THE BEHAVIORAL RESPONSE OF THE CASTRATED MALE GUINEA PIG TO TESTOSTERONE PROPIONATE

by

Jerome A. Grunt

B. S. Rutgers University 1947
M. S. Rutgers University 1948

Submitted to the Department of Anatomy and the Faculty of the Graduate School of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Advisory Committee

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June 1952

ACKNOWLEDGMENTS

The author wishes to express his appreciation to Professor William C. Young for his advice and friendship throughout this work. He also wishes to acknowledge gratefully the aid of Mrs. Joanne Comer and Mr. Edward Bishop in the preparation of the graphic material used in this thesis.

This investigation was supported in part by research grants from the National Institutes of Health, U. S. Public Health Service, in part by a grant from the Committee for Research in Problems of Sex, National Research Council, and in part by grants from the University of Kansas Research Fund.

Testosterone propionate was supplied by the courtesy of Ciba Pharmaceutical Products, Inc.

TABLE OF CONTENTS

INTRODUCTION

The investigations here reported contain contributions basic to endocrinology and to psychology. In general these disciplines are widely separated; endocrinologists as a group have not concerned themselves with studies that are primarily psychological, and most psychologists are not interested in problems that are essentially endocrinological. For this reason it has seemed advisable to prepare two articles, one intended for an endocrinological journal and dealing with the endocrinological phases of the work, and the other intended for a psychological journal and dealing with the behavioral aspects of the work. This manner of presentation has been adhered to in the preparation of the thesis.

Part I. Differential Reactivity of Individuals and the Response of the Male Guinea Pig to Testosterone Propionate[1]

Many investigators have directed attention to the close relationship between the reactivity of tissues, sometimes referred to as sensitivity or responsiveness, and the degree of response to hormonal stimulation. The literature in which the subject is discussed has never

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[1]Submitted to Endocrinology

been reviewed completely, but a few references will indicate something of the extent to which differences in reactivity influence endocrine function.

Smith and Engle (1927) reported that the response of immature rats and mice to pituitary transplants increased with age; that in older animals fewer transplants were required to produce precocious sexual maturity. Bradbury (1944) and McCormack and Elden (1945) found an inherent seasonal variation in the sensitivity of the rabbit to pituitary extracts. Albright, Burnett, Smith, and Parson (1942) presented evidence that in certain clinical cases of idiopathic hypoparathyroidism the disturbance was not a lack of hormone, rather a resistance to it. Selye and Albert (1942) described a differential reactivity of the adrenal gland. They found that estradiol administered to immature male rats in large doses was not followed by the adrenal cortical hypertrophy that was produced in the adult, in fact, it tended to decrease the size of the tissue. Sprague (1951) writes that in many conditions of seeming adrenal insufficiency, no deficiency of the adrenal hormones exists. Apparently, there had been an alteration in the manner in which the target organs were responding to the hormones.

The importance of the relationship of reactivity for tissue response is not restricted to mammals. Lillie

(1932) showed that different feather tracts of the brown Leghorn fowl have inherently different growth rates, and exhibit correspondingly different thresholds of reaction to the female hormone. The response of the oviducts in young New Hampshire Red chicks to injections of stilbestrol was shown to depend on the level of folic acid intake (Hertz, 1945). Williams (1942), early in his work on the metamorphosis of the native silkworm moth, concluded that the ultimate result is determined by the ability of the tissues to react.

Early reports of differences in the reactivity to gonadal hormones and an enumeration of some of the factors which might influence reactivity have been reviewed (Young, 1941; Beach, 1948), but there are more recent additional studies. The seminal vesicles of the rat are most sensitive to stimulation by androgens at 40 to 60 days of age, a time when this tissue is differentiating most rapidly (Hooker, 1942). Price (1944) indicated that at 26 days there is a marked increase in the reactivity of the uterus and seminal vesicle of gonadectomized rats to testosterone propionate. A similar change was found in the male and female prostate on the thirty-sixth day. Hamilton (1948) found that no correlation exists between certain secondary sexual characteristics of the human male, such as baldness and the presence of auricular hair, and the titers of excreted

steriods. He concluded that the action of the hormones in endocrine-dependent states is controlled by genetic, aging, environmental, and other factors. Lyman and Dempsey (1951) working with hibernating, castrated, male hamsters showed that following the injection of testosterone, the seminal vesicles of the animals which returned to hibernation revealed little enlargement or histological change, whereas those of the animals which remained awake showed an increase in weight and histological alteration. They concluded that it is not the amount of circulating hormone which determines the condition of the affected organ, rather the transient condition of the organ.

It will be apparent that most of these differences in reactivity have been associated with age, season, and nutrition. Other factors, however, may be involved. Regulation of the reactivity of tissues by endocrine substances, such as the thyroid hormone, has been suggested (Smelser, 1939; Salmon, 1941; Langham and Gustavson, 1947; and others). Another example is the priming effect of an initial dose of estrogen on the sensitivity of the vaginal mucosa (Kahnt and Doisy, 1928). Differences in reactivity may have a genetic basis. Bates, Riddle, and Lahr (1941) report that two hereditary strains of chicks showed differential thyroid responsiveness to thyrotrophin. Chicks from one source required four times as much hormone to produce an amount of stimulation equal

to that obtained in chicks from the other.

In few if any of the studies cited above were the investigators concerned primarily with reactivity. Most information came as a by-product of experiments directed toward other problems. Lacking was a study of the extent and importance of differences in the reactivity of tissues for hormonal action in animals homogeneous with respect to age, diet, the season of experimentation, methods of handling, and general endocrine balance as judged by the condition of the individuals at the beginning of the investigation.

MATERIALS AND METHODS

Reproductive behavior of the male is particularly well adapted for investigations of this type. The end points are definite. The strength of sex drive displayed by individual male guinea pigs is extremely variable from animal to animal, but for individuals quite constant from test to test. Long range experiments requiring comparatively few animals are possible. Individual animals can be used repeatedly giving continuous information throughout the experimental period with a minimum of operational trauma. The importance of this last point can be illustrated briefly. In this investigation each animal was given 41 tests, consequently much more information was obtained from single animals than would have been possible had procedures been employed that involved

sacrifice of the animals following each test.

Sexual behavior patterns of the adult, male guinea pig and their development have been described (Avery, 1925; Louttit, 1927; 1929; Sollenberger and Hamilton, 1939; Seward, 1940; Young and Grunt, 1951; and Webster and Young, 1951), but since an understanding of what follows depends on some familiarity with the behavior, a brief description is given.

When a female guinea pig in heat is placed with a male the following sequence of behavior is usually seen. The male follows the female and there is frequently a generalized sniffing and licking, or pulling of the hair with the teeth. The term nibbling is used to describe these actions. Shortly afterwards, the male centers his attention on the ano-genital region; nuzzling is used for this localized sniffing and licking. In the next type of action the male mounts the female and executes a series of pelvic movements. Most often this occurs posteriorly; frequently, however, in his excitement the male mounts elsewhere. In either case, the action is called mounting. In the display of the complete pattern terminating in ejaculation, intromission with pelvic thrusts usually follows mounting. In those cases in which ejaculation occurs, the activity is brought to an abrupt end with a grasping of the female's back, and a convulsive drawing in of the flanks. This position is held for a number of seconds following which the male dismounts and licks his penis. If watched, he will be seen to drag his

pudendum along the floor of the cage. Usually the time required to achieve ejaculation is less than 10 minutes. More frequently than not, ejaculation is followed by a period of quiesence which lasts at least an hour (Grunt and Young, 1952). This sequence of behavior is not invariable. At times the lower degrees of the behavior pattern are omitted and mounting with intromission or even ejaculation takes place almost immediately. At other times there is little sexual behavior beyond nuzzling or mounting.

Although there is wide variation in the age at which these elements of the sexual behavior pattern are first displayed, the approximate age at which each component appears is known. Generally nibbling is first seen about the fourteenth day, nuzzling about the seventeenth day, mounting about the forty-fifth day, intromission about the fifty-fourth day, and ejaculation about the sixty-fourth day (Avery, 1925; Louttit, 1929; and Webster and Young, 1951). All this information was utilized in the development of the method (Young and Grunt, 1951) by which the strength of sex drive was measured in this investigation.

When determining the strength of sex drive a female displaying good heat responses (Young, Dempsey, Hagquist, and Boling, 1937) was placed in the cage occupied by a male. The amounts of the five measures of behavior,

nibbling, nuzzling, mounting, intromission and ejaculation, displayed by the male during a 10-minute period were recorded. Each minute of the test was divided into four 15 second periods, and a measure was recorded only once during each period in which it was shown. Intromission and ejaculation, being more discrete and of shorter duration, were recorded only in the period during which the measure of behavior began.

In determining the score for each test, the number of 15-second periods was counted during which each measure of behavior was displayed. Only the highest measure of behavior displayed during each period was used in the calculations. Therefore, the maximum number of measures in each test was 40. Since, however, ejaculation usually is achieved in less than 10 minutes, the number of measures was less. The number of 15-second periods during which a given measure of behavior was displayed was then divided by the duration of the test. The quotient represents the number of times per minute when that measure of behavior was the highest degree shown. Each quotient was then multiplied by a factor arbitrarily chosen as representing the importance of the measure; 1 for nibbling, 2 for nuzzling, 3 for mounting, 4 for intromission, and 5 for ejaculation. These values were chosen because, as was indicated above, the elements of the behavior pattern appear in this order during maturation. The sum of the

products was taken as the score of the test. When this procedure is followed, an animal that mates within the first 15 seconds is scored 20.0 while one that does nothing for the entire 10 minutes of the test is scored 0.0. A male having an average of 8.50 or higher for 10 tests is considered high drive. If the score averages between 6.25 and 8.50, he is considered medium drive; if below 6.25, low drive.

In the first of two experiments, each of 39 male guinea pigs, 80 to 150 days of age, was isolated in a cage 24 inches square. Beginning approximately seven days later each male was given tests at weekly intervals to determine the strength of his sex drive. After 10 tests all but 10 of the animals, the intact controls, were castrated. Their average scores ranged from 2.2 to 11.1. For the following 31 weeks both experimental and control animals were tested weekly. In all, 1599 tests were made. During the first 16 of the 31 weeks no therapy was given. This was the period during which sexual activity decreased from the precastrational level to a constant low level, which is referred to as the base line. During the following 15 weeks, each of 22 of the castrated males was injected with testosterone propionate. The androgen was administered daily in doses of 25γ per 100 grams body weight daily for the first 10 weeks of this period, and 50γ per 100 grams body weight for the

last 5 weeks. The volume of injected sesame oil containing dissolved hormone was kept constant for each 100 grams body weight. Seven of the 29 castrates were given sesame oil and served as the castrate control group.

At the end of the experiment the scores for each week were averaged. In a first analysis of the scores the animals were divided into intact controls, castrate controls, and castrates given testosterone propionate, thus revealing the effects of castration and subsequent androgen therapy. A second type of analysis was suggested by the great differences between individuals. For this analysis the animals were divided into high, medium, and low drive groups, thus relating the performance of each group during the period of therapy to the strength of drive prior to castration.

In the second experiment 31 animals were used. On the basis of the scores of 10 tests prior to castration, these males were divided into four balanced groups whose scores averaged 7.8. Each group contained 7 or 8 animals. Following castration, tests were made at weekly intervals for 31 weeks. During the first 16 weeks no androgen was given, and the scores decreased to the base line. At the beginning of the seventeenth week following castration and for the remaining 15 weeks, the animals in each of the four groups were given daily injections of testosterone

propionate in doses of 12.5, 25, 50, or 100 γ per 100 grams body weight. These amounts were used in order that the effects of a variable dosage could be compared. In all, 1271 tests were made.

Following the last test, the weekly scores were averaged. In a first analysis, the averages for each of the four groups were plotted in order to show the effects of castration and therapy with these amounts of androgen. In a second analysis the performance was related to the strength of drive prior to castration.

After the last test, the animals were sacrificed and portions of the endocrine and reproductive systems were fixed for histochemical and histological study. The results of the microscopic findings will be reported elsewhere.

Throughout the work the temperature was maintained between 70° and 75° F. The diet always included rabbit pellets, oats, green vegetables, alfalfa hay, and water. All the animals were healthy, and showed little if any ill effect of the operation or daily injections.

RESULTS

The results obtained from the experiment involving observation of males prior to castration, during the period of castration without therapy, and while testosterone propionate was being administered in the same amount per 100 grams body weight to each animal are

summarized in figure 1.

