The Association Between Brain Size and Maze

Ability in the White Rat

By

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PUBLICATIONS

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Acknowledgment

It will be apparent to the most casual reader that the findings which are reported in this paper are the direct outcome of Dr. R. C. Tryon's investigation of the inheritance of maze ability. Rather than thank Dr. Tryon for what is obviously his, the writer wishes but to express his appreciation of the cooperation which has been characteristic of Dr. Tryon throughout the entire experiment.

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SECTION 1.

INTRODUCTION

The experiments to be reported in this thesis were the result of any hypothesis formulated by Dr. N. W. Shock of the Department of Physiology at this University, and by the writer, with regard to the nature of such differences as might exist between the bright and dull strains of animals developed by R. C. Tryon. In the course of an experiment on the inheritance of maze ability in the rat, Tryon (74) has run twelve generations of animals on a self-recording 17-unit maze, described by Tolman, Tryon, and Jeffress (70). The parental generation was composed of 142 animals from heterogeneous stocks maintained by the Department of Psychology, and the Department of Anatomy, at this University. These animals, after receiving preliminary training, were given one trial per day for a period of 20 days on the maze. The scores for each animal were the errors made from days 2 to 19, and ranged from 11 to 198 errors. Insofar as possible, animals from the extremes of the distribution were selected as parents for the first filial generation. When these animals, known as the F_1 generation, were run, the mean score of the offspring of superior parents was slightly less than the score of the offspring of inferior parents.

A similar selection from the extremes of the distribution of bright and dull animals was continued for each succeeding generation. In order to maintain the continuity of the lines it was necessary to select animals which were healthy and fertile, in the case of both bright and dull strains. The probable fertility of an animal was judged by the number of litter mates in his litter, and by the number of litters and of offspring produced in other mating of his parents. The most important criterion for selection, however, was the maze score.

Our hypothesis specifically concerned the nature and magnitude of such anatomical or physiological differences as might be found between the bright and dull strains. According to current theories regarding the nature of the maze-learning function, maze ability might be determined largely by either differences in the peripheral nerves, sense organs and specific projection areas, or largely by differences in the whole brain. Hunter (34,35) emphasizes the importance of multiple sensory factors, and feels that the maze habit is localized in definite projection areas. On the other hand, Tryon (78), Lashley (36,37), and more recently, Honzik (31,32), have presented experimental data in support of the theory that the maze habit involves large areas of cortical tissue which function in a more or less integrated fashion. Our investigation tended to follow the latter interpretation, insofar as our

experimental studies were confined to anatomical and phy-
siological aspects of the whole brain. It should be point-
ed out, however, that the findings to be presented in this
thesis do not constitute a critical test of the truth of
either type of explanation.

Another aspect of current psychological theory was
of some importance, in the determination of our procedure.
Current opinion is divided into two schools with regard
to multiple factors as opposed to general factors as de-
terminers of ability. According to strict multiple factor
theory, maze ability might be the result of a very large
number of specific traits. In the case of the strains
developed by Tryon, it might be expected that bright ani-
mals were superior to normal or dull animals by virtue of
possessing superiority in a great many minor characteris-
tics of their nervous systems. If this were the case one
might expect to find, in the case of bright animals, in-
numerable minor superiorities. Only in the event that
these innumerable minor differences additively combined to
form a major difference would we expect to find such a
major difference.

As opposed to the multiple factor theory, Spearman
(62) has long advocated a general theory of ability.
According to this theory, all individuals differ in learn-
ing or intellectual ability by virtue of possessing varying
amounts of general ability or G. In the case of each func-
tion the individual's ability is the result of his g, endow-

ment plus varying amounts of specific abilities. Spearman has, however, never given evidence with regard to the anatomical or physiological nature of $\underline{G}$, except in such vague terms as "intellectual energy."

It should be emphasized that our hypothesis was not dependent upon either a multiple factor or a general theory of ability. We postulated, however, that such differences as might exist between the nervous systems of the bright and dull animals, would exist in magnitude comparable to the difference between the maze scores of bright and dull animals. If an anatomical characteristic related to maze ability differed quantitatively between the two strains, we expected the difference to be quite marked. Whether or not this difference was due to the additive effect of numerous minor difference, was of little immediate concern.

Our preliminary procedure was thus greatly simplified. We had but to compare the brains of bright and dull animals for gross differences. If no gross differences were found in the case of any single anatomical or physiological trait, that trait was eliminated from consideration. Dr. Shock made a number of chemical analyses of brains from bright and dull animals. The results of these analyses are not yet ready for presentation. The writer confined himself to the investigation of anatomical features of the brains.

The literature was particularly barren of suggestions in this regard. As is presented elsewhere in this thesis (Section II) the investigations of brain size in relation to intelligence in the human species have found no large corre-

lation between cranial or brain measurements and intellectual ability.

Two investigators have studied the relationship between maze ability and brain size in animals. The results of Shirley (59) were definitely negative (cf. Section IV). Bassett (5) compared the maze ability of a strain of rats having small brains with animals from the Wistar colony having brains of average size, and found that the Wistar animals were somewhat superior. Paterson (46), however, showed that Bassett's results did not demonstrate statistically significant differences between the two strains.

Consequently we turned to other possibilities in search of anatomical correlates of ability. The work of Hindzé (26,27,28,29) on the vascularity of the brains of superior persons seemed suggestive. With the cooperation of Dr. Alexis Koneff and Miss Yvonne Champreux, of the Department of Anatomy, a technique was developed for staining the vascular tree of the pia mater. In a few cases the pia mater was removed but it was later deemed advisable to leave it on the brains. The brains of ten dull and ten bright animals were prepared in this manner. The complexity of the vascular tree precluded direct measurement of vascularity, so the psychological method of ratings was employed. Five observers were requested to arrange the brains in order of complexity of vascular structure. There was considerable agreement among the observers with

regard to rank order of complexity, but the ratings did not seem to be at all related to whether the brains were from bright or dull animals.

The brains of five brights and five dulls were then sectioned and stained according to a technique described by Sugita (66). Thickness of cortex was measured at a number of comparable loci, but no differences appeared between the bright and dull animals. Complete serial sections were not studied in detail, but a cursory examination of them revealed no striking differences.

A few crude measurements were then taken on the brains of several bright and dull animals. The bright animals had consistently larger brains. It seemed advisable to add brain weight to the measurements, so 22 animals from the dull strain and 26 animals from the bright strain were studied. The animals of each group were about equally divided as to sex. The average brain weight of the dull animals was 1.45 grams, with a standard deviation of $\pm$. 099, while the average brain weight of the bright animals was 1.71, with a standard deviation of $\pm$.089. The critical ratio of the difference, .26 grams, was 3.37, indicating that the two averages were significantly different.

Before definite conclusions could be drawn with regard to the association between maze ability and brain size a number of factors had to be considered. A large portion of this thesis is concerned with a description of methods

used in measuring and controlling these factors. It
might be well, however, to indicate the general nature
of the factors in question.

