However, the 22% pigeons and 22% chickens did not differ significantly from the 14% pigeons.

Figures 9 and 10 show R and NR performance over blocks of problems, for chickens and pigeons respectively. It can be seen that there appears to be no apparent change in the difference between R and NR days, across problem blocks, and substantiated by the non-significant Blocks X Days interaction.

Reversal Index

As described earlier, the reversal index (RI) has been suggested as a promising indice of phyletic separation. RI data was derived for each experimental group. The mean RI for each group can be found in Table 14. A simple 2 X 2 X 4 (species, incentive, drive) analysis was performed. The results of this analysis may be found in Table 15. The main effect of species was the only significant finding ($F = 7.54$, $p < .01$). The mean RI for pigeons was higher than that for chickens.

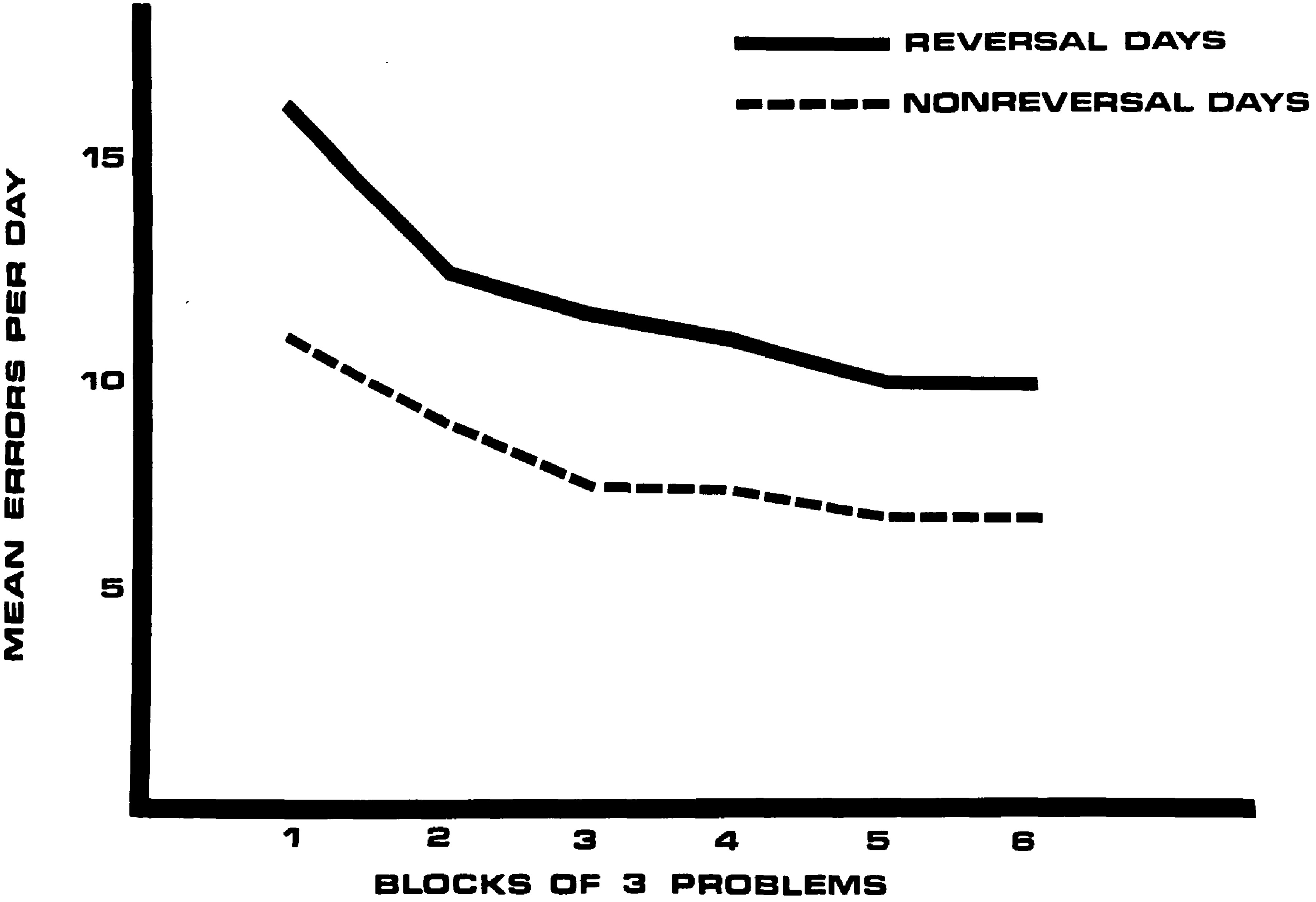

FIGURE 9. MEAN ERRORS ON R & NR DAYS ACROSS ALL D & K LEVELS, OVER BLOCKS OF 3 DAYS, FOR CHICKENS.

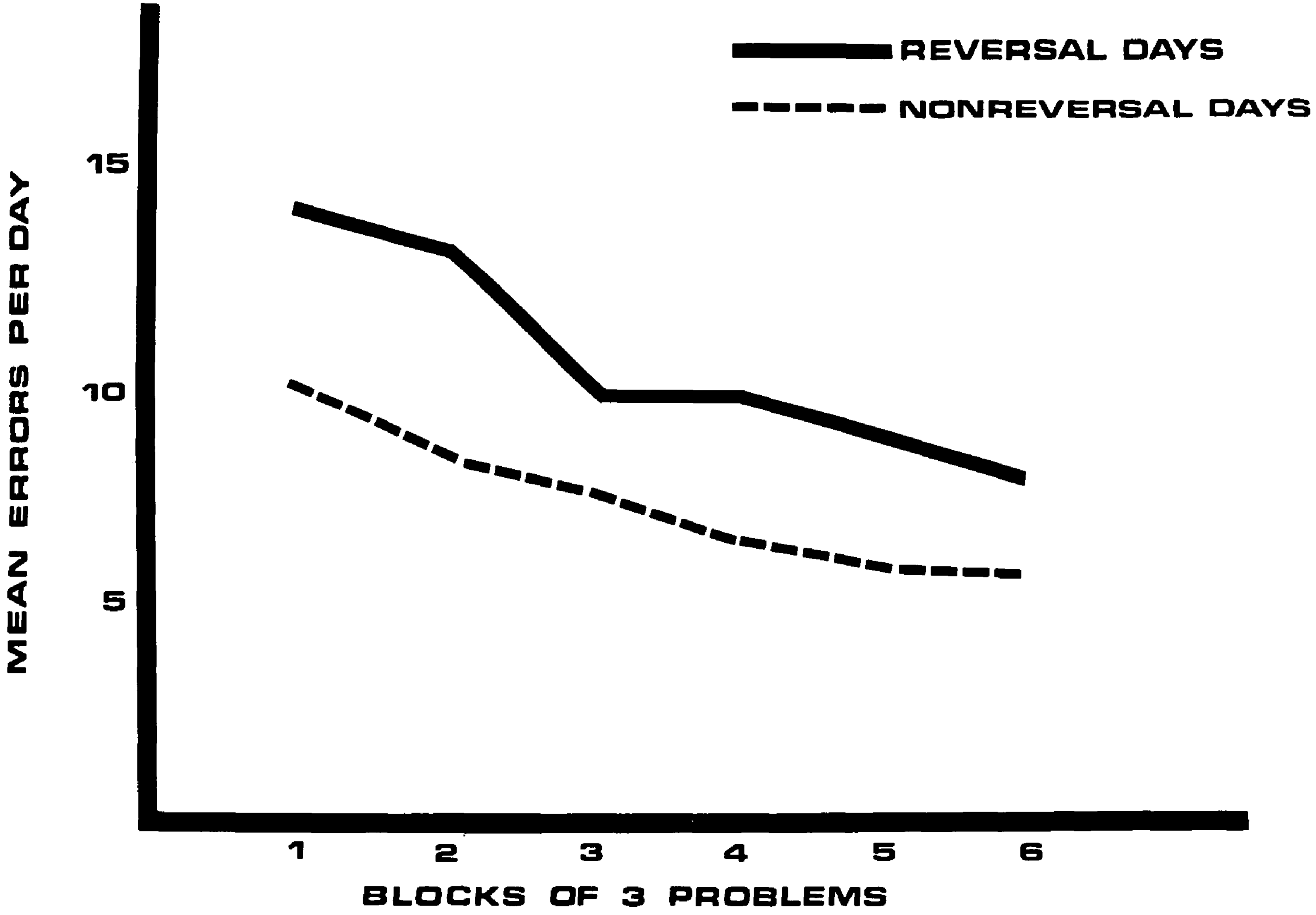

FIGURE 10. MEAN ERRORS ON R & NR DAYS ACROSS ALL D & K LEVELS, OVER BLOCKS OF 3 DAYS, FOR PIGEONS.