During the 41 weeks of the experiment the intact controls showed a very slow decline in sexual activity. By the end of the period approximately 18% of the original drive had been lost. This loss manifested itself mainly in a decline in the frequency of ejaculations which was possibly associated with aging. Removal of the gonads in the animals to be studied experimentally was followed by a gradual decline in sexual activity. The base line was reached within 14 weeks, during which time more than 75% of their original drive was lost. The activity at this level consisted basically of nibbling and the score achieved was approximately 2.0. The activity of the animals which received no treatment save the daily injection of sesame oil remained at this level during the remainder of the experiment. When the experimental animals were given testosterone propionate beginning the seventeenth week following castration, their sexual activity increased. By the tenth week after the start of therapy, they returned to a level of drive similar to that of the intact controls, and only slightly lower than that seen prior to castration.

It will be recalled that the 22 castrated animals given testosterone propionate were divided into three groups according to the strength of their sex drive prior to castration. The average scores of these groups before

castration, during the period of castration without therapy, and after androgen treatment was begun are shown in figure 2. Almost immediately after the beginning of testosterone propionate therapy a redistribution of the animals into the groups seen prior to castration became apparent. The high drive animals showed the highest amount of sexual activity, the low drive animals the lowest, and in general, the activity of the medium drive animals was between the two. Not once during the period of androgen therapy did the score of the low drive group equal that of the medium or high drive groups. In all three groups the strength of drive following androgen administration was comparable with that prior to castration.

The significance of the differences between the groups was tested by the "Student t" test. In doing so the scores of the tests for the thirty-fourth, thirty-fifth, and thirty-sixth weeks were used. This was the end of the period during which therapy consisted of 25γ testosterone propionate per 100 grams body weight. It was found that the differences between the low drive group and the other two were significant at the 2% level or better. Because of the variability within the medium drive group, the difference between this group and the high drive group was not significant, nevertheless, the trend was apparent. Similar comparisons were made for

the thirty-ninth, fortieth, and forty-first tests. This was the end of the period during which therapy consisted of 50 γ testosterone propionate per 100 grams body weight. Although the same trend manifests itself, the increase in variability was sufficient to decrease the significance of the differences. Only that between the high and low drive animals remained significant, but at the 3% level. The correlations of the data from all the castrates given androgen, when compared with the average of the precastrational scores, were found to be significant at the 1% level or better.

With few exceptions, the results of the experiment in which four different doses of androgen were administered were comparable with those obtained when each animal received the same amount (figure 3). As before, sexual drive of the four groups decreased to the base line after castration and, following the injection of testosterone propionate, there was an increase in sexual behavior. The only conspicuous deviation from the rule that individuals return to the level displayed prior to castration, was that the rate of increase in the sexual activity of the group given daily injections of 12.5 γ testosterone propionate per 100 grams body weight was slower than in the other animals. Never during the 15 weeks of therapy did this group reach its precastrational average, although at the end of the experiment there were

indications of a return to this level. The low scores were due basically to the failure to achieve intromission and ejaculation.

By the eighth week after the beginning of testosterone propionate therapy, the sexual drive of the animals in the other three groups had returned to the precastration level. With minor exceptions, they continued to display sexual activity of this degree for the remainder of the experiment. The behavior of the animals given 100 ✓ testosterone propionate was comparable with that of the others, except that, starting 9 weeks after the beginning of therapy, the scores always equalled or surpassed by a slight degree, the highest scores of the other groups. The differences were tested for significance. Using the means of the last five tests, it was found that only the differences between the group given 12.5 ✓ testosterone propionate and each of the other groups were significant at the 5% level. None of the other differences was significant. It is seen, therefore, that once the threshold was reached, 4-fold differences in dosage did not cause significant variation in sexual behavior.

In the first part of the experiment it was shown that when male guinea pigs are injected with a given dosage of androgen, the high drive animals returned to a high level of activity, and the low drive animals

returned to a low level. It became of interest therefore, to see whether this would also be true when the range of experimental dosages was varied as in the second experiment. Even though the number of animals in each group was less, comparable data were obtained (figures 4, 5, and 6). The strength of drive following castration and androgen therapy was related to that prior to castration. The responses of the eight animals receiving 25γ testosterone propionate are not summarized here because they were similar to those of the animals used in the first part of the experiment (figure 2).

DISCUSSION

Although the importance of the reactivity of a tissue or organ for its responsiveness to hormonal stimulation has been widely noted, this study is believed to be one of the first, if not the first, in which adult animals, homogeneous with respect to age, diet, the season of experimentation, method of handling and caging, have been used. The degree of variation in the hormonally induced reaction that was studied is of interest. More so, however, is the demonstration of the faithfulness with which the strength of the precastrational sex drive of individuals was restored by hormonal treatment following castration, and, in the second part of the experiment, the demonstration that within the limits of a 4- to 8- fold increase above the threshold, variation

in strength of drive was attributable to the reactivity of the tissues on which the hormone was acting rather than to variation in the amount of hormone. Increased emphasis is thereby given to the principle that the response to a hormone is influenced by the character of the soma.

The reader will want to know whether this suggestion is consistent with other data that are reported by those who have followed the effects of androgens on adults. Hamilton's (1948) demonstration that testosterone propionate will not cause alopecia in some eunuchs, particularly those having relatives that are not bald, is similar in principle. The point was also made by Dempsey (1951) when he called attention to the observation that certain patients with interstitial cell tumors, although producing great amounts of androgen, fail to exhibit any of the symptoms usually associated with high levels of testosterone. The results from two other studies, on the other hand, indicate that the response may be proportional to the amount of hormone. Gordon and Fields (1942) showed that large amounts of androgen, when given to hypogonadal individuals often cause excessive penis growth, priapism, and "over strong sex interest". Beach and Holz-Tucker (1948) indicated that castrated male rats receiving 100 to 500 ✓ testosterone propionate per day exhibited sexual behavior that was

equal or superior to that shown prior to gonadectomy. Species differences may account for the lack of agreement, but even this suggestion is premature because no two studies are more than remotely comparable. Additional work must be done before the principle that is postulated can be fully evaluated. Also of importance is the full meaning of reactivity in terms of what is taking place within the cells that are being stimulated by hormones. No approach to the problem was made during this study, nor is any suggested in the literature.

SUMMARY

The strength of sex drive displayed by individual male guinea pigs is extremely variable from animal to animal, consequently the tissues mediating this behavior are well adapted for a study of the relationship between tissue reactivity and the response to testosterone propionate. Male guinea pigs, homogeneous with respect to age, diet, the season of experimentation, methods of handling, and general endocrine balance as judged by the conditions of the individuals at the beginning of the investigation, were used. The administration of 12.5, 25, 50, or 100 γ of the androgen per 100 grams body weight daily led to the demonstration that the strength of sex drive displayed by individuals during therapy is similar to that shown prior to castration. With androgen therapy, animals that were characteristically high drive prior

to gonadectomy returned to the high level, while the animals that were low drive returned to the low level. It is postulated from the results obtained when the tissues mediating sexual behavior in the male guinea pig were used as the target organ, that much of the difference between individuals is attributable to the reactivity of the tissues rather than to differences in the amount of hormone. The strength of the reaction to the androgen was not altered significantly by a 4- to 8- fold increase in dosage.

Figure 1. Strength of sex drive in male guinea pigs before and after castration and following therapy with testosterone propionate daily.

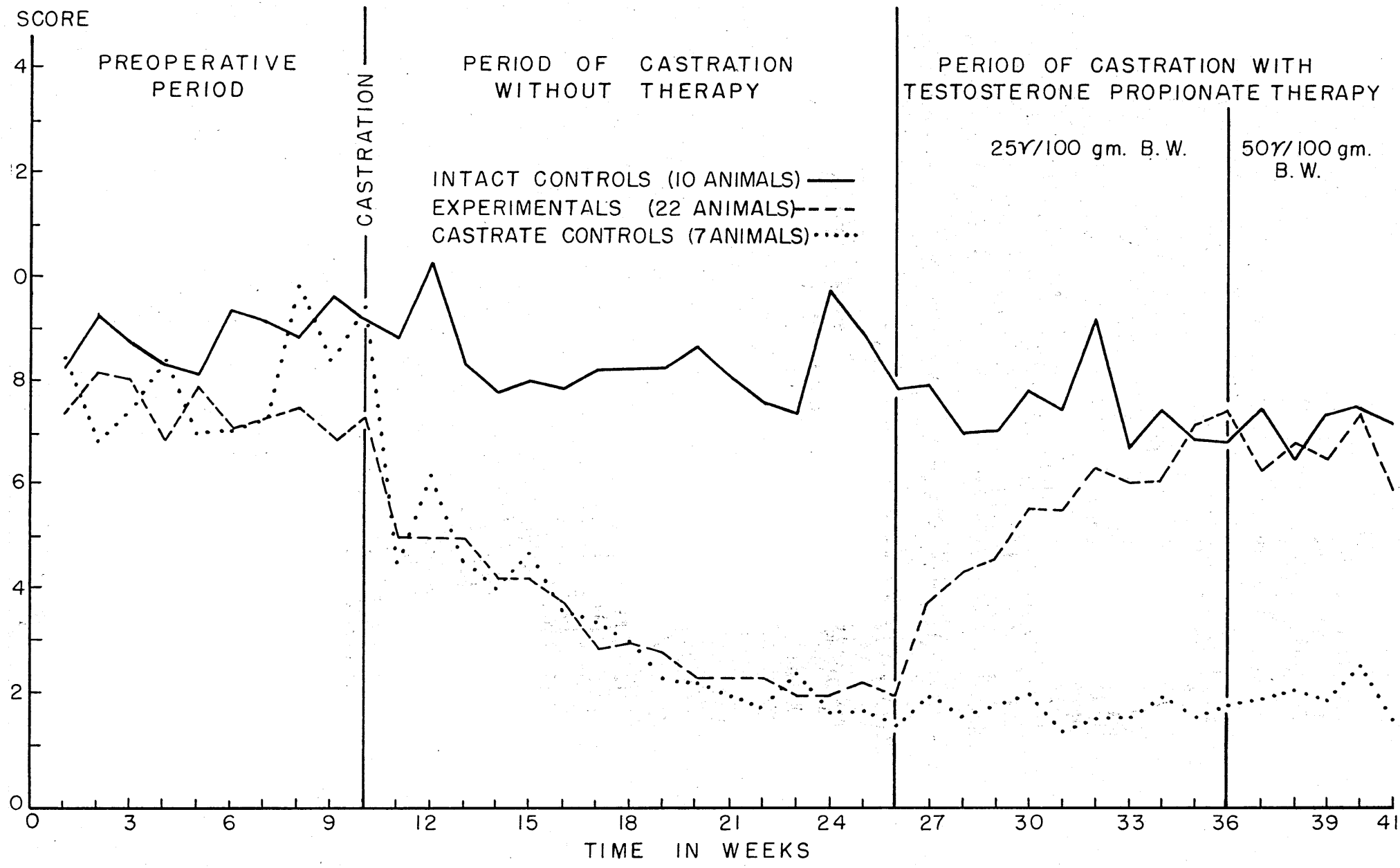

SCORE
PREOPERATIVE PERIOD
CASTRATION
PERIOD OF CASTRATION WITHOUT THERAPY
PERIOD OF CASTRATION WITH TESTOSTERONE PROPIONATE THERAPY
25γ/100 gm. B. W.
50γ/100 gm. B. W.
INTACT CONTROLS (10 ANIMALS)
EXPERIMENTALS (22 ANIMALS)
CASTRATE CONTROLS (7 ANIMALS)
4
2
0
8
6
4
2
0
0
3
6
9
12
15
18
21
24
27
30
33
36
39
41
TIME IN WEEKS

Figure 2. The effect of castration and therapy with testosterone propionate daily on the sex drive of high, medium, and low drive male guinea pigs.