1. Gross Body Size. We wished to learn whether
the bright animals were simply large animals with propor-
tionally large brains, or whether their brains were large
irrespective of body weight. In order to learn this it
was necessary to have not only body weight, but several
indices of skeletal size.

2. Technique of Dissection and Measurement. It
was necessary to develop a technique which would enable us
to obtain accurate and reliable measurements of brain size.
Fortunately Sugita (65) had worked out such methods in
considerable detail. It was possible for us to make several
improvements on his technique, particularly with regard to
the problem of ascertaining the reliability of measurements.

3. Normal Controls. We wished to learn if both bright
and dull strains differed from an unselected group of normal
colony rats in brain size. It might have been possible, for
example, that bright animals, had brains which were larger
than unselected animals, while dull animals did not differ
from unselected animals in brain size. In order to invest-
igate such possibilities it was necessary to make anatomical
measurements on a large number of unselected animals.

4. Concomitant Genetic Effect. It would be impossible
to conclude, from data regarding the brains of bright and
dull animals, anything regarding the relationships which
might exist between brain size and maze ability in normal

animals. It was thus necessary for us to run our un-
selected normal animals on a maze which might adequately
measure individual differences in maze ability, and to
correlate maze scores with anatomical measures.

5. Age and Sex. In our preliminary studies we did
not take pains to have groups which were comparable with
regard to age, nor did we separate sexes. These data, of
course, were available and were controlled in the subsequent
groups. Under ideal conditions it would have been desirable
to restrict the animals used to a narrow age range. This
was done in the case of the unselected normal animals.
It was necessary, however, to use bright and dull animals
of various ages. About half of Tryon's animals were de-
livered to the writer upon completion of the maze schedule.
Other animals were not run on the maze, and were delivered
to the writer at ages varying from 90 to 120 days. Certain
aspects of the statistical treatment of the data were de-
signed to control the factor of age.

Sections III. and IV. are devoted to a detailed de-
scription of the methods which were used in investigating
and controlling the above factors. Before these methods
are presented, however, it might be desirable to review the
literature which is related to the general problem of the
association between anatomical features of the brain and
ability. This is done in the following section.

SECTION II.

A History of Experimental Investigations of
the Association between Intellectual Traits
and Features of the Brain or Cranium

The problem of discovering anatomical correlates or determiners of intelligence has intrigued many of the most notable anatomists, biometricians, anthropologists, and psychologists of the last hundred years. Among those who have conducted such research are Tiedemann, Broca, Galton, Binet and Pearson. Recently Pearl, Donaldson and Hull have attempted to contribute to our knowledge of these relationships.

The great bulk of the literature is devoted to the description of investigations of features of the brain and cranium, as related to intellectual ability or achievement, in the human species. Only two studies have been done with animals. Since our problem has obvious implications with regard to the nature of brain function irrespective of species, it seemed desirable to present the findings of the studies on human beings in some detail. There is, moreover, no comprehensive review of the literature of this subject.

We will first consider the studies which have been done on the human brain. Several kinds of approach have been made to this problem. The earliest investigators were concerned largely with gross brain size and the possible relation between brain size and intellectual achievement. It was not long, however, before anatomists began to search for other

features which might differentiate the brains of inferior, normal and superior persons. These studies are so intimately bound up with the investigations of brain size that it seems desirable to consider them together.

Shortly after 1900 a large number of investigators used cranial measurements of living persons as indices of brain size. Although such measurements were not exact measures of brain size or development, the workers had the advantage of somewhat more accurate estimates of intelligence than was the case when anatomists were restricted by the necessity of using estimates of the intellectual ability of persons who had died. Another advantage of cranial measurements was the feasibility of including a large number of cases of more or less homogeneous chronological age.

More recently Hindźe (26,27,28,29) has suggested the study of the vascular system of the brain and its possible relation to intellectual achievement. The vascular tree of the pia mater of several noted Russians has been compared with that of normal and retarded persons. Although Hindźe's findings have not been corroborated or disputed by other investigators, they present a novel attack upon the problem of anatomical correlates of intelligence. Since the pia mater is not usually considered a part of the brain, these studies will be considered under a separate heading.

A final discussion will consider the two animal studies which bear directly upon the present study.

Studies of the Brain.

The anthropologist Topinard (66) has reviewed the studies of the human brain up to 1885. In 1830 Sir William Hamilton

reported the weights of 61 brains in "The Anatomy of the Brain," which was published in Edinburg. Frederick Tiedemann, in 1836 wrote "Sur l'encéphale du Nègre comparé à celui de l'Europèen et celui de l' orangoutang," which was published in the Philosophical Transactions of London. Tiedemann is quoted by Bain (3) as establishing "an indisputable connection between the size of brain and the mental energy displayed by the individual man or animal." Tiedemann did this by weighing the brains of three microcephalic idiots, and finding the largest of these to weight $25\frac{3}{4}$ ounces.

By 1885 Topinard (71) was able to report that 10,182 brains had been weighed by 35 investigators, R. Wagner (Vorstudien zu einer Wissenschaftliche Morphologie und Physiologie des Menschenliches Gehirns," Göttingen, 1860) started the first collection of brains of superior persons, and made the first attempt to discover relationships between complexity of fissures and intelligence. Topinard (72) states that Wagner had small faith in brain size as a determiner of intelligence, partly because of the fact that the heaviest brain in the Göttingen collection was that of a 3-year-old hydrocephalic idiot. Donaldson (17) is authority for the statement that within Bischoff's series of 559 males there was no difference in weight between the brain of elite, ordinary men, and criminals.

Another important series of brain weighings is that of Broca (11) in 1861, who suggested that if the reports of extremely large brains of geniuses could be depended upon, it was probable that such men achieved distinction in spite of, rather than because

of their heavy brains. Twenty years later Topinard (72)
went through Broca's original clinical reports and class-
ified the cases by age, sex, and body weight. Topinard re-
ported that there seemed to be no consistent association be-
tween brain size and ability in Broca's cases.

The only extensive bibliography of the earliest lit-
erature is that of Topinard (71), and many of his citations
are so incomplete as to preclude consultation of the original
papers. Such titles as are given suggest that much of the
great mass of investigation which was carried on prior to
1885 was done with the notion that somehow such studies
might lead to anatomical correlates of ability. It is in-
dicative of the interest in the subject that in the second
volume of the memoirs of the Societe d'Anthropologie de Paris,
published in 1861, over half of the papers and almost all of
the discussions are devoted to the topic of brain studies.
This volume contains Broca's (11) series of brain measurements,
as well as his first attempt to estimate brain size from
skull measurements. (12)

The finding of Broca, Wagner, Topinard (after Broca),
and Bischoff ("Das Hirngewicht des Menschen," Bonn, 1880) are
almost universally combined in some form for the purpose of
comparison with individual brains. There is but one large-
scale investigation of the size of the normal human brain
after 1885 which has been used as a standard of normality,--
that of Marchand (41,42) in 1902. Marchand pointed out clear-
ly the technical and interpretative pitfalls in brain studies,

and attempted to overcome them. His work was done at Marburg
between 1885 and 1900, and comprises 1173 cases. In discussing
the factor of age he states that the occurrence of a war may
result in a different distribution of "normal" brain weights,
as a result of the large number of young men who come to hos-
pitals during such a period. In discussing the heavy brains of
geniuses reported by sporadic investigators, he states, "Derartige
Gehirne können dabei gut, ja sogar sehr gut funktionieren (Cuvier,
Turgenieff), ohne dass sie einen Schluss auf das Verhältnis
zwischen Gehirngewicht und Geisteshaltigkeit im allgemeinen
zulassen, denn in anderen Fällen sind die Funktionen solcher
übergrossen Gehirne keineswegs hervorragend."