Table 14

Mean Reversal Index

Species	D	K	Reversal Index
Chicken	6%	2	.48
		6	.36
	14%	2	.47
		6	.45
	22%	2	.52
		6	.53
	30%	2	.49
		6	.40
Pigeon	6%	2	.51
		6	.56
	14%	2	.69
		6	.71
	22%	2	.59
		6	.58
	30%	2	.50
		6	.61

Table 15

Three-way analysis: Reversal Index

Source	df	Mean Square	F
Drive (D)	3	376.77	
Incentive (K)	1	6.25	
Species	1	2809.00	7.54*
D X K	3	17.79	
D X Species	3	231.38	
K X Species	1	390.06	
D X K X Species	3	113.10	
Error	48	372.30	

$*p < .01$

DISCUSSION

This study attempted to determine the extent to which inter-species performance differences on SDR tasks vary as a function of D and K. The final goal of such research is the isolation of the control ranges of these variables across species, since it is quite possible that differences in performance may be a consequence of the mismatching of D and K levels rather than true species differences. These control ranges must be determined before any fine-grain analysis of inter-species differences is undertaken. In a recent discussion of just this question, Wilcock (1972) has contended that it is virtually impossible to devise experimental conditions to match for such a presumably important variable as motivation, across species. The present findings suggest that such a contention is not justified.

Inspection of the control range of the D variable leads to the conclusion that equation of species on this dimension is not only possible, but imperative. Apparently, D can exert a sufficiently powerful effect to erase inter-species SDR differences on a task such as employed here. Gossette (1969) had previously demonstrated that the SDR performance levels of pigeons can drop to a level equal to or inferior to that of Galliforme species, when run under conditions of high D. The present results support this finding, in that species differences became obscured when pigeons at

30% reduction were compared to chickens at 14, 22 or 30% reduction.

Overall analysis reveals that, on an absolute basis, generally superior performance is obtained at the intermediate levels of D, as suggested earlier by Gossette (1969), who argued for a curvilinear function. Inspection of Figures 4 and 5 suggest such an interpretation. The superiority of the intermediate D levels is more pronounced for the pigeon groups, but the consistent absolute superiority of the intermediate D chickens cannot be dismissed, especially in light of the fact that differences fell between two customarily established levels of significance.

On all major measures, the overall species variable reached statistical significance. Pigeons outperform chickens as hypothesized.

In addition, reversal index data provided equivalent species differences. Since this measure has been shown to be insensitive to either D or K, and is relatively easy to obtain, it appears to hold promise as an expediant tool for cursory evaluation across phyletic levels. One drawback, however, is it's relative insensitivity (in comparison to the other measures employed) to inter-species differences, which limits it's value in fine-grain analysis of such differences.

Examination of the D X Species interaction reveals statistical significance for both errors per problem and percent errors on session one data. Further analysis showed that, on an absolute basis, pigeon performance is optimal at the 14% D level and chicken performance at the 22% D level. Errors per problem data showed a significant difference between the pigeon 14% condition and all other pigeon groups. Examination of all mean scores shows that the 14% pigeon group was consistently superior on every measure.

The effects of D for the chicken groups was generally less pronounced than for the pigeons. While the 22% D group consistently displayed superior SDR performance, in absolute terms, there was generally no significant difference between the 14, 22 and 30% groups. However, the performance of the 6% group was always inferior and, for the errors per problem data, this difference was statistically significant. As with the pigeons, the intermediate D groups obtained mean error scores lower than either the high or low D conditions.