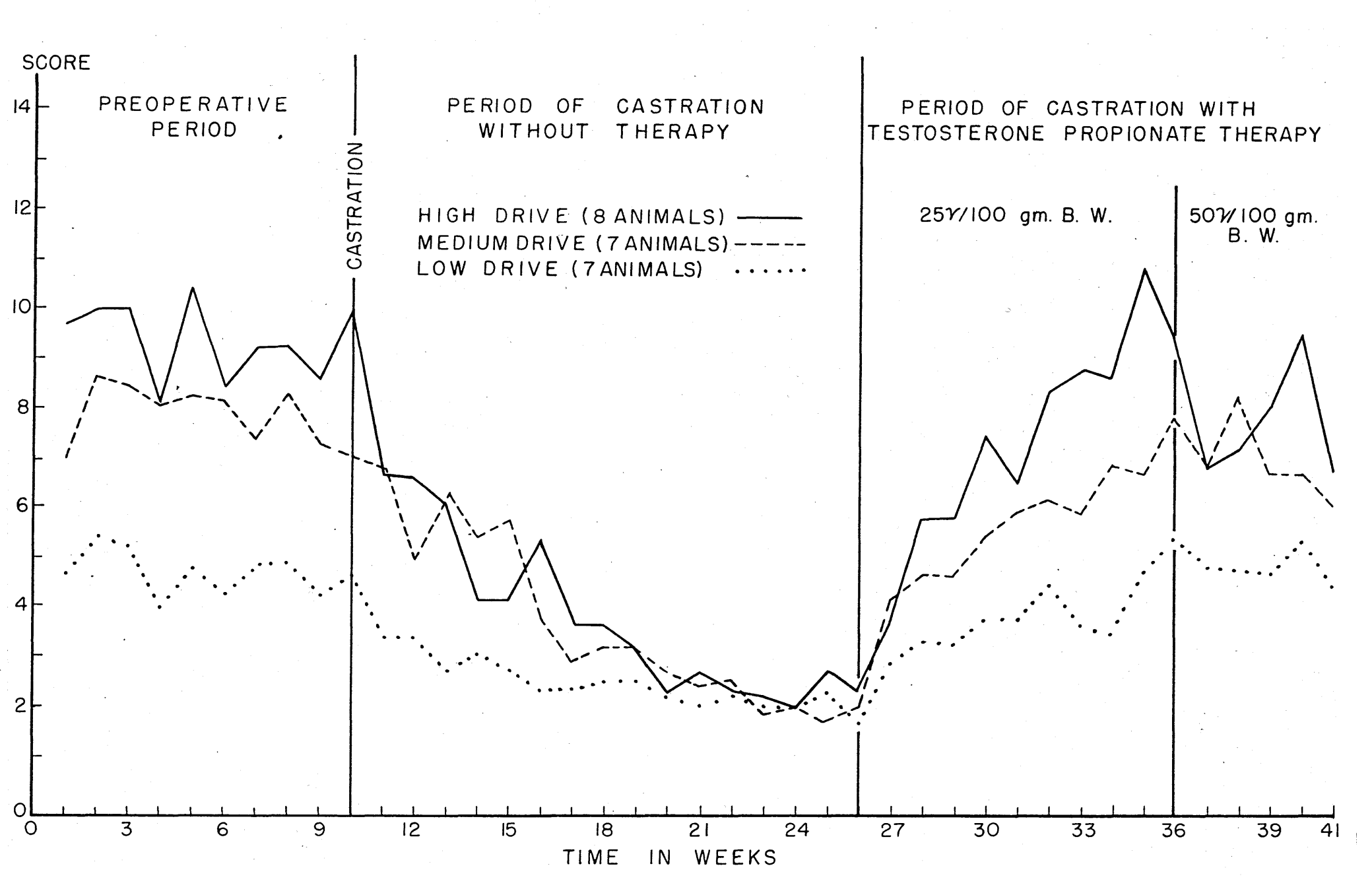

SCORE
PREOPERATIVE PERIOD
CASTRATION
PERIOD OF CASTRATION WITHOUT THERAPY
PERIOD OF CASTRATION WITH TESTOSTERONE PROPIONATE THERAPY
HIGH DRIVE (8 ANIMALS)
MEDIUM DRIVE (7 ANIMALS)
LOW DRIVE (7 ANIMALS)
25γ/100 gm. B. W.
50γ/100 gm. B. W.
0
2
4
6
8
10
12
14
0
3
6
9
12
15
18
21
24
27
30
33
36
39
41
TIME IN WEEKS

Figure 3. Strength of sex drive in male guinea pigs before and after castration and following therapy with different quantities of testosterone propionate daily.

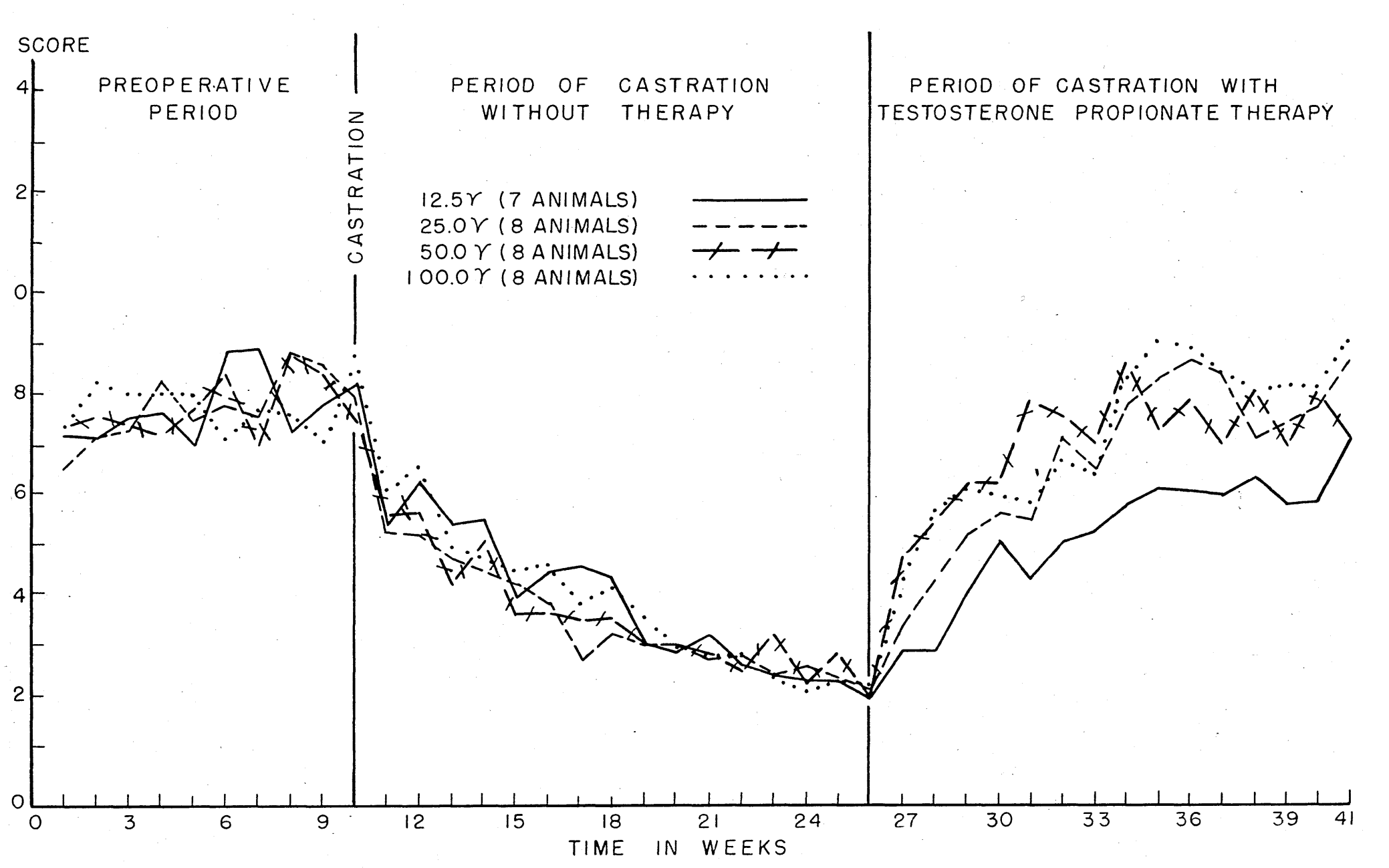

SCORE
PREOPERATIVE PERIOD
CASTRATION
PERIOD OF CASTRATION WITHOUT THERAPY
PERIOD OF CASTRATION WITH TESTOSTERONE PROPIONATE THERAPY
12.5γ (7 ANIMALS)
25.0γ (8 ANIMALS)
50.0γ (8 ANIMALS)
100.0γ (8 ANIMALS)
4
2
0
8
6
4
2
0
0
3
6
9
12
15
18
21
24
27
30
33
36
39
41
TIME IN WEEKS

Figure 4. The effect of castration and therapy with 12.5γ testosterone propionate daily on the sex drive of high, medium, and low drive male guinea pigs.

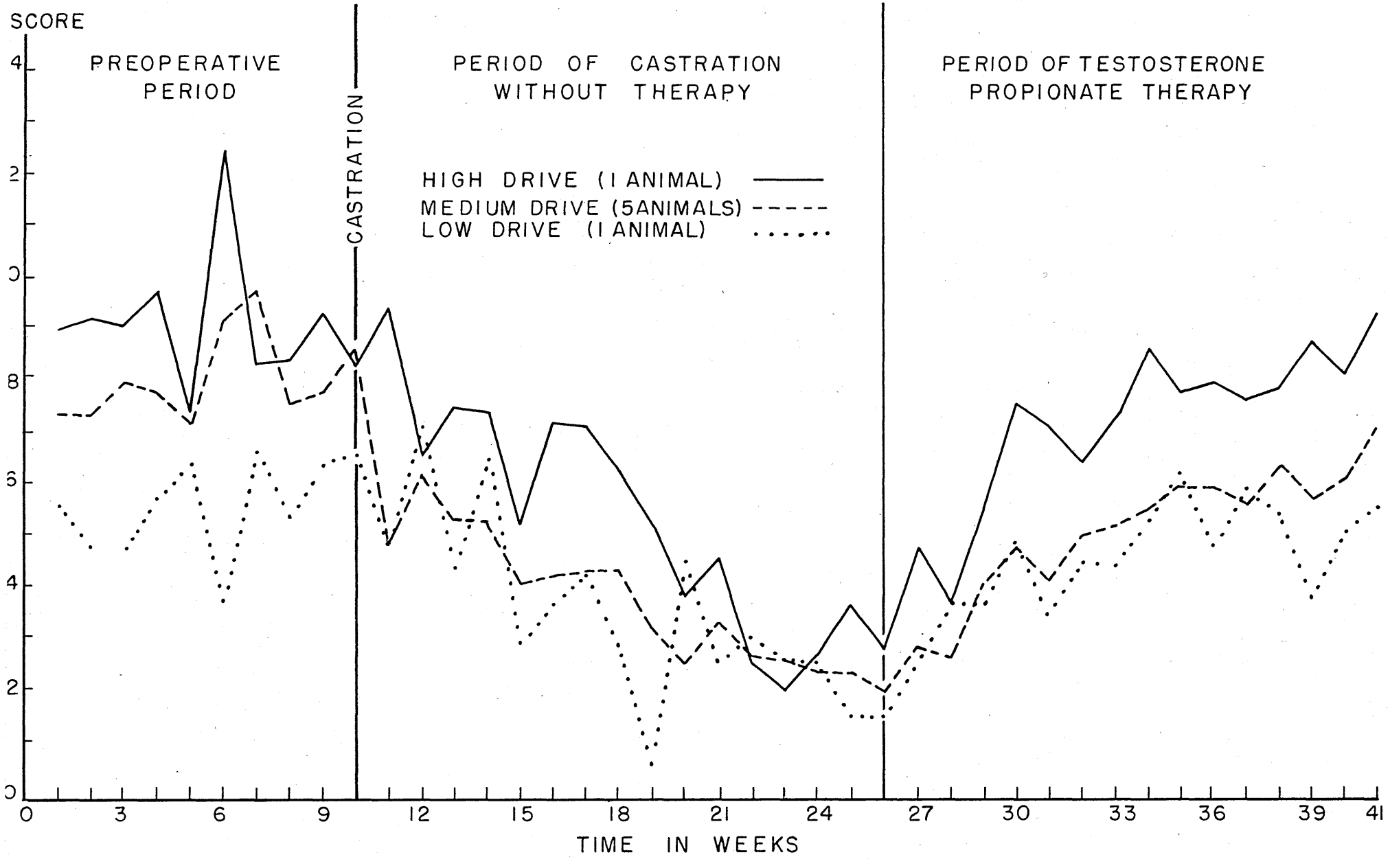

SCORE
PREOPERATIVE PERIOD
CASTRATION
PERIOD OF CASTRATION WITHOUT THERAPY
PERIOD OF TESTOSTERONE PROPIONATE THERAPY
HIGH DRIVE (1 ANIMAL)
MEDIUM DRIVE (5ANIMALS)
LOW DRIVE (1 ANIMAL)
TIME IN WEEKS

Figure 5. The effect of castration and therapy with 50.0γ testosterone propionate daily on the sex drive of high, medium, and low drive male guinea pigs.