The elaborate monograph of Spitzka (63) recites the inter-
esting history of various societies organized for the purpose
of accumulating large collections of the "brains of the élite."
Their method was patterned after that in the bequest of Tiede-
mann, who said in his will, "Den Körper lasst öffnen; es
gewährt diess vielleicht enigen Nutzen. Finded sich ein Theil,
der den Aerzten Belehrung gewähren kann, so nehme ihn in eine
anatomische Sammlung auf."

Members of the societies signed mutual wills regarding
the disposal of their respective brains. The first of these
societies was the Societé d'Antopsie de Paris, which was
founded in 1881, as a subsidiary group withing the Societé
d'Anthropolgie. It was followed in 1889 by the American An-
thropometric Society, and shortly after by the Cornell Brain
Association, under the leadership of Professor Burt G. Wilder.

As the "brains of the élite" began to accumulate, the
literature became flooded with scores of extremely detailed
descriptions of the brains of famous men. Well over one-
hundred investigators are cited by Spitzka, and their findings
in the case of 150 brains are summarized. It should be noted
that this summary of necessity consisted of a description of
each brain treated as an individual, and the only data capable
of quantitative comparison was brain weight.

As time went on and the early supposition with regard
to the intimate relationship between brain size and ability
was borne out only in very slight degree, investigators began
to look for other indices of ability in the brains which com-
prised their collections. Elaborate methods were devised for
measuring depths of fissures, total area of the cortex, and the
relative sizes of various lobes. One of these methods is de-
scribed by Donaldson (16,19), who also refers to many of the
other methods. Enthusiasm at Cornell began to wane after the
autopsy of the noted mathematician and philosopher Chauncy
Wright, of who brain Wilder says, "The simplicity of the fiss-
ures, and the width and flatness of the gyres are paralleled
in the Cornell collection only in the much smaller brain of an
unknown mulatto. Some approach to this condition occurs in
Ruloff, a murderer, and perhaps in a German shown by Wagner."

We have already mentioned that the weight standards for
"normal" brains were furnished by Wagner, Broca, Bischoff and
Marchand. It is reasonable to assume that each of these men
established uniform conditions for the preparation of brains
for weighing, and uniform landmarks for determining the point
at which the spinal cord was severed. It is possible that

the same conditions were adhered to by all four investigators. We have, however, no assurance that these same conditions were not adhered to in the case of the 150 brains reported by Spitzka (63). Since scores of anatomists from all parts of the world contributed to the literature cited by Spitzka, it would be a most reasonable assumption that uniform conditions were not adhered to.

Some idea of the factors affecting variability in preparation may be obtained from the study of the brain of H. L. F. von Helmholtz, by Hansemann (24,25).

The brain as removed from the cranium weighed 1,700 grams. This would place Helmholtz in the ninety-third percentile of Spitzka's list of the elite. The blood coagulum was then removed, which reduced the weight to 1,540 grams (seventy-third percentile). So much blood still remained on the brain that Hansemann estimated that the "real" weight of the brain was from 1,420 to 1,440 grams (forty-fourth percentile). This single test of the reliability of measurement might well excite our suspicion of the investigators who report no such ambiguities of measurement.

Spitzka's graphic representation of the difference between normal brains and brains of eminent men is open to serious criticism. The brains of 100 élite are classified according to weight, and are displayed in the form of a histogram. The Bishoff-Marchand-Broca-Topinard series of 1,334 cases is distributed in similar class intervals and reduced in the ratio of 100/1334. This distribution in the form of a second histogram is then superimposed on the élite distribution, with the

result that, for every class interval in the heavier brackets, there is a proportionally greater number of élite brains, while in each light class there are more brains of normal men. It should be noted that a few microcephalic brains among the "normal" series would be sufficient to shift the entire series in the direction desired. The difference between the means of the two distributions differ by but 75 grams, the average weight of élite brains being 1,473 grams.

An interesting example of the personal equation in brain measurement is brought out in two recent publications of Henry Donaldson (19, 20). The first of these publications reports detailed measurements of the brains of G. Stanley Hall, Sir William Osler, and Edward S. Morse. The actual measurements were made by Dr. Myrtelle M. Canavan, according to a technique worked out by Donaldson. The frontal and occipital areas of the cortexes of all three scholars were more extensive than those found by Dr. Canavan (13) in the case of three other brains measured by her.

These findings suggested the necessity for a large control group, so Donaldson (20) supervised the measurement of brains of 30 white males and 27 negro males. The actual measurement, in this case, was done by Dr. Addison. When the results for the normal controls were compared with those previously presented by Donaldson, it was apparent that the scholars had a marked deficiency in parietal area, and an excess of temporal area. In order to assure himself that the differences found

were real, Donaldson had Dr. Addison remeasure the brains
previously measured by Canavan. The proportional distri-
bution of cortical areas in the case of the scholars was
identical with that found in the case of the white and negro
controls. The differences found had apparently been due to
differences in technique, despite the fact that the work, in
each case, was done with the same system and was supervised
by the same person.

Studies of the Size and Shape of the Cranium.

The latter half of the nineteenth century produced enough
investigations of cranial measurements and their relation to
intelligence for A. Binet (8) to write an extensive review
of the subject in 1898. This review contains a full reprint
of P. Broca's privately-printed memoire, "De l'influence de
l'education sur la volume et la forme de la tete." The date
of original publication of Broca's study is not given. Broca
had found small differences between averages of skull measure-
ments taken on normal and inferior adults, and had inferred
that the process of acquiring knowledge tended to increase the
size of the brain.

At the meetings of the Anthropological Institute on April
24, 1888, a paper was read by Dr. A. Venn describing preliminary
results from anthropometric measurements taken on Cambridge
students. There is no record of the publication of this paper.

On the following day Francis Galton (22,23,82), who was then president of the Institute, commented on Dr. Venn's study, and presented a rearrangement of the Cambridge data. Measurements of height, width and length of skull were multiplied together to give an approximate index of the cranial capacity of the men. Galton concluded, "Accepting these curves as a true statement of the case--and they are beyond doubt an approximately true statement--we find that a 'high honor' man possesses at the age of nineteen a distinctly larger brain than a 'poll' man in the proportion of 241 to 230.5, or one that is almost 5 per cent larger. By the end of his college career, the brain of the 'high honor' man has increased from 241 to 249, that is, by 3 per cent of its size, while the brain of the 'poll' man has increased from 230.5 to 244.5 or 6 per cent."