It is therefore possible to conclude that while D does exert differential effects across species, species can be equated along the dimensions of this variable. For example, if one wished to compare pigeons and chickens, it would be possible to preselect some level of performance (e.g. optimal performance) and maintain the two species at that D condition which had been shown to result in the level of performance preselected. Once the two species were tested at this preselected performance level, differences between species could not be attributed to mismatching of this variable.

The finding that K failed to exert a statistically significant effect on the performances of either chickens or pigeons is at odds with most previous studies employing SDR methodology (Feldman, 1968; Gossette & Hood, 1968; Gossette, Birnbaum & Ramsey, 1970). In these studies increased K was found to enhance performance.

Despite such reports, there have been studies failing to support this finding. Employing SDR methodology, Gonzalez, Berger and Bitterman (1966) studied the effect of K on the performance of rats and found an inverse relationship between magnitude of reward and performance. An earlier study (Behrend, Domesick & Bitterman, 1965) failed to demonstrate any K effect, although the study employed subjects (fish) whose performance under different K conditions differs from that of other organisms (Gonzalez, Eskin & Bitterman, 1961).

Pubols (1961) employing single reversal methodology found K effects, but upon further inspection of his data he concluded that it was the delay of reward, not the magnitude of reward, that was responsible.

Investigators employing different types of tasks have also reported K effects to be non-significant. Lawson (1957) used a brightness discrimination task and found no K effect on performance. Reynolds (1949) found no difference in the discrimination learning of rats using 160 versus 30 mg. food rewards. Fehrer (1965) failed to discover any relationship between amount of drinking time allowed thirsty rats and running time in a straight alley or U maze.

As mentioned earlier, several studies have failed to find K effects on measures of resistance to extinction, when K effects on acquisition are eliminated (Metzger, Cotton & Lewis, 1957; Fehrer, 1956; Ison & Cook, 1964). Reynolds, Marx and Henderson (1952) obtained no significant differences in the number of trials to extinction of barpressing response following 120 versus 30 mg. food reward. Lawrence and Miller (1947) also found no K effect on trials to a running response extinction criteria, following 1 versus 4 pellets during training.

Since inter-species extinction rate differences constitute the basis of a major theory of SDR performance (differential-extinction hypothesis) such studies may help explain why K failed to exert a strong influence on performance. Since K apparently does influence performance during the acquisition phase, it's effect on SDR may represent it's differential influence on this phase. The previously mentioned studies in which K exerted a significant effect on SDR performance typically involved a more difficult discrimination (form) which would provide a longer period for acquisition and therefore a greater opportunity for K to affect performance.

It remains difficult, however, to completely explain the uniformity of studies which have found K effects on SDR. One additional explanation may be suggested by a study concerning K effects on multiple discrimination learning in rhesus monkeys (Schrier, 1958). This investigator found no differences in performance when reward magnitude was either 1, 2, or 4 food pellets. However, when 8 pellets were used, errors decreased. Since there have been no reported studies of K effects on avian SDR performance employing feeder presentation time as the independant variable, it remains unclear as to just how the present K manipulation corresponds to other techniques. Perhaps greater values of K are required to produce significant changes in performance, although differences of rather small magnitude have been shown to affect performance with other techniques. Thus, such a possibility must await further study.

It has been established that significant species differences arise across successive reversals. Of major interest to the student of comparative SDR learning is the question of the locus of improvement (i.e. error reduction) or, by what mechanism does such improvement take place. Three formulations have been offered; the attention, retention-decrement and differential-extinction hypotheses. The first has not been sufficiently developed and contains several important weaknesses which have been already outlined.

The retention-decrement hypothesis as advanced by Bitterman and his colleagues (Bitterman, 1968) is couched in terms of proactive inhibition, as discussed above. This hypothesis fails to differentiate between the varieties of transfer, provides no adequate basis for a comprehensive evaluation of interspecies differences and fails to account for such typical findings as one-error solutions and error levels which fall below that of the original problem.