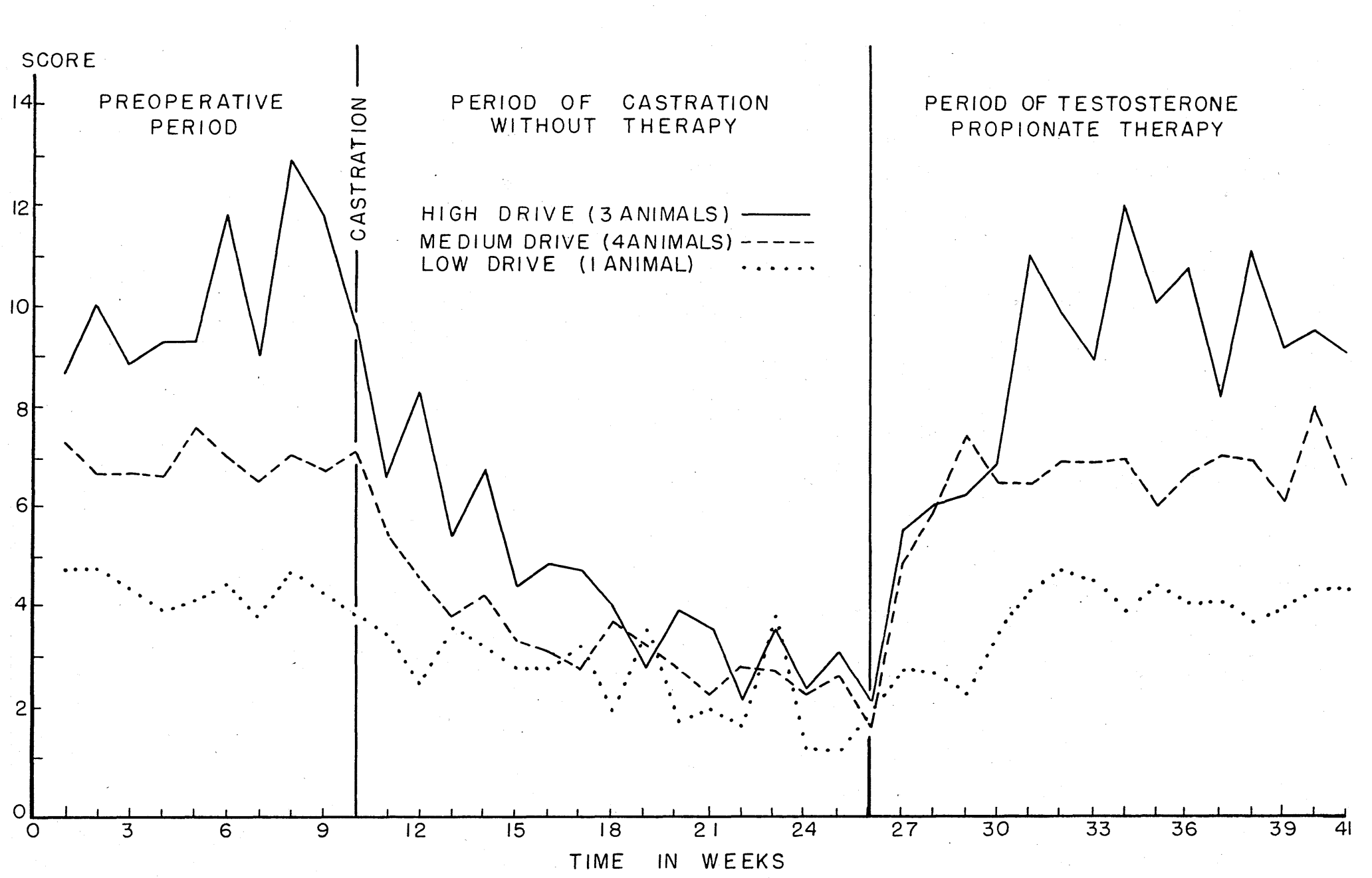
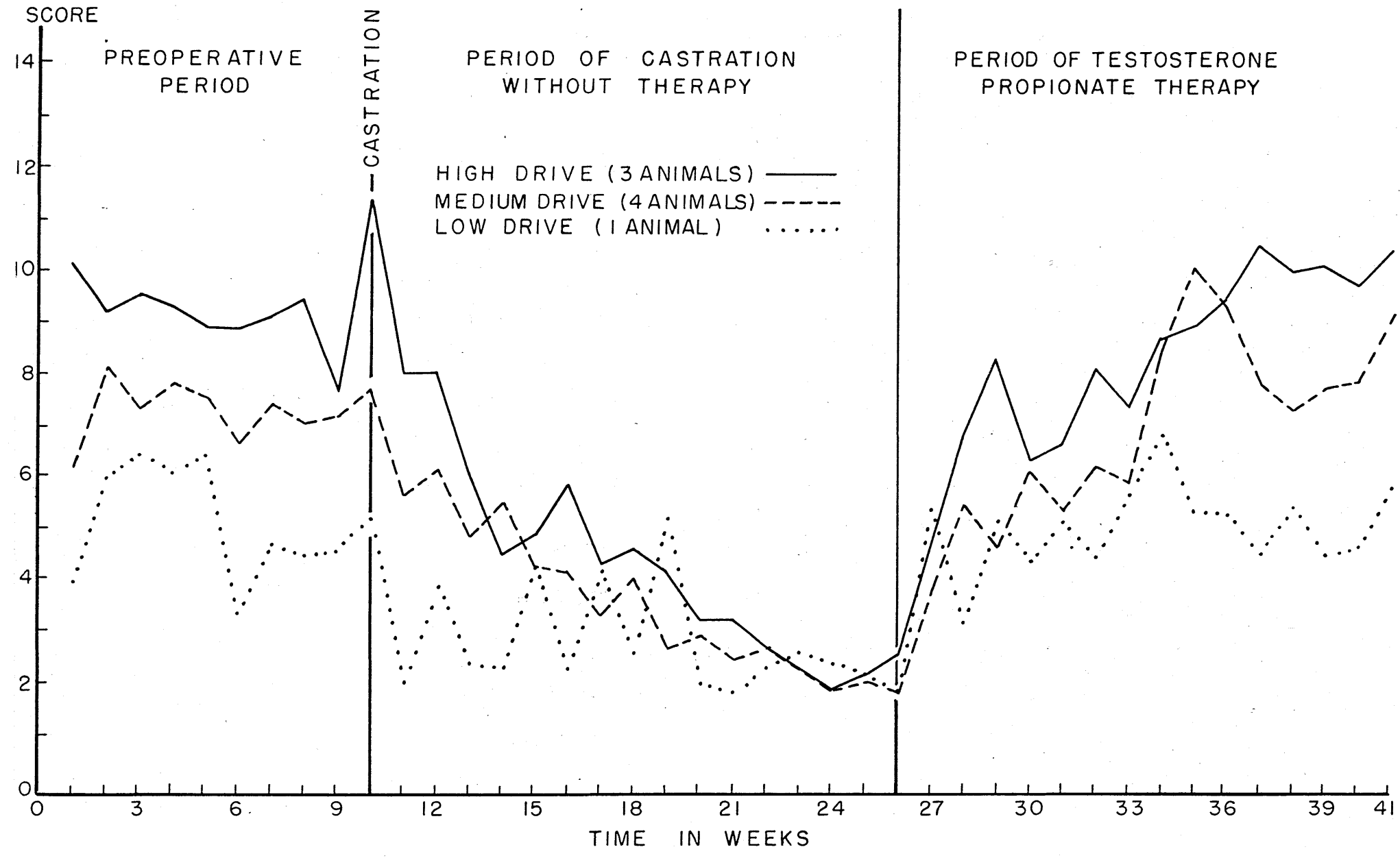

SCORE
PREOPERATIVE PERIOD
CASTRATION
PERIOD OF CASTRATION WITHOUT THERAPY
PERIOD OF TESTOSTERONE PROPIONATE THERAPY
HIGH DRIVE (3 ANIMALS)
MEDIUM DRIVE (4ANIMALS)
LOW DRIVE (1 ANIMAL)
0
2
4
6
8
10
12
14
0
3
6
9
12
15
18
21
24
27
30
33
36
39
41
TIME IN WEEKS

Figure 6. The effect of castration and therapy with 100 γ testosterone propionate daily on the sex drive of high, medium, and low drive male guinea pigs.


SCORE
PREOPERATIVE PERIOD
CASTRATION
PERIOD OF CASTRATION WITHOUT THERAPY
PERIOD OF TESTOSTERONE PROPIONATE THERAPY
HIGH DRIVE (3 ANIMALS)
MEDIUM DRIVE (4 ANIMALS)
LOW DRIVE (1 ANIMAL)
0
2
4
6
8
10
12
14
0
3
6
9
12
15
18
21
24
27
30
33
36
39
41
TIME IN WEEKS

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Part II. Consistency of Sexual Behavior Patterns in Individual Male Guinea Pigs Following Castration and Androgen Therapy[2]

The effects of castration and subsequent treatment with androgen on the sexual behavior of several species of male mammals have been described (Shapiro, 1937; Moore and Price, 1938; Sollenberger and Hamilton, 1939; Stone, 1939; Seward, 1940; Beach, 1944; Beach and Holz, 1946; Beach and Holz-Tucker, 1949; Beach and Pauker, 1949; and others), but for the most part these studies have contributed little information bearing on the hypothesis that the pattern of sexual behavior in individual animals is strongly influenced by an inherent reactivity of the tissues mediating this behavior (Young, 1941; Beach, 1947; Beach, 1948). Beach and Holz-Tucker (1949) are among the few who related the behavior after gonadectomy and androgen treatment to that prior to the operation. They stressed, however, the effects of different amounts of injected hormone rather than the possible influence of the reactivity of the tissues, although Beach (1948) in a review had previously suggested that variation in sexual responsiveness, in addition to being dependent on the amount of hormone, is influenced by the genetically

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[2]Submitted to J. Comp. and Physiol. Psychol.

determined reactivity of the nervous mechanisms mediating sexual arousal and mating behavior. Using different methods and the male guinea pig, data supporting this suggestion have been obtained.

METHODS

Two experiments were performed in which sex drive was measured by the method of Young and Grunt (1951). When this is done, animals that achieve an average score of 8.50 or higher for 10 tests are considered high drive, those that fall between 8.49 and 6.25, medium drive, and those that receive less than 6.25, low drive.

In the first of the two experiments each of 39 male guinea pigs, 80 to 150 days of age was isolated. Starting 7 days later 41 weekly tests of sexual behavior were begun. The first 10 tests were used to determine the score during the precastrational period. Following the tenth test, all but 10 of the animals, the intact controls, were castrated. During the next 16 weeks no therapy was given and sexual behavior decreased to a constant low level, referred to as the base line. Following the twenty-sixth test which was 17 weeks after castration, 22 of the castrates were given testosterone propionate daily by subcutaneous injection. They received 25γ per 100 grams body weight for the first 10 weeks, and 50γ for the last 5 weeks. The remaining seven animals were injected with sesame oil and served as the castrate controls.

In the second experiment 31 animals were used. They were divided into four closely matched groups, each having an average score of 7.8 during the precastrational period when the first 10 tests were given. Following castration these animals were tested for the next 16 weeks when no therapy was given. Beginning the twenty-seventh week and for the remaining 15 weeks of the experiment, each group was injected daily with 12.5, 25, 50, or 100γ testosterone propionate per 100 grams body weight and given weekly tests. This range of hormonal dosages was used in order to determine the effect of different levels of hormone on the restoration of the sexual behavior characteristic of the precastrational period.

In analyzing the data obtained from the two experiments it was necessary to make allowance for a feature of the method of scoring which has not hitherto been considered. The score is a composite of the various elements of the behavior pattern: nibbling, nuzzling, mounting, intromission, ejaculation, and the length of the interval between the beginning of the test and ejaculation. It is conceivable that a large amount of behavior of a low order, for example nuzzling, and a small amount of behavior of a high degree, such as intromission, might give the same score. If so, change in patterns of behavior rather than change in score would be more indicative of the extent to which the behavior

restored by hormonal therapy resembles that displayed prior to castration. The data were treated accordingly. Several elements of the sexual behavior pattern were measured and the results plotted as three point running averages. The elements are the per cent of males achieving at least one ejaculation, the per cent achieving at least one intromission, and the per cent mounting at least once during the test period, and the length of the interval from the start of the test to the accomplishment of each of these acts. This latter is called the latency period.