Binet's investigations of the problem, covering a period from 1900 to 1910, was dominated by an interest in establishing limiting boundaries (frontières anthropométriques) for the diagnosis of feeblemindedness in children. Following much the same statistical procedure as was later used by him in his intelligence testing, he established norms for stature, length and breadth of head, and various indices derived from these measurements, for children from the age of 6 to 18. (9). These norms were amplified in 1910 to include the sum of five cranial measurements (10). He suggested that a retardation

of six years or more in cranial development was significant
evidence of abnormality, while a retardation of from three
to six years, if confirmed by inferior scholarship or un-
satisfactory scores on psychological examinations would be
valuable diagnostic evidence. Investigations of cephalic
measures of feebleminded children by Simon (60) confirmed
his opinion regarding the diagnostic value of such measures.

Contemporary with the French investigations were studies
by German, English and American investigators. The German
and American investigations were similar in method and con-
clusion to those of the followers of Binet. The general
procedure was to divide a sample of children into two or more
groups on the basis of estimates of ability, and compare av-
erages of cranial measurements for the groups. Investigators,
as a rule, established their own anthropometric landmarks and
their own classification of ability. The results are thus
not comparable but in almost every case point in the same
direction as the French studies. Rose (57) compared 884
"sitzengebliebenen" children with 621 "weiterkommenden" chil-
dren and found a difference of .17 cm. in cranial length and
.04 cm. in width. Loewenfeld and Eyerich (40) collected
data on 935 Bavarian soldiers who were grouped into four classes
by their superiors on the basis of ratings. Measurements of
head length and head diameter were then taken, and the average
measurements for the four groups were in the same order as the

ratings. Bayerthal (7) reported the measurement of 10,000 heads, but subdivided his subjects into so many groups that his figures are meaningless.

Two American studies resulted in the assembling of a vast amount of data concerning relationships between morphological factors and intelligence. Porter (53,54) supervised the measurement of 33,500 St. Louis school children. Most of these data were never analyzed, but one summary of 1,067 boys aged 10 is available. These boys were classified by school grade, and head width was found to increase according as the boys were in the first, second, third or fourth grade. The average head width for first-grade 10-year olds was 145.86 mm, while fourth-graders averaged 147.21 mm.

The second extensive American study was that of McDonald (43), who made a number of anthropometric and "psycho-physical" measurements on 5,000 Washington school children. He took the average head circumference at various ages from 6 to 18, and se-cured teachers' ratings as to whether the children were bright, average or dull. For most age groups there was about 1/6 inch difference in head circumference between bright and dull pupils. As is the case with most of the other American, French and German studies, no measures of variability are reported. McDonald concludes, "As circumference of head increases, mental ability increases."

In contrast to the investigations reported above, most of

the English studies after Galton were characterized by an
attempt to arrive at more accurate quantification and analysis
of experimental data. Lee (38) devised formulae for arriv-
ing at an approximation of the exact size of the brain from
cranial measurements, and reports a negligible relationship
between estimated cranial capacity and estimated intellectual
capacity in the case of 60 men and 30 women.

Pearson (50) using four-fold tables, correlated breadth
of head with scholastic ability in the case of 524 Cambridge
students, and found the r to be +.0843 + .024. He averaged
correlations for 5,000 pupils of various school grades and
for Cambridge grades, and concluded that the mean r of both
breadth and length of head was of the order of +.065. He
states, "For practical purposes it seems impossible either
in the case of exceptionally able men or in the bulk of the
population to pass any judgment from size of head to ability
or vice versa."

More elaborate analysis of the data on 5,000 school chil-
dren and 1,000 Cambridge undergraduates is presented by Pearson
in a later paper (51). The Cambridge students were classified
into four groups on the basis of scholarship, and the school
children were classified into six groups. Correlations with
width of head ranged from +.097 to +.113, with N's for all
correlations between 1,000 and 2,100. Stature and head length,
however, correlated to the extent of +.28, and stature and head

width correlated to the extent of +.15, in the case of the
Cambridge students.

Pearl (48,49) applied the method of mean square con-
tingency to the data of Loewenfeld and Eyerich (40) on 935
Bavarian soldiers rated into four classes by their superiors,
and found an r of +.14 ± .04 between head circumference and in-
telligence. His conclusions from this study are an extremely
appropriate evaluation of the meaning of all the findings in
this field. He says, "If further statistics (of which there
is great need) should show that generally there is a just
sensible positive correlation between these characters, the
correct interpretation of the fact would, it seems to me,
probably be physiologic rather than psychologic. That is to
say, the association between vigor in growth processes (lead-
ing to a well-developed body) and vigor in mental processes
would most probably be the result of the action of good con-
ditions of nurture. Other things being equal groups of men
with well-nourished bodies are on the average likely to be
more able intellectually than groups in which bad conditions
of nutrition prevail. Such an interpretation of the facts
seems at present to have much better justification than any
which in effect implies that a big brain connotes per se an
able mind. Rightly interpretated the facts regarding the
correlation between size of head and intelligence, seem to me,
simply to furnish, so far as they go, direct statistical evi-
dence in favor of the adage: mens sana in corpore sano."

More recently Porteus and Berry (54) have presented
data based on head measurements taken on 10,000 school chil-
dren and university students in Australia. Cranial capacity
was estimated by means of a formula devised by Lee (38) which
makes use of length, width and height of skull. Ages ranged
from 7 to 30. Percentile norms for cranial capacity were es-
tablished for several age groups. Mental tests indicated that
over half the lowest 10 per cent in head size were subnormal
in intelligence. No correlational analyses are presented in
this paper. In a later publication Porteus and Babcock (55)
criticize the interpretation of Karl Pearson that head measure-
ments have but a very slight relation to intelligence. They
insist that, had Pearson used a more adequate index of cranial
capacity than single measurements, much larger correlations
might have been found. They state, "Investigations by Porteus
show that while the correlation is not high it is probably
about the order of +.3, which is much larger than Pearson found
with single measurements." Details of Porteus' investigation,
in which correlations of +.3 were found, have not been published.

One of the most interesting of the later studies is that
of Murdock and Sullivan (45) on 600 pupils of the Punahou
school in Hawaii. The subjects range in age from 6 to 16, but
this factor was controlled by expressing anthropometric data in
terms of deviations from norms for the several age groups. The
subjects were all of American or northern European stock. Stan-
dard intelligence tests were used, and a correlation of +22 ±.03

was found between I.Q. and head diameter. Weight was found to

correlate with I.Q. to the extent of +.16, and stature to the

extent of +.14, the probable error in each case being ±.03.

Still another study of the relation of cranial measurements to

intelligence was that of Reed and Mulligan (56), who correlated

scholastic performance of 449 Aberdeen University students with

head diameters. The r found was +.08 ±.03. When age and stature

were held constant by the method of partial correlation, the r

fell to +.07. Sommerville (61) correlated several head di-

mensions with intelligence test scores of Columbia students.

His r's in the case of individual measurements did not exceed

+.10. When indices composed of several head measurements were

used, the correlations with intelligence did not exceed +.11.

Before we consider the next study it might be well to re-

view the findings of the various investigators who have studied

the relation between head measurements and mental ability.