The differential-extinction hypothesis (Gossette, 1970) is based upon the role of inhibitory processes and would predict that differences in magnitude of negative transfer from problem to problem are responsible for inter-species performance differences. To assess the role of negative transfer, three measures were devised for analysis; problem two errors, O.D.-peak errors and percent errors on session one of problem two. As noted earlier, these measures differ in the degree to which they represent pure negative transfer effects (e.g. resistance to extinction of the previously correct response). It appears that those measures which are the purest indices of negative transfer (O.D.-peak and percent errors on session one of problem two) are also those least affected by D variation. The purest measures of negative transfer are also those which represent measures of resistance to extinction, according to the differential-extinction model. Since resistance to extinction has not been shown to be uniformly sensitive to variation in D (Campbell & Kraeling, 1954; Kendler, 1945; Strassburger, 1950) the insensitivity of these measures to D provides strong empirical support for the differential-extinction hypothesis. The fact that the major measures are influenced by D may indicate that they are importantly contaminated with positive transfer effects, since D is more likely to have it's effects on the acquisition process than on extinction (Kimble, 1961).

A rather imprecise index of positive transfer is the blocks X days interaction of the R-NR analysis. Since positive transfer should constitute a major component of the decrease in errors from a R to an NR day, improvement across problems would be expected to be seen in the R-NR difference. This interaction and the blocks X day X species interaction are both non-significant. This suggests that species do not differ along the dimension of positive transfer. When this is considered in conjunction with the previously mentioned measures of negative transfer, support is again lent to the differential-extinction formulation. The corresponding analysis of negative transfer, of course, would be a comparison of the NR day with the next R day. However, such an analysis is not reasonable with the present design, since a performance rather than trials criterion was used. Therefore, different numbers of days follow any given NR day, thereby contaminating such an analysis.

The retention-decrement account of SDR performance has also included the proposal that not only is there a decline in transfer of a preference from problem to problem, but from session to session within a problem. Thus, while this formulation predicts a progressive decline in errors on R days, it also predicts an accompanying increase in errors on NR days (Gonzalez, Behrend & Bitterman, 1967; Behrend, Jennings & Bitterman, 1968). The curves for these two functions should converge during later problems. While the present design allowed for only 20 problems (these investigators have often used as many as 40 to 60 problems), inspection of Figures 9 and 10 show no such tendency. The functions remain parallel throughout the course of 20 problems, displaying no sign of a developing convergence.

From the data described above it is apparent that interspecies performance comparisons are not only feasible, but are in fact of considerable value in assessing the relative phyletic importance of critical dimensions of discrimination learning. It is commonplace observation of students of animal behavior that certain key parameters of learning must very across different phyletic levels by virtue of variation in the complexity of the central nervous system. Yet, as noted above, significant interspecies performance differences have been singularly absent in the literature, despite the employment of a wide repertoire of behavioral tasks and methodologies. To a large extent, these past failures, and in fact the few reported successes, have been extensively criticized for failing to compare performances of different species under comparable methodological conditions. As recently as Wilcock (1972), the position is stated that it may be almost impossible to achieve this goal. The major aim of the present research was to bring to bear an empirical answer to the questions posed by these problems.

The strategy selected in the present investigation was designed to evaluate species performances at several levels of D and K. The full range of behavioral variation that can be attributed to variation of an environmental variable has been termed the "control range" of that variable. The actual value of a given variable may yield optimal performance for one species, but not another. Therefore, performance differences can be interpreted as taxonomically meaningful only after it is clear that such differences have not resulted from a mismatch of control ranges across species. Once the control ranges are calibrated, the magnitude of inter-species differences can be determined through comparisons of performance levels at predetermined sectors of the control range.

The present study has examined the feasibility of this comparative approach and has found it to be not only possible, but desirable. Determination of the control ranges for other species and other variables known to affect performance can and should be undertaken.

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Appendix 1

Duncan's New Multiple Range Test: Errors per Problem[a]

Conditions: Ranked from lowest to highest mean

1	2	3	4	5	6	7	8
P14	C22	P22	P30	C14	P6	C30	C6

Appendix 2

Duncan's New Multiple Range Test: Percent Errors on Session One[a]

Conditions: Ranked from lowest to highest mean

1	2	3	4	5	6	7	8
P14	C22	P22	P30	C14	P6	C30	C6

Appendix 3

Duncan's New Multiple Range Test: R-NR Performance (Errors)[a]

Conditions: Ranked from lowest to highest mean

1	2	3	4	5	6	7	8
P14	C22	P22	P30	C14	P6	C30	C6

[a] Groups not underlined differ at .01 level