The animals used in both experiments were homogeneous as to age, diet, the season of experimentation, methods of handling, and general endocrine balance as judged by the conditions of the individuals at the beginning of the experiment. They were members of a well stabilized, healthy colony and showed no ill effects of the operation or the daily injections.

RESULTS

The effects of castration and subsequent androgen treatment as revealed by the scores are of interest to endocrinologists and have been summarized (Grunt and Young, 1952). Briefly, castration was followed by a gradual reduction in the strength of sex drive until the base line was reached (figure 1A). Following treatment with testosterone propionate, the behavior of the injected animals returned to the level maintained by the

controls.

The animals responded to androgen in relation to the drive prior to castration; those that were high drive returned to the high level, while those that were low drive returned to the low level (figure 1B). The significance of these differences was tested by the "Student t" test. Using the scores of the thirty-fourth, thirty-fifth and thirty-sixth tests, the end of the period during which therapy consisted of 25γ testosterone propionate per 100 grams body weight, it was found that the differences between the low drive group and the other two were significant at the 2% level or better. Although the scores of the medium drive group were generally between those of the other two, the differences between this group and the high drive group were not significant. Similar comparisons were made for the thirty-ninth, fortieth, and forty-first tests. The dosage during this period was 50γ per 100 grams body weight. Again the difference between the high and low drive animals was significant, but at the 3% level. An increase in variability accounted for the lack of significance between the medium drive group and the other two. A product moment correlation of .79 is obtained when the individual scores following androgen are plotted against their own precastrational average score. This is significant at the 1% level or better.

Once the threshold which is between 12.5 and 25 γ had been reached, 4-fold differences in hormone dosage did not cause significant differences in the response (figure 1C). It was concluded, therefore, that differences from individual to individual seen in this experiment were not attributable to differences in hormonal level.

An observation not previously recorded, had to do with the rate of decrease (per cent change) in the strength of sex drive following castration and androgen therapy. When the average of the precastrational scores for each group was taken as 100% and the subsequent change taken as the per cent variation from this level, the scores of the high, medium, and low drive animals decreased at the same rate to approximately the same base line. The difference between the low drive group and the other two groups during the last weeks of castration without therapy was not significant. Subsequently, with androgen therapy, the scores of the three groups returned to the precastrational level at approximately the same rate (figure 2).

Changes in the pattern of behavior following castration and androgen therapy are indicated by the data bearing on the per cent of animals ejaculating, the per cent achieving intromission, the per cent mounting and the latency period for ejaculation, intromission and

mounting. Ejaculation was achieved by the intact animals in more than 50% of the tests during the precastrational period (figure 3A). A rapid decline was seen following castration. Within 2 weeks less than 20% of the castrates ejaculated; within 4 weeks less than 5% and within 6 weeks less than 2%. By 9 weeks after castration ejaculation was generally eliminated. Occasionally, however, an individual may again become active and ejaculate. This was seen in the present experiment when one male ejaculated 15 weeks after castration. With the start of androgen therapy, the animals regained their ejaculatory ability. By 2 weeks approximately 2% of these animals ejaculated; by 4 weeks, 10%; by 6 weeks, 20%; and by 8 weeks, more than 25%. The per cent of animals ejaculating remained at this level until the end of the experiment; and although it was considerably below the precastrational percentage, it was the same as that of the intact controls of the same age. Doubling the amount of hormone after the thirty-sixth test did not increase the per cent ejaculating, in fact, there was a slight decrease. At no time during the period of androgen therapy did the castrate controls ejaculate.

When the castrates given 25γ followed by 50γ testosterone propionate were divided into three groups on the basis of the score prior to castration (figure 3B) it became obvious that there also existed wide differences

in the ability of these animals to ejaculate, and that the differences were closely correlated with the score. Approximately 75% of the high drive animals, 55% of the medium drive, and only 5% of the low drive animals achieved ejaculation. Following castration, these percentages declined rapidly. Within one week the low drive animals ceased to ejaculate; the medium drive animals followed suit by the third week; and by the ninth week, with the exception mentioned above, the high drive animals were no longer achieving ejaculation. With the administration of the same amount of testosterone propionate per 100 grams body weight, there was soon a redistribution into the same groups which existed prior to castration.

When four different dose levels of androgen were maintained, the same general pattern of response followed (figure 3C). Provided 25γ or more testosterone propionate were given, the per cent of animals ejaculating was similar to that prior to castration; a 4-fold increase did not effect the result significantly. A dose level of 12.5γ was obviously subthreshold, for in only 2 of 105 tests did these animals achieve ejaculation.

When the per cent of animals reaching intromission was subjected to analysis, it was found that approximately 85% of the animals displayed this measure of sexual behavior during the precastrational period (figure 4A). Following castration the per cent decreased to 0, but

the change was not as abrupt as it was in the case of ejaculation. With therapy the increase in the per cent achieving intromission was rapid, by the second week approximately 15% of the castrates had achieved intromission; and this per cent increased steadily until the ninth week when more than 55% achieved intromission.

Changes in the per cent of high, medium, and low drive animals achieving intromission are shown in figure 4B. Prior to castration and subsequent to androgen therapy there is an overlapping of the high and medium drive animals, but the performance of the low drive animals was always much below that of the others.

The injection of different amounts of androgen (figure 4C) gave results similar to those obtained for ejaculation. About 70% of the animals receiving 25, 50, or 100γ of androgen reached intromission, whereas only approximately 35% of the animals given 12.5γ did so.

Mounting was seen at least once during each test in approximately 95% of those made prior to castration (figure 5A). Among the intact controls, there was no decrease in this percentage during the 41 weeks of the experiment. Although castration decreased the percentage, the rate of reduction was slow; as long as 31 weeks after castration approximately 35% of the castrate controls were still achieving at least one mounting per test. Treatment with testosterone propionate was followed

by a prompt increase in the number of animals mounting; within 2 to 3 weeks the precastrational level was reached.

When high and medium drive animals were compared, few differences were seen (figure 5B). Prior to castration almost all of these animals mounted at least once during each test. Six weeks after castration decreases occurred; but with androgen therapy both groups returned to a level near that maintained before castration. The low drive animals behaved differently. During the precastrational period, approximately 65% of the animals mounted at least once during each test. Following castration this proportion decreased to about 15%; and during the period of androgen therapy about 45% mounted at least once.

Even the smallest amoung of injected androgen returned all of the castrates to approximately the level seen prior to gonadectomy (figure 5C). The per cent of animals mounting at least once was about the same whether 12.5 or 100 γ testosterone propionate per 100 grams body weight were injected.

The latency periods for ejaculation, intromission, and mounting constitute a part of the pattern of behavior and were studied accordingly. The results were almost identical with those obtained from analysis of the data bearing on the per cent of animals ejaculating, the per cent having at least one intromission, and the per cent

mounting at least once per test. The latency periods of the groups given therapy were similar to those before castration. For all three measures, 25, 50, or 100 γ testosterone propionate restored the latency periods to about the length seen prior to castration. A dose of 12.5 γ was completely effective in restoring the latency periods to the precastrational length only for mounting. The supporting data have been summarized graphically (figures 6, 7, and 8).

Examination of the data bearing on the per cent of animals achieving at least one ejaculation, at least one intromission and at least one mounting in each test, and the latency periods, reveals that, as with the scores, the response to androgen is strongly influenced by the reactivity of the tissues mediating this behavior. The evidence is perhaps clearest for ejaculation, slightly less so for intromission, and least for mounting, but even in the case of mounting, the sharp separation of the low and high drive groups before and after therapy reinforces this conclusion.

DISCUSSION

Of the material presented above, some is new, some is confirmatory of observations made on other species, and some is at variance with results previously reported. In the first category is the validity given the use of the composite score by the results obtained when the

separate elements of the behavior pattern are analyzed. Also new is the demonstration that behavior patterns characteristic of the precastrational period tend to be restored in castrate males injected with androgen; and that once the threshold is exceeded there is no significant alteration in the behavior of males receiving 4-fold differences in hormone dosage. These findings reinforce the hypothesis that differences in sexual behavior of laboratory mammals can be attributed, in part at least, to differences in the reactivity of the tissues mediating that behavior stimulated by gonadal hormones.

An effect of aging does not seem to have been pointed out. The general decrease in strength of drive in the male has been noted (Grunt and Young, 1952), but there is no reference to a change in the display of the elements composing the pattern. During the 41 weeks of this experiment the per cent of animals ejaculating decreased approximately 50%; the per cent of animals achieving at least one intromission per test decreased only about 20%, while the number of animals mounting at least once per test remained constant throughout the experiment.

The data which give confirmation to the results from other species are of interest. Stone (1939) and Beach (1944) showed that following castration the ejaculatory reflex of the rat is eliminated prior to

the copulatory response (intromission). In addition, the action of testosterone propionate restores the copulatory response before the ejaculatory reflex. Comparable data were obtained from the guinea pig. With castration the order of disappearance of the elements of the sexual behavior pattern is ejaculation, intromission, and mounting; and, as in the rat, the order of return is reversed when androgen therapy is given.

In the rat the different elements of the pattern have different thresholds for androgen (Beach and Holz-Tucker, 1948). Daily injections of 25γ testosterone propionate caused approximately 80% of a group of castrated male rats to achieve copulation, while only about 60% achieved ejaculation. Comparable results were obtained when 12.5γ daily of the androgen were injected into the guinea pig. This amount of hormone was scarcely enough to elicit ejaculation, but was sufficient to cause over 35% of the group to achieve intromission, and to bring the entire group back to the precastration level of mounting.

Confirmation is given to a suggestion by Stone (1932) for the rabbit, that the time interval necessary to drop the copulating drive below the effective minimum for copulation varies directly with the strength of drive at the time of castration. In this work low drive animals ceased to ejaculate within one week, medium drive animals

by the third week, and high drive animals by the ninth week. This observation is not inconsistent with the statement that the high, medium, and low drive animals decreased at the same rate (p. 34). The score is a composite of several elements of the pattern, whereas ejaculation is but one of the elements. More important, the decrease for the three groups of males plotted in figure 2 is from a precastrational level taken for comparative purposes as 100%, regardless of the strength of drive.

The data which are at variance with other species require comment. Those obtained from the guinea pig do not support the hypothesis that within the normal limits of sexual excitability castration depresses mating tendencies least in the most vigorous copulators, and most in the less active individuals (Beach, 1948).

Rats display wide differences in their sexual behavior after castration (Beach and Holz, 1946). In contrast, guinea pigs following castration soon showed a very constant low level of sexual activity. Beach and Holz-Tucker (1948) state that the administration of 25 to 50γ androgen per day to castrated male rats was followed by a significant increase in sexual behavior. Doses of 75γ testosterone propionate per day or more increased sexual behavior above that seen before castration. In the guinea pig there were indications that

increments of androgen up to a point between 12.5 and 25 γ per 100 grams body weight per day increased sexual behavior. On the other hand, once the threshold was reached, as much as 100 γ of the androgen per day did not modify the character of the behavior significantly beyond that seen prior to castration.

SUMMARY

The display of elements of the sexual behavior pattern of male guinea pigs homogeneous as to age, diet, and handling was tested during the period prior to castration, after castration, and during a period when 12.5, 25, 50, or 100 γ testosterone propionate per 100 grams body weight were injected daily. Differences between individuals were great and permitted a division of the animals into high, medium, and low drive groups. Using the precastrational scores as 100%, and the subsequent change as the per cent variation from this level, the scores of the high, medium, and low drive animals decreased at the same rate to approximately the same base line.

The decrease in the behavior following castration, and the restoration of the precastrational pattern with androgen therapy were noted. Provided 25 γ or more testosterone propionate were given, the pattern was similar to that prior to castration; a 4-fold increase did not effect the results significantly. A dose level of 12.5 γ was

subthreshold for all the elements save mounting. The data support the hypothesis that the behavorial response to gonadal hormones is strongly influenced by the reactivity of the tissues.

Figure 1. Strength of sex drive in male guinea pigs before and after castration and following androgen therapy.

a) Intact controls, castrate controls, and castrates given 25 γ followed by 50 γ testosterone propionate.

b) Castrates given 25 γ followed by 50 γ testosterone propionate, divided into high, medium, and low drive groups.

c) Castrates given 12.5, 25, 50, and 100 γ testosterone propionate.