Most of the studies have used the method of group differences

between averages of various head measurements and intelligence.

A number of more recent studies have employed correlation tech-

niques, and have rarely reported r's exceeding +.11. The highest

correlation supported by experimental details was that of +.22

by Murdoch and Sullivan, between head diameter and intelligence

test scores. It would thus seem reasonable to conclude that

while there is a definite relationship between cranial capacity

as indicated by skull measurements, this relationship is certair-

ly of a very low order.

It seems worthwhile, therefore, in view of the imposing mass of evidence which has been collected throughout the past fifty years, to give special consideration to a study which has recently been reported by Hull (33). Data were taken from the A.B. thesis of Elsie Sherman. These data consisted of a large number of cranial measurements taken on 78 freshmen students of engineering at the University of Wisconsin. The measurements were correlated with grades received by the men. Hull applied a multiple regression technique to the data and found that a combination of three head measurements and two facial angles correlated with scholarship to the extent of +.50. Hull points out that such a correlation is of the order of magnitude usually found between scholarship and intelligence test scores, and thus indicates the possibility that some sort of cranial index might be valuable in the prognosis of ability.

Since the correlation of +.50 seemed completely out of line with the other findings regarding such associations, it seemed advisable to consult the original manuscript (58) from which Hull took his data for the application of the multiple regression technique. Sherman had fortunately been most explicit with regard to the details of her experiment. The subjects were of German, Chinese, Norwegian, Russian, Bohemian, and American stock, and ranged in age from 16 to 34. Inter-

correlations were made between grades in 6 courses and 17 anthropometric measures taken with a radiometer devised by Hull. The largest of her correlations was +.3961 $\pm$.65, and was between length of auricular axis and semester grades in a laboratory course in forge known as Shop I. This same measurement correlated with grades in Shop 2 (machine shop) to the extent of -.04. There were a number of similar irregularities in Sherman's correlations which suggested the possibility that systematic factors related to the peculiarities of her population were exerting an undue influence on her results.

There is, of course, no reason for doubting the validity of Sherman's results nor of Hull's analysis of them, as applied to the particular sample with which she was dealing. It is the opinion of the writer that the data of Sherman are of little value in predicting relationships in a universe of population. We suggest that Hull's conclusion with regard to the possibility of predicting ability from head measurements is, to say the least, somewhat premature.

In a recent critical summary of the literature related to the problem of the association of cranial measurements with intelligence, Paterson (44) concludes, "A critical review of available evidence tends to dissipate claims put forth in behalf of an intimate relation between head size and intelligence. Although inadequate statistical methods characterize most of the research studies and although no satisfactory standardized

method of measuring head size is adopted in them, it can be said with considerable assurance that whatever positive correlation exists must be of a low order."

The Vascular System of the Brain.

Within the last decade the Russian anatomist Hindzé (26, 27, 28, 29) has suggested a new approach to the problem of anatomical correlates of intelligence. In one publication (29) he shows sections from the vascular tree of the pia mater of the psychiatrist A. Bernstein and of the mathematician P. Nekrasoff, and compares them with the vascular tree of a bandit and an unknown hospital patient. Differences in complexity are very apparent. Donaldson (20) has suggested that this approach may be extremely significant. It is important to note, however, that Hindzé has reported specifically on less than ten cases, and has developed no quantitative method for estimating the degree of complexity of the vascular system of the pia mater. There is, however, the possibility that Hindzé has finally hit upon the touchstone for which anatomists have been searching for the last hundred years.

Before accepting his results wholeheartedly one should remember that in 1864 (3) the presence of an intimate association between brain size and intelligence in the human species was considered to be definitely established. Only when other investigators, using adequate measurements and large numbers of cases,

have reported similar findings may we feel certain that the complexity of vascular system of the pia mater is an important correlate of intellectual ability.

Animal Experiments

In the entire literature of animal investigations there are but two studies which bear upon the problem of the relation of brain size to maze ability in the rat. The first of these was the study of Bassett (5), who investigated the maze-learning ability of a strain of rats having less than average brain weight. In the course of a study of inbreeding at the Wistar Institute of Anatomy a progressive decrease in brain weight was observed for four generations.

The animals of the fourth generation seemed to lack general vitality, and their average brain weight was about six and one-half per cent below that of normal animals. Inbreeding was continued for six more generations, but the progressive decrease in brain weight did not continue.

At the suggestion of Henry Donaldson, Bassett undertook to determine whether the decrease in brain weight observed in the case of these animals might be accompanied by a similar decrease in ability to form habits. Thirty-one males and thirty-one females from the inbred strain were compared with a similar number of normal controls on the Watson circular maze, and on learning and relearning of the inclined plane box. Bassett con-

cluded, "In all these experiments the strain of rats of lesser
relative brain weight learned less well, on the average, than
the normal control series. In the maze and inclined plane ex-
periments the average number of days required to learn and re-
learn, and the time of absolute retention, was far greater in
the case of the inbred rats than in that of the normal control
series. In the maze experiment, two inbreds and one control
failed to learn; two inbreds failed to relearn. In the in-
clined plane experiment, eleven inbreds and two controls
failed to learn."

The data presented by Bassett is in such a form as to
render it impossible to learn anything concerning the vari-
ability within his normal and control groups. Time and days
to learn are the only criteria of learning used. The time
curves for his experimental and control groups on the maze
differ but slightly from each other. The average number of
days required for the inbred animals to learn was 36.62, while
the average number of days for the control group was 24.62.

Paterson (46) attempted to analyze Bassett's original
data for statistical significance. When four particularly
poor inbred rats and one poor control rat were excluded, the
distributions of learning scores for the two groups were almost
identical. He also determined the median number of days re-
quired for the inbred and control animals to learn the maze.
The difference between these medians was but five days. The
probable error of the median of the inbred rats was 11 days,

while the probable error for the median of the control animals
was 8.5 days. It is obvious that the difference of five days
between the two medians is not significant.

The other experiment on the relation of maze ability to
brain size was that of Mary Shirley (59). Twenty-nine male
rats were trained on an 8-blind Lashley maze, the odd-even
error reliability of which was +.80 ±.048. The odd-even time
reliability was +.95 ±.013. The number of errors required to
reach a criterion of three successive errorless runs correlated
with total brain weight to the extent of +.29 ±.129. Maze
time and brain weight correlated +.19 ±.136. The correlation
between number of trials required to reach the criterion and
total brain weight was +.13 ±.139. The correlation between
maze errors and per cent brain weight to body weight was
+.23 ±.134. She concludes, "The coefficients are all too low,
and their probable errors are too high to suggest any relation-
ship between brain weight and maze ability. The only relation-
ship which is at all consistent is that between maze errors and
brain weight. Whether relative or absolute weight is used, the
correlations between brain weight and errors are above +.20.
The relationship between maze learning and brain weight, insofar
as one exists at all, is, then, the heavier his brain, the more
rat blunders. This is not a relationship to be expected, or one
in which dependence can be put. Although this minor study can-
not be taken very seriously, its results are in agreement with
the general mass of evidence which has been accumulating since

the beginnings of phrenology, which can be summed up by saying
that measures of the gross structure of the brain are very poor
indicators of the excellency of its function."

Summary

Few problems have so engrossed the attention of biologi-
cal scientists during the past hundred years as the quest for
anatomical determiners of mental ability. Hundreds of investi-
gators have examined the human brain for a neurological key to
the explanation of individual differences in intelligence.
Many hypotheses have been formed and discarded. The intro-
duction of correlational methods shortly before the turn of the
century served to dispel much of the hope which had survived up
to that time. Results from two animal experiments were equally
inconclusive.

A few tentative conclusions, however, can be drawn from
the mass of data which has accumulated. It is not likely that
complexity of convolutions, depth of sulci or general config-
uration of the brain are related to mental ability. There is
some evidence of slight differences in gross brain size as be-
tween superior, normal and inferior persons. There is no good
evidence that these differences are more than a reflection of
differences in body size. The more dependable correlational
studies of cranial and mental measurements have indicated that
the maximal r in normal populations is between +.10 and +.15.

Few investigators have taken the precaution to correlate their mental measurements with measurements of body size. When this has been done, the <u>r</u> is found to be positive, but somewhat smaller than the correlations with cranial measurements.

On the basis of the experimental data available, it would seem likely that such relationships as have been conclusively demonstrated between intelligence and features of the brain or cranium are of a very low order, and lend little support to the theory that excellence in mental function is closely related to the mass of brain tissue available.

SECTION III.

The Development of Methods Designed to Permit Accurate and Reliable Anatomical Measurements of the Brain and Skeleton of the Rat

The most careful investigation of the size and growth of the rat brain is that of Sugita (65,67). The anatomical methods of the present study followed, in general outline, the work of Sugita. We deemed it advisable, however, to differ from his procedure with regard to several details of his brain preparation. Sugita was principally interested in the size and shape of the whole brain, and in the effect of growth on these factors. Consequently he took pains to include the whole brain in his preparation. The writer, on the other hand, was interested in individual differences between adult brains. It was thus of particular importance, in this study, to prepare brains in such a manner as to minimize the effect of preparation on measurements and weighings.

The olfactory bulbs are extremely variable from animal to animal, and are quite susceptible to damage in dissection. Since the writer was not particularly interested in this part of the brain, the olfactory bulbs were severed from the rest of the brain on a plane parallel to the transverse and vertical axes of the brain, just anterior to the anterior poles of the cerebral hemispheres.

The distal end of the paraflocculus lies within the floc-

cular fossa, and may be removed intact only by careful dissection of the fossa. Even with most careful dissection the paraflocculus may occasionally become torn from the rest of the cerebellum. In order that all brains might be comparable in this respect, the paraflocculi, which together comprise less than five per cent of the total weight of the brain, were removed.

Sugita's measurement of brain height was from the stalk of the hypophysis to the dorsal surface of the brain, and vertical to the plane on which the brain is resting. Ordinarily this measurement is also the greatest height of the brain. Since it is impossible to see the stalk of the hypophysis while the brain is resting on an horizontal plane, we disregarded this landmark, and took, in each case, the greatest height of the brain as measured from the horizontal plane upon which it rested.

In order to study accurately and in detail the association between brain weight and maze ability, it was necessary for us to have accurate and detailed information regarding other factors which might possibly be associated with brain size, such as body weight, skeletal size, age, and sex. Specifically, we wished to know, in the case of bright and dull animals, whether brain size was unique in its association with maze ability, as compared with other measures of gross anatomy.

Almost all strictly anatomical studies of the rat reported by Donaldson (18) satisfy themselves with averages of observations, and are not concerned with measures of reliability or variability. It was our purpose to learn, in the case of each measure employed, not only the variability of our sample, but

also the accuracy with which our measurements were measuring the
variables in question. This would ordinarily be determined by
correlating duplicate measurements in each case. Wherever possi-
ble this was done. Certain peculiarities of the present experi-
ment made it necessary for us to obtain our reliabilities in a
somewhat different manner, for certain variables.

In the case of brain weight, for example, the prepared speci-
mens were weighed to one-tenth of a milligram. Excepting the
possibility of a major error in weighing, the correlation between
duplicate weighings would be almost unity. There are, however,
several other factors which might reduce the accuracy of an in-
dividual determination, and which would not reduce the reliabil-
ity coefficient between duplicate weighings. The brain, in situ,
is connected directly with the olfactory lobes, and with the
spinal cord. In the process of dissection the brain was severed
from the olfactory lobes and from the spinal cord at landmarks
which are described later in this section. It is obvious that
the error involved in preparing the brains would be many times as
great as the error involved in weighing the prepared specimen.

It was therefore necessary to obtain a measure of brain size
which was independent of the landmarks used in preparing the brains.
For this purpose we selected three linear measurements similar to
those used by Sugita (65). These measurements are expressed in
the data as L (length), W (width), and H (height). The details of
measurement and the landmarks used are described later in this
section. These three measurements, H, L, and W were later multi-
plied together to give a rough measure of volume. Actually, how-

ever, this measure, which we will hereafter call M, is the volume
of a cube, bounded by the three dimensions of brain width, mean
length of cerebral hemispheres, and maximum brain height. That M
is closely related to brain weight, although entirely independent
of it in measurement, is shown by the correlation of $+.76 \pm.030$
between brain weight and M, in the case of 88 normal male animals,
age 180-200 days.

Special Problems of Gross Body Size

Probably the most inadequate measure of gross body size is
body weight. In the course of running a maze for 20 days, animals
frequently lose as much as 30 grams. Minor illness will often re-
duce the weight of an animal 50 grams in the course of a week.
Animals reduced from an unlimited supply of food to an adequate
daily ration of 15 grams, will frequently lose 50 grams in two or
three weeks. Consequently it was necessary to secure more stable
indices of body size. Three measurements were taken for this
purpose,-- length from snout to tip of tail, length from snout to
base of tail, and tibia length. A special instrument was devised
for measuring body lengths. The incisors of the anaesthetized
animal were hooked under a clamp which pinioned him to a vertical
board. A millimeter scale was attached to the board, and readings
were taken from the tip of the nose to the base of the tail, and
from the tip of the nose to the tip of the tail. Duplicate measure-
ments were taken in the case of the 50 normal males comprising

Series R[*], and the reliability of the nose-to-base measurement was
found to be +.90 ±.018, while that of the nose-to-tip was found to
be +.94 ±.011. When nose-to-base was correlated with nose-to-tip,
the r was found to be +.92 ±.015, in the case of the animals com-
prising Series R.

The other index of skeletal size chosen was the tibia. Im-
mediately after preparation of the brain for measurement and
weighing, the tibia was removed and tagged. It was later placed
in a solution of 25 per cent soap solution, 15 per cent ammonia,
and 60 per cent water, and kept at a temperature of 100° for a
period of two hours. Measurements were taken with vernier cali-
pers from the intercondyloid fossa to the tip of the medial
malleleous. Duplicate measurements were taken, and the reli-
ability was +.96 ±.007, in the case of 65 normal males.

Cranial Measurements.