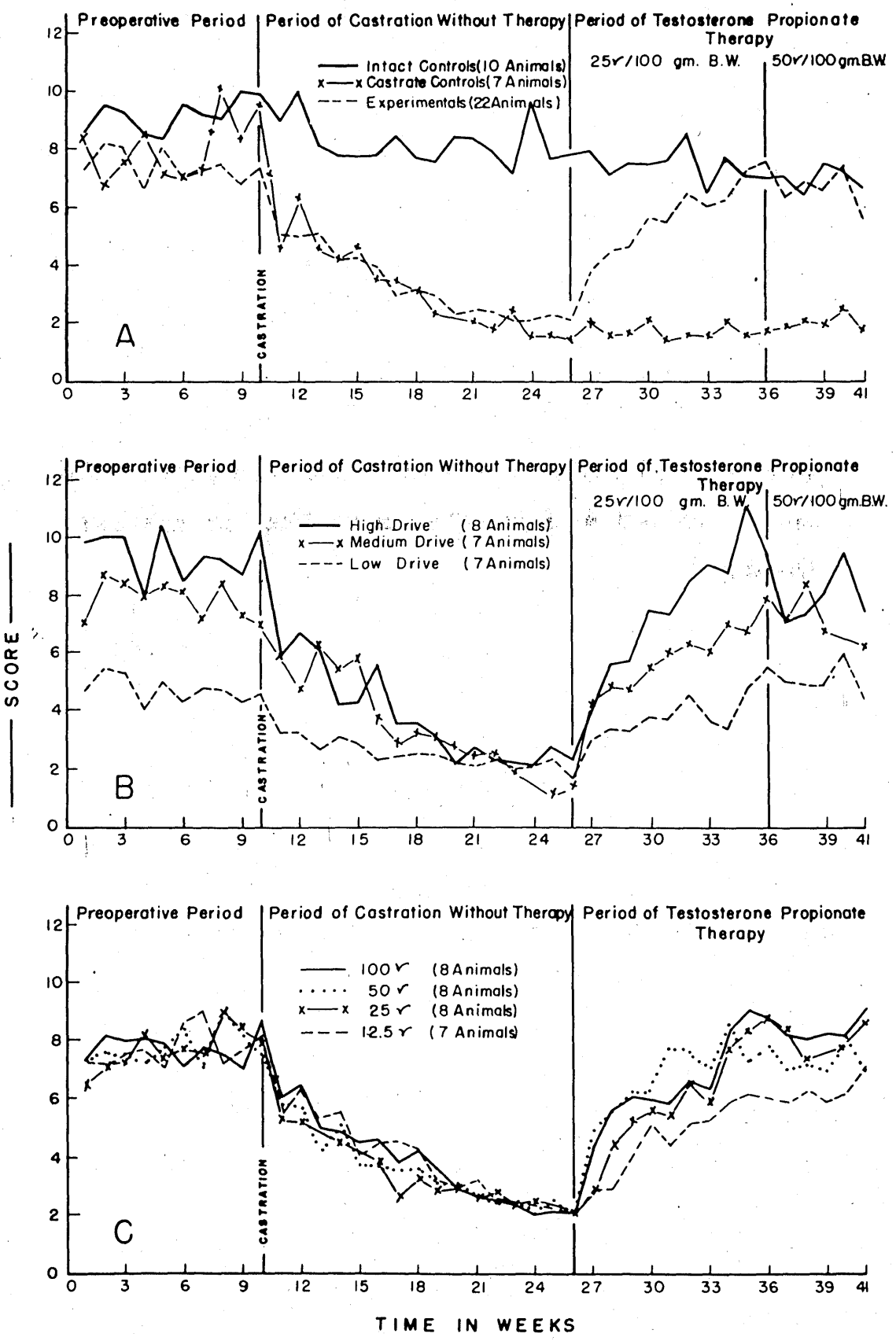

Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
25γ/100 gm. B.W.
50γ/100 gm.B.W.
Intact Controls(10 Animals)
x—x Castrate Controls(7 Animals)
Experimentals(22Animals)
CASTRATION
A
Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
25γ/100 gm. B.W.
50γ/100 gm.B.W.
High Drive (8 Animals)
x—x Medium Drive (7 Animals)
Low Drive (7 Animals)
CASTRATION
B
SCORE
Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
100γ (8 Animals)
50γ (8 Animals)
25γ (8 Animals)
12.5γ (7 Animals)
CASTRATION
C
0 3 6 9 12 15 18 21 24 27 30 33 36 39 41
TIME IN WEEKS

Figure 2. Per cent variation in strength of sex drive of male guinea pigs from the precastrational level.

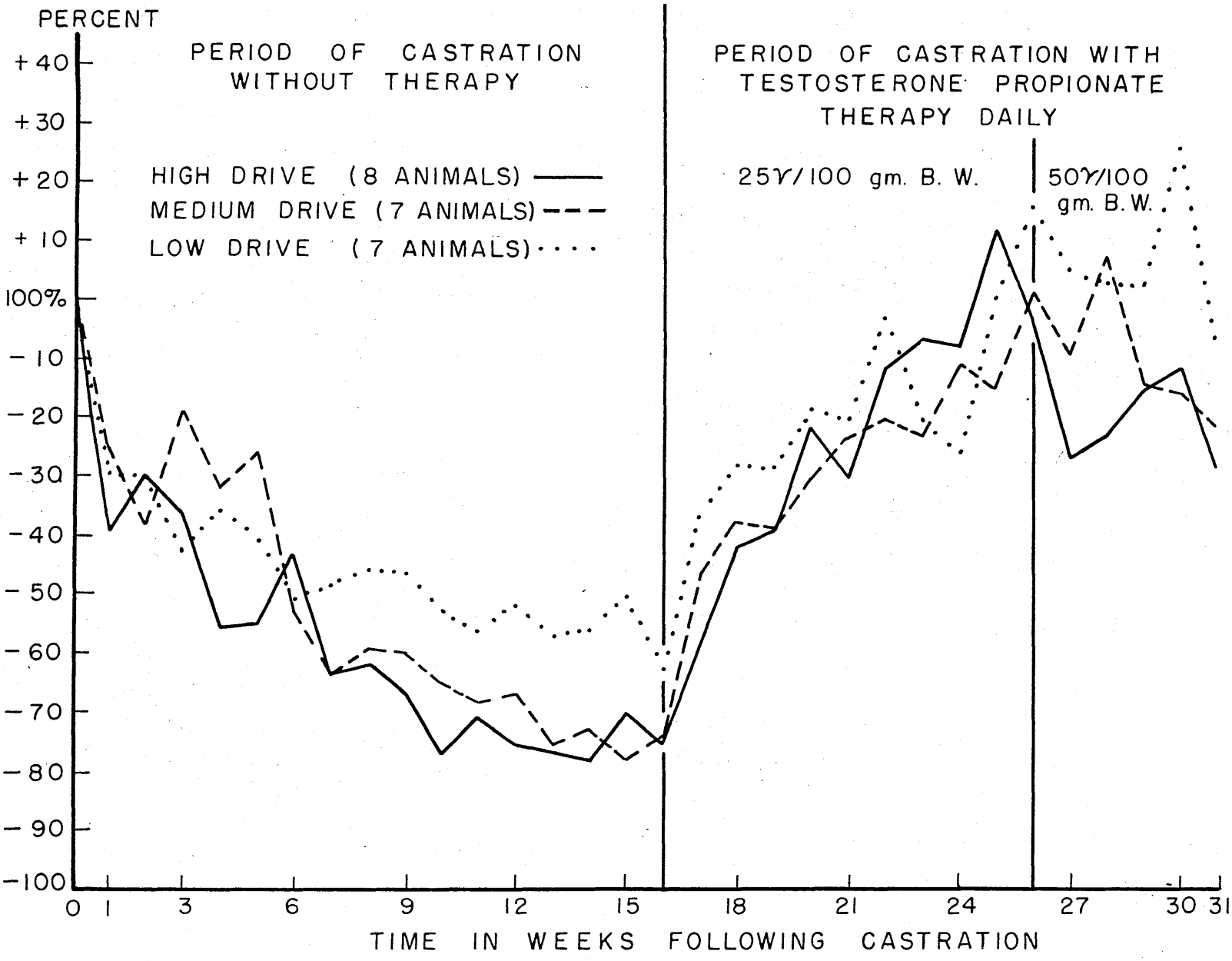

PERCENT
+40
+30
+20
+10
100%
-10
-20
-30
-40
-50
-60
-70
-80
-90
-100
PERIOD OF CASTRATION WITHOUT THERAPY
PERIOD OF CASTRATION WITH TESTOSTERONE PROPIONATE THERAPY DAILY
HIGH DRIVE (8 ANIMALS)
MEDIUM DRIVE (7 ANIMALS)
LOW DRIVE (7 ANIMALS)
25γ/100 gm. B. W.
50γ/100 gm. B. W.
0 1 3 6 9 12 15 18 21 24 27 30 31
TIME IN WEEKS FOLLOWING CASTRATION

Figure 3. Per cent of male guinea pigs achieving ejaculation before and after castration and following androgen therapy.

a) Intact controls, castrate controls, and castrates given 25γ followed by 50γ testosterone propionate.

b) Castrates given 25γ followed by 50γ testosterone propionate, divided into high, medium, and low drive groups.

c) Castrates given 12.5, 25, 50 and 100γ testosterone propionate.

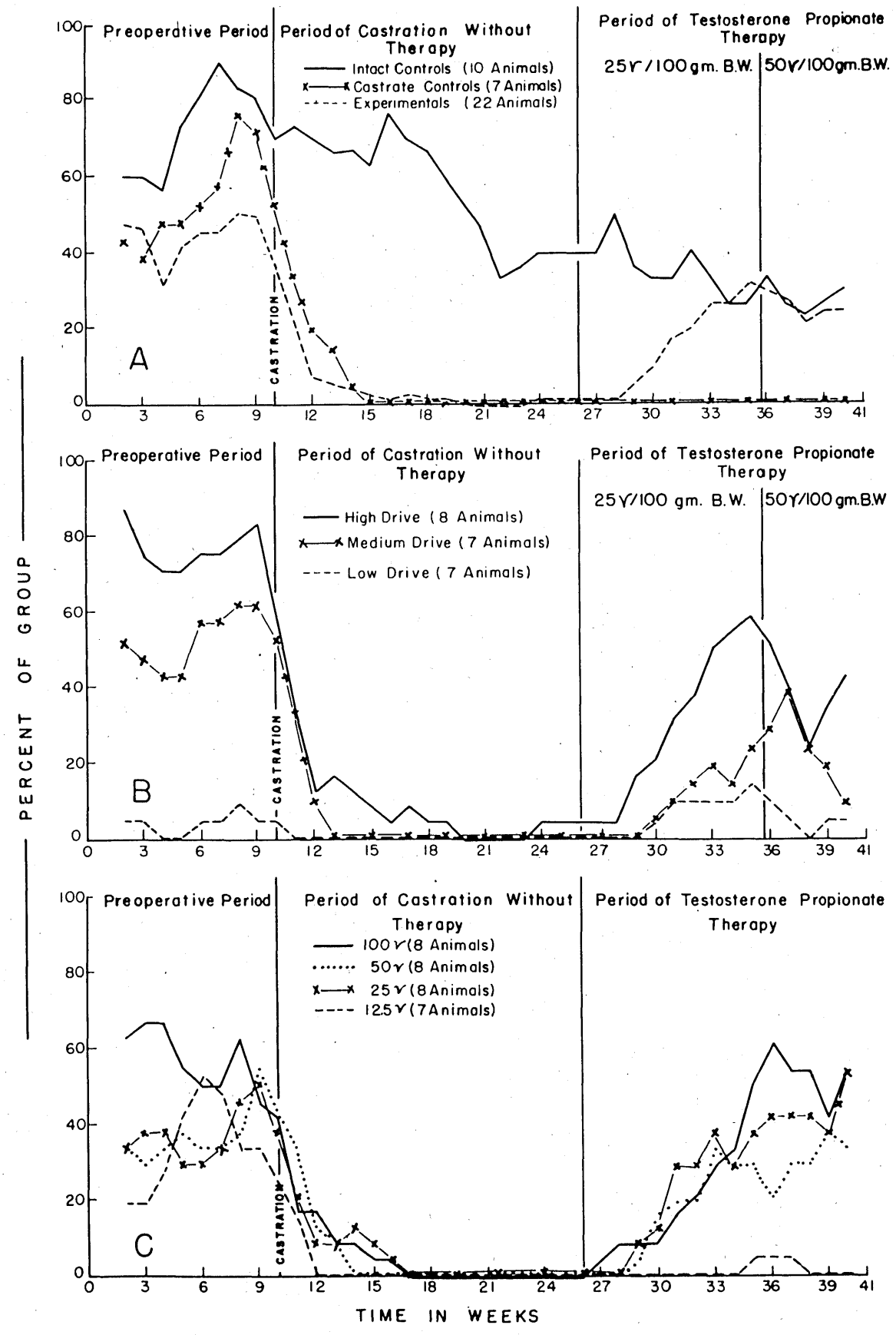

Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
25γ/100 gm. B.W.
50γ/100 gm. B.W.
Intact Controls (10 Animals)
Castrate Controls (7 Animals)
Experimentals (22 Animals)
CASTRATION
A
High Drive (8 Animals)
Medium Drive (7 Animals)
Low Drive (7 Animals)
B
100γ (8 Animals)
50γ (8 Animals)
25γ (8 Animals)
125γ (7 Animals)
C
PERCENT OF GROUP
TIME IN WEEKS

Figure 4. Per cent of male guinea pigs achieving intromission at least once during each test before and after castration and following androgen therapy.

a) Intact controls, castrate controls, and castrates given 25γ followed by 50γ testosterone propionate.

b) Castrates given 25γ followed by 50γ testosterone propionate, divided into high, medium, and low drive groups.

c) Castrates given 12.5, 25, 50 and 100γ testosterone propionate.