Since the brains examined in the original groups revealed
such a striking difference between the bright and dull strains
of animals, it seemed worthwhile to discover whether these dif-
ferences might be reflected in the size or shape of the cranium.

Two measurements were selected which promised to give rea-
sonably accurate estimate of the length and width of the cranium.
Length was measured from the center of the coronal suture to the

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[*]Fifty unselected colony males were used for the purpose of ob-
taining reliability coefficients of anatomical variables which
were not otherwise obtained. These animals constituted series R,
and data from their measurement appears only in this Section.
The factor of age was not rigidly controlled, but the distribution
of individual scores was similar in range and variance to that of
the unselected colony males.

lambdoidal ridge, along the suture of the parietal bones. Width of the cranium was taken as the greatest width of the paired parietal bones. Measurements were taken with dividers similar to those used for brain measurements. No cranial measurements were made on the normal animals, except the Series R group, for the purpose of obtaining reliability coefficients. The findings in the case of cranial measurements are reported in Appendix I.

Details of Dissection and Measurement

Throughout the entire experiment the writer was aided by two assistants. The writer did all of the dissection and preparation for measurement. The brain was then transferred to the first assistant, who made all measurements, and who in turn, transferred the brain to the second assistant, who was responsible for weighing and bottling. The first assistant was trained personally by the writer for a period of three months before the first data presented in this thesis were collected. The second assistant was a graduate pharmacist. When bright and dull animals were worked on, neither assistant was told which animals were bright and which animals were dull. The assistants were not familiar with the numbering system used by Tryon which distinguished bright from dull strains.

Two factors made it imperative that the entire operation, from dissection to the moment at which the brain was placed in an enclosed receptacle for weighing, be conducted as rapidly as possible. Preliminary studies showed that evaporation might account for the loss of as much as 20 mg. per minute, after removal from

the cranium. Probably an even greater weight loss was caused by
fluids which ran from the surface of the brain and collected on
the glass plate under the brain. Practice on preliminary animals
made it possible to reduce the interval during which the brain
was exposed to less than one minute. Although it would have been
desirable to take duplicate measurements on all experimental prep-
arations, we felt that such a procedure would delay the weighing
of the brains for too long a time. Reliability coefficients for
brain and cranial measurements were obtained from Series R ani-
mals. The coefficients obtained were:

Cerebrum Width	+.96	±.007
Cerebrum Length	+.98	±.004
Cerebrum Height	+.96	±.007
$M = L \times H \times W$	+.97	±.005
Cerebellum Width	+.97	±.005
Cerebellum Length	+.92	±.015
Cranium Width	+.97	±.005
Cranium Length	+.96	±.007

The various steps in the procedure are outlined below:

1. Anaesthesia. The animals, in a state of 22-26 hours
hunger, were placed in a bell jar and anaesthetized with ether.
They were removed, thoroughly anaesthetized, but living, after a
period of from two to three minutes.

2. Body-Weight. The weight of the animals was taken accurate-
ly to 2 grams. As has been pointed out above, this accuracy was
far greater than diurnal, dietary, and other factors which affect
body weight. As mentioned above, there was a maximum difference
of four hours between final feeding and determination of body
weight. While this difference may have effected body weights to

the extent of two or three grams, the effect was unsystematic as between bright and dull animals. Brights and dulls were taken from their cages and prepared in random order.

3. Body Lengths. The incisors of the animals were hooked into a specially designed device which pinioned them vertically to a measuring board. The distances from tip of snout to tip of tail, and tip of snout to base of tail were taken to the nearest millimeter.

4. Dissection. The anaesthetized animal was killed by decapitation. Skin and muscles were removed from the head as completely as was found necessary for the subsequent operations, and the lower jaw was removed. The spinal cord was severed posterior to the cranium. The top of the skull was then removed, and the pia mater was slit and removed from the surface of the brain. The olfactory lobes were then severed from the brain on a plane parallel to a transverse section of the brain, and just anterior to the poles of the cerebral hemispheres. The brain was then lifted from the floor of the skull. The optic nerve was cut at the chiasma, but other nerves were allowed to break at any point. The hypophysis remained in the cranium when the brain was removed, and the stalk of the hypophysis was allowed to break at any point. The brain was then transferred to a glass plate of known thickness. The medulla oblongata was severed at the posterior pole of the cerebellum. The preparation was then handed to the first assistant for measurement. The writer meanwhile removed, tagged, and partially cleaned the tibia of the left hind leg.

4-A. In the case of bright and dull animals, two additional measurements were taken. Length of skull was measured from the center of the coronal suture to the lambdoidal ridge, and width was taken as the greatest width of the paired parietal bones. Measurements were taken just prior to the removal of the roof of the cranium.

5. Width. For this and subsequent measurements of the brains, a series of metal dividers was used. These dividers were adjusted by means of a screw to the landmarks bounding the desired dimension, and were later measured with a steel measuring rod to a tenth of a millimeter. The measurement of width was the greatest width along the frontal plane, dimension W-W' in Figure 1. (Figures and tables will be found at the end of the text).

6. Length. Since the brains of many animals are somewhat asymetrical, measurements were taken of both cerebral hemispheres, and were from the frontal pole to the occipital pole of each hemisphere. Both readings were recorded, and their mean was used for subsequent treatment of the data. Measurements are L-L' and l-l' in Figure 1.

7. Height. In the case of this measurement, considerable improvement was made over the method used by Sugita (60). He states, "I brought the brain to the edge of the glass plate, inserted one end of the calipers under the basal surface at the stalk of the hypophysis and, holding the calipers vertically to the plate, carefully measured the distance to the dorsal surface of the brain."

As has been previously stated, the glass plates used for measurement in this experiment were of known thickness. They were selected from several hundred plates, and were between 1.224 and 1.226 mm. in thickness. A micrometer stage from a microscope was set up vertically on a platform in such a fashion that the greatest height of the brain could be measured on the vernier scale of the stage accurately to one-tenth of a millimeter. This measurement is shown in Figure 2. The brains were then transferred to the second assistant.

8. Brain Weight. The brain weights of the first seventy-five animals were determined in a manner which was later abandoned. The brains were removed from the glass measuring plate and inserted in a pyknometer. This container was stoppered and weighed accurately to .002 grams. The pyknometer was then opened and filled with a solution of physiological saline. The concentration of this solution was 9 grams of NaCl to one liter of water. Bottle, brain, and saline were then weighed. It was our intention to use this second weighing for the dual purpose of determining specific gravity of the brains and as a check on the original weighing. The method was found to be unsatisfactory. Even though the pyknometers used were specially designed to hold a constant volume of liquid, the magnitude of error in filling the pyknometer was so great as to preclude accurate determinations of specific gravity. There was, moreover, a dangerous possibility of more serious error in the use of the pyknometers for original weighings. The weights of the pyknometers were checked each day.

On several occasions a material decrease in weight was observed.
Apparently, a minute piece of glass had been chipped from either
the cover or the bottle. A total of more than 25 brains had to be
discarded for this reason. Since the elimination of animals was
contingent upon conditions unrelated to the maze scores of the ani-
mals, it is improbable that the results from remaining animals were
systematically affected by the selection. This is equally true in
the case of animals eliminated for other incidental reasons, as
noted elsewhere in this Section and Section IV.

The second procedure adopted was much less susceptible to
error. A glass weighing plate was prepared by smoothing the edges
of a thick cover glass with a fine emery. The brain was placed on
this weighing plate after removal from the measuring plate. It
was immediately covered with a glass bottle, the edges of which
were fused. In order to avoid possible errors in subtraction, a
plate and bottle of equivalent weight were placed on the other
pan of the balance. The equivalence of these, as well as the ac-
curacy of the balance, was checked each day. The actual weight
of the preparation could thus be read and recorded directly.

9. Preservation of Brains. After weighing, the brains were
transferred to a small bottle containing a 4 per cent solution of
formaldehyde. This bottle was immediately corked, labeled, and
paraffined.

9-A. After a period of from 15 to 20 days from the time of
immersion in formaldehyde, the brains were removed with a fine
needle, immersed for three seconds in distilled water, then for
three seconds in 90 per cent alcohol, then in ether. The brains

were then exposed to the air for 30 seconds. The purpose of this
operation was to free the surface of the brains from adhering
formaldehyde solution. After 30 seconds of exposure the brains
were transferred to the weighing plate, covered, and weighed.
This was followed by re-measurement, with the same procedure as
used in the case of the fresh preparations.

As has been indicated earlier in this section, time was an
extremely important factor in the original handling of the brains.
Had it not been for this, the ideal procedure would have included
duplicate measurements taken on the fresh preparations. This was
actually done in the case of animals composing Series R, as above
reported. However, for the purpose of this study it was thought
particularly important to have a check on major errors in measure-
ment or recording. It was found that the effect of 15-20 day im-
mersion in 4 per cent formaldehyde solution was to increase the
weight of the preparations quite uniformly to from 65 per cent to
75 per cent above their original weight. Whenever the per cent in-
crease was less than 65 per cent or more than 75 per cent, such
brains were discarded. Reweighing thus served as a rough check on
the original weighing of the brains. The correlation between the
weight of the original preparation was +.87 ±.018 in the case of
the 88 normal males. Correlations between measurements before and
after preservation in formaldehyde were:

M	+.47	±.056
W	+.34	±.063
L	+.66	±.040

It will be seen that there is considerable distortion of the

brain, particularly in the transverse diameter, as a result of form-
aldehyde fixation.

As has been previously stated, brains whose percentage increase
was less than 65 per cent or more than 75 per cent were discarded.
Altogether about 20 records out of a total of over 300 were dis-
carded for this reason. It seemed inconceivable that these had all
been errors in original weighing. The writer has recently discovered
what seems to be a likely explanation of the too-frequent aberrations.
Donaldson (18) on page110 summarizes the results of a number of in-
vestigations of the effect of fixatives on the weight of brain prep-
arations. There is some reason for believing that a minor deviation
in the pH of the fixative may materially alter the amount of liq-
uid absorbed by the preparation. At the time the experiments re-
ported in this paper were performed the writer was ignorant of this
fact, and consequently failed to control the pH of the formaldehyde
solution. On the whole it would seem wise in further experiments
to use M as a check on brain weight, rather than to resort to pre-
servation and re-weighing.

SECTION IV

The Development of Methods for Studying the Association between Brain Size and Maze Ability in Unselected Animals*

The preliminary findings concerning the association between

brain size and maze ability in the case of Tryon's bright and

dull strains of animals suggested the possibility that this as-

sociation might be found to exist in the case of unselected

animals. As has been stated in Section II, the only comparable

animal studies of this association were those of Bassett (5)

and Shirley (59). The results of the former investigator showed

a slight superiority in maze and problem box performance on the

part of Wistar rats as compared with a strain of animals char-

acterized by the possession of small brains. Paterson (46) has

analyzed the data of Bassett and found that the differences be-

tween the two groups of animals were not significant.

The results of Shirley were negative. It should be empha-

sized, however, that as late as 1928 very little was known about

the factors affecting reliability and validity of maze scores.

The maze which she used, although containing 8 culs-de-sac, was

extremely simple. The median number of trials to reach the cri-

terion of 3 successive errorless trials was 10 trials, and all

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*The term "unselected animals" will hereafter be used
to denote animals from the colony maintained by the Depart-
ment of Psychology at the University of California, as dis-
tinguished from Tryon's bright and dull strains of animals.

her animals had learned the maze by the twenty-seventh trial.
She states, "Those who have worked on the maze say that the
simpler the maze, the more consistently it measures whatever it
does measure." This statement might well be contrasted with
Tryon's (75) first experimental-statistical principle (Cf.infra).

In addition to the inadequacy of the measuring instrument
used for determining maze ability, there are several other ques-
tionable aspects of her study. There is no assurance that her
animals were of similar age when dissected. The number of cases
is much smaller than should be used in a study which attempts to
investigate relationships of this nature.

The writer was particularly interested in using the best
possible method for measuring individual differences in maze
ability. Since it was our purpose to use the animals studied
in this experiment as a control group for the bright and dull
strains, it would have been desirable to run these animals on
the self-recording maze developed by Tolman, Tryon, and Jeffries
(70), and used by Tryon (74) in his study of the inheritance of
maze ability. This maze, however, is in continuous use and was
not available for our investigation.

It was our task, then, to devise a maze which would measure
individual differences as adequately as possible. In doing this
we attempted to follow the eight cardinal experimental-statistical
principles laid down by Tryon (75) for securing highly reliable
and valid maze scores. These principles are briefly summarized
below:

1. The amount of "material" to be learned should be large.

2. Individuals should be well "test-broken" before actual experimentation begins.

3. The experimental situation should be carefully controlled.

4. Scoring should be as objective as possible.

5. A large "spread of talent" is desirable.

6. The greater the heterogeniety of correlated "irrelevant factors," the higher the reliability coefficient, other things being equal."*

7. The two sets of measurements correlated to give the reliability coefficient should be as "comparable" as possible.

8. A large number of cases should be used.

The remainder of this section is devoted to the details of apparatus, animals and procedure.

Apparatus

1. Maze pattern. The study of reliability of maze-measures for rats reported by Tolman and Nyswander (69) in 1927 indicated that the 14-unit multiple-T maze was the most satisfactory type at that time. The highest reliability of any maze which has been used for animal experimentation is that of Tryon's (74,75) 17-unit Maze X. The writer felt that even these mazes might not adequately measure the higher ranges of ability, so a more complicated pattern of 22 units was devised. This pattern is shown

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* While heterogeniety of age, weight and sex does make for high reliability, the peculiarities of our experiment demanded that special care be used in controlling just such factors.

in Figure 4. The Tolman-Nyswander maze pattern is included in our pattern and consists of units 5 to 19.

The correct path involved 12 right choices and 10 left choices. There were eight choice points at which centrifugal swing (4) would force animals into a blind, and thirteen choice points where centrifugal swing would force animals into the true path.

2. Maze Construction. The maze was of the elevated block type described by Dennis (15), and was constructed of