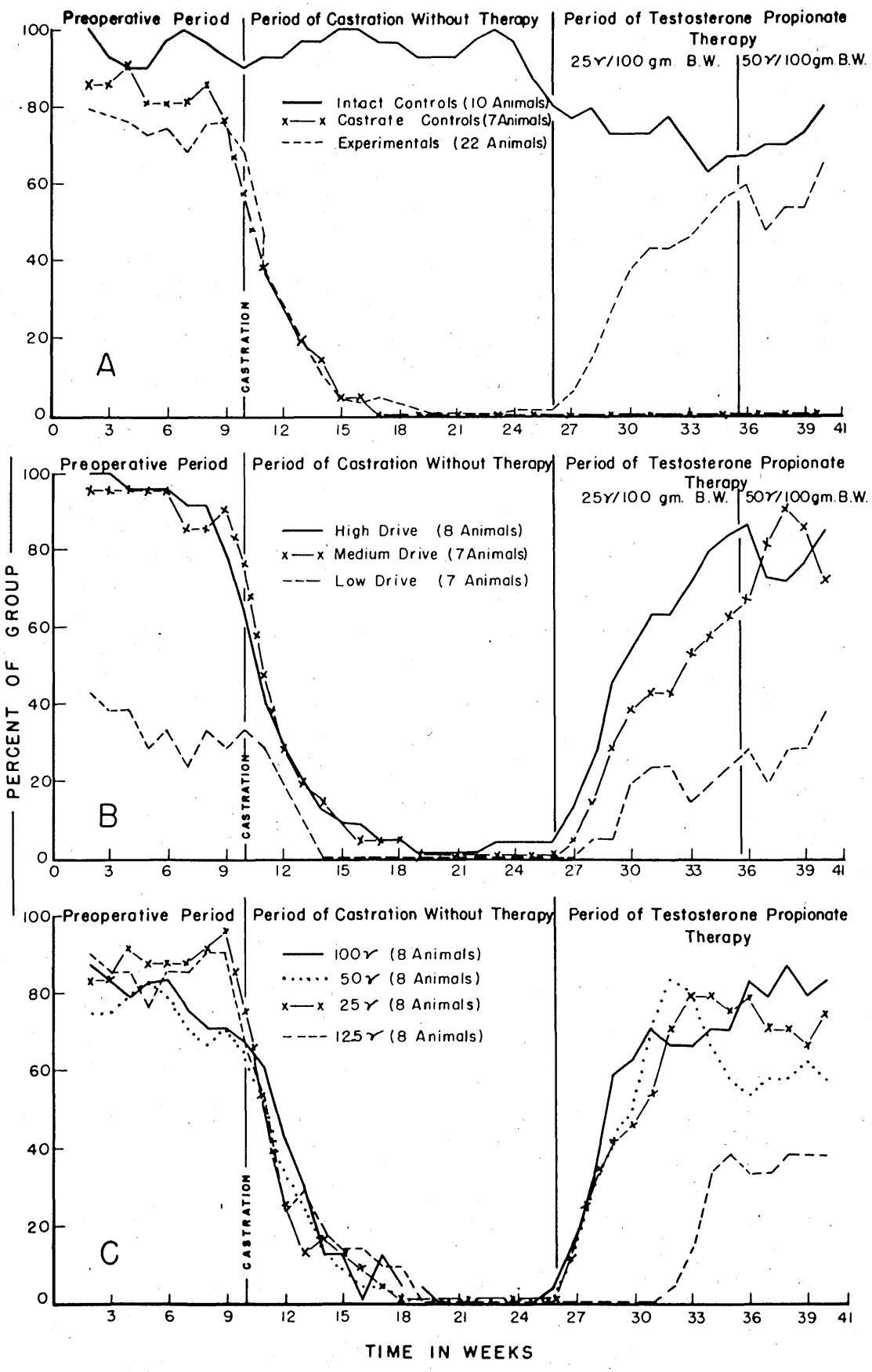

Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
25γ/100 gm. B.W.
50γ/100gm.B.W.
Intact Controls (10 Animals)
Castrate Controls (7Animals)
Experimentals (22 Animals)
CASTRATION
A
PERCENT OF GROUP
High Drive (8 Animals)
Medium Drive (7Animals)
Low Drive (7 Animals)
B
100γ (8 Animals)
50γ (8 Animals)
25γ (8 Animals)
12.5γ (8 Animals)
C
TIME IN WEEKS

Figure 5. Per cent of male guinea pigs mounting at least once during each test before and after castration and following androgen therapy.

a) Intact controls, castrate controls, and castrates given 25✓ followed by 50✓ testosterone propionate.

b) Castrates given 25✓ followed by 50✓ testosterone propionate, divided into high, medium, and low drive groups.

c) Castrates given 12.5, 25, 50, and 100✓ testosterone propionate.

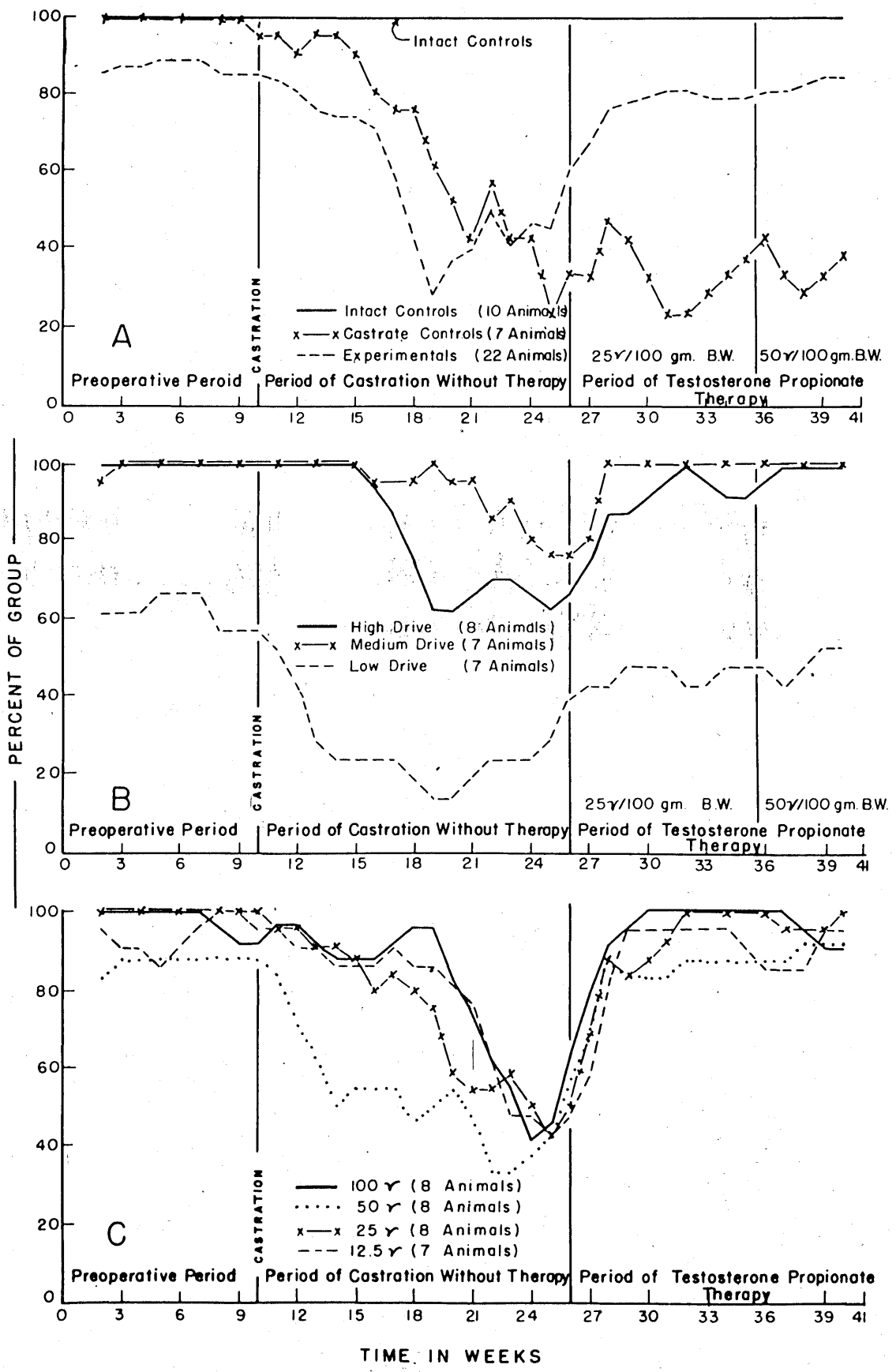

PERCENT OF GROUP
100
80
60
40
20
0
Intact Controls
CASTRATION
A
Intact Controls (10 Animals)
Castrate Controls (7 Animals)
Experimentals (22 Animals)
25γ/100 gm. B.W.
50γ/100 gm. B.W.
Preoperative Peroid
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
0 3 6 9 12 15 18 21 24 27 30 33 36 39 41
B
High Drive (8 Animals)
Medium Drive (7 Animals)
Low Drive (7 Animals)
Preoperative Period
C
100 γ (8 Animals)
50 γ (8 Animals)
25 γ (8 Animals)
12.5 γ (7 Animals)
TIME IN WEEKS

Figure 6. Time required for male guinea pigs to achieve ejaculation before and after castration and following androgen therapy.

a) Intact controls, castrate controls, and castrates given 25γ followed by 50γ testosterone propionate.

b) Castrates given 25γ followed by 50γ testosterone propionate, divided into high, medium, and low drive groups.

c) Castrates given 12.5, 25, 50, and 100γ testosterone propionate.

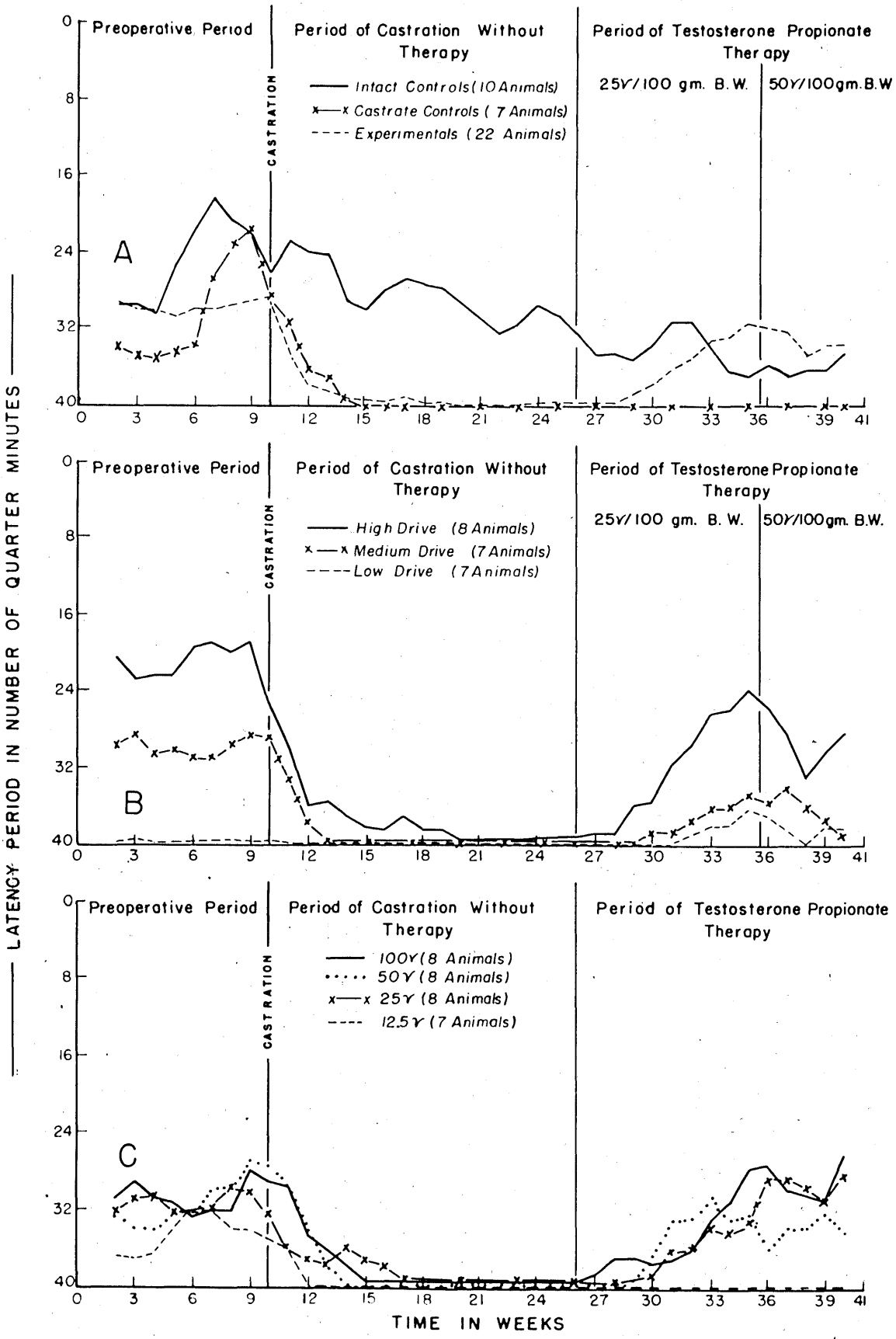

Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
CASTRATION
Intact Controls (10 Animals)
Castrate Controls (7 Animals)
Experimentals (22 Animals)
25γ/100 gm. B.W.
50γ/100gm.B.W
A
High Drive (8 Animals)
Medium Drive (7 Animals)
Low Drive (7 Animals)
B
100γ (8 Animals)
50γ (8 Animals)
25γ (8 Animals)
12.5γ (7 Animals)
C
LATENCY PERIOD IN NUMBER OF QUARTER MINUTES
TIME IN WEEKS

Figure 7. Time required for male guinea pigs to achieve first intromission before and after castration and following androgen therapy.

a) Intact controls, castrate controls, and castrates given 25γ followed by 50γ testosterone propionate.

b) Castrates given 25γ followed by 50γ testosterone propionate, divided into high, medium, and low drive groups.

c) Castrates given 12.5, 25, 50, and 100γ testosterone propionate.

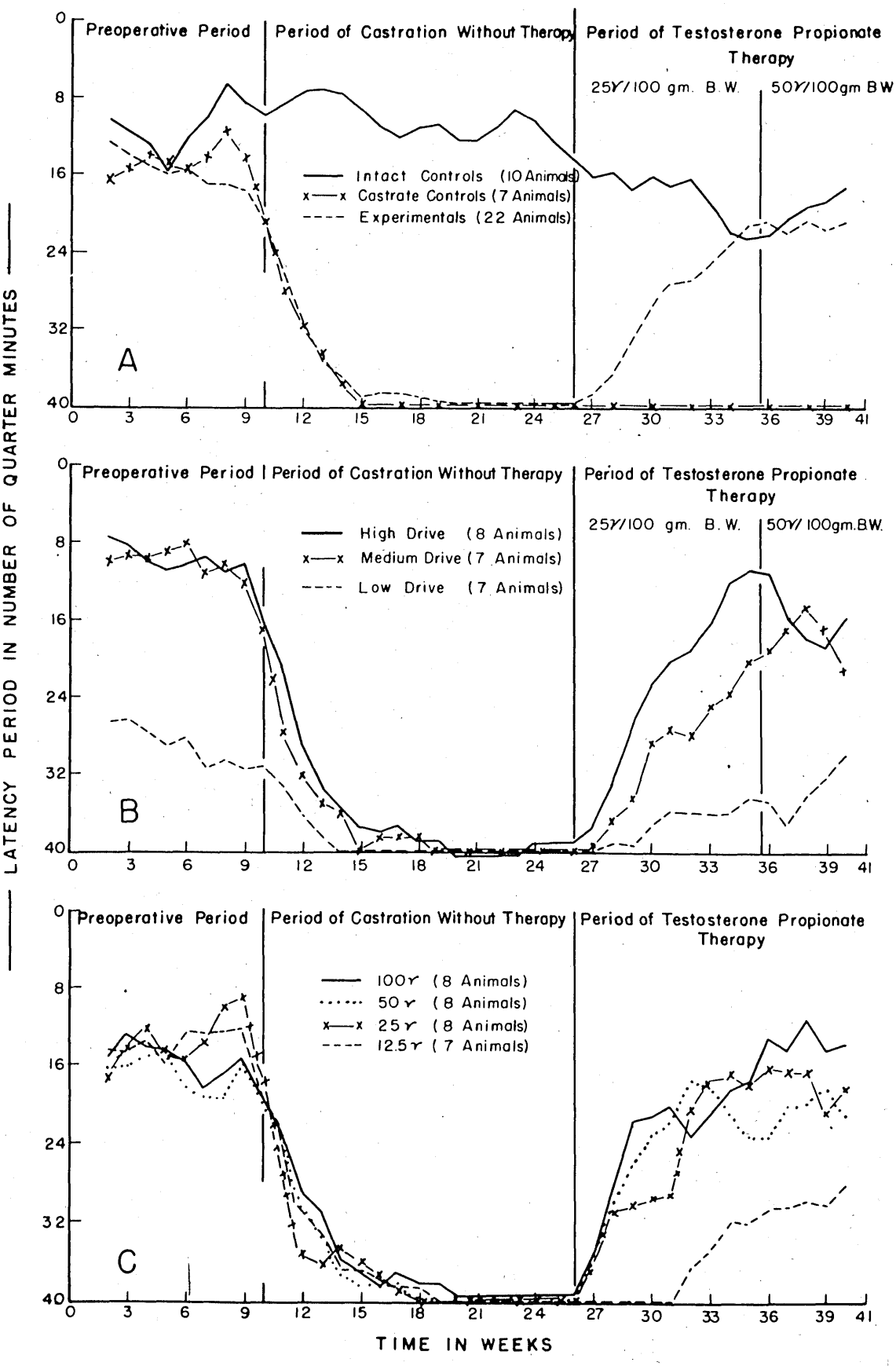
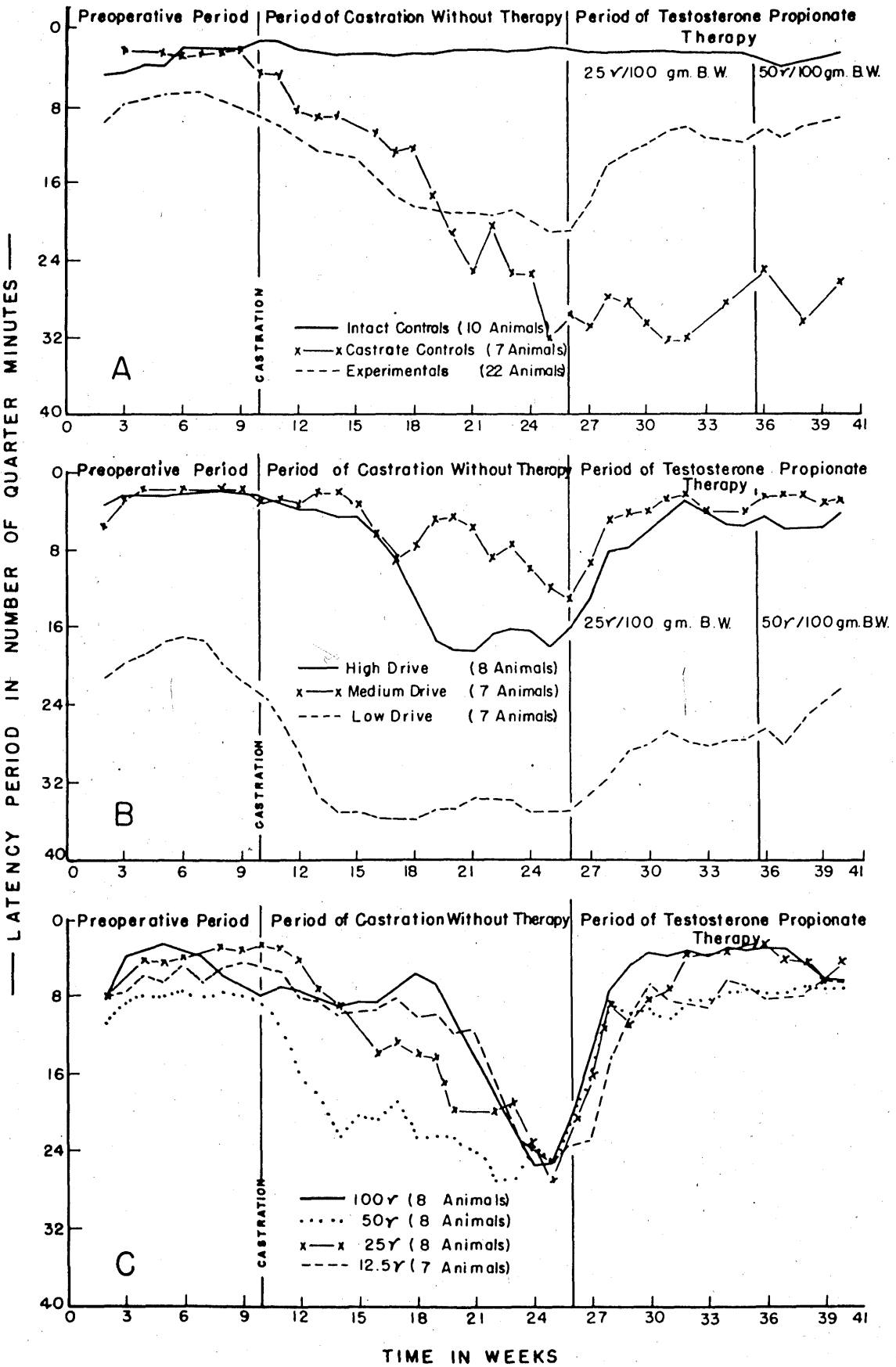

Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
25γ/100 gm. B.W.
50γ/100gm BW
Intact Controls (10 Animals)
Castrate Controls (7 Animals)
Experimentals (22 Animals)
A
High Drive (8 Animals)
Medium Drive (7 Animals)
Low Drive (7 Animals)
B
100γ (8 Animals)
50γ (8 Animals)
25γ (8 Animals)
12.5γ (7 Animals)
C
LATENCY PERIOD IN NUMBER OF QUARTER MINUTES
TIME IN WEEKS

Figure 8. Time required for male guinea pigs to achieve first mounting before and after castration and following androgen therapy.

a) Intact controls, castrate controls, and castrates given 25✓ followed by 50✓ testosterone propionate.

b) Castrates given 25✓ followed by 50✓ testosterone propionate, divided into high, medium, and low drive groups.

c) Castrates given 12.5, 25, 50, and 100✓ testosterone propionate.


Preoperative Period
Period of Castration Without Therapy
Period of Testosterone Propionate Therapy
25 γ/100 gm. B.W.
50 γ/100 gm. B.W.
CASTRATION
Intact Controls (10 Animals)
x—x Castrate Controls (7 Animals)
Experimentals (22 Animals)
A
High Drive (8 Animals)
x—x Medium Drive (7 Animals)
Low Drive (7 Animals)
B
100 γ (8 Animals)
50 γ (8 Animals)
25 γ (8 Animals)
12.5 γ (7 Animals)
C
— LATENCY PERIOD IN NUMBER OF QUARTER MINUTES —
TIME IN WEEKS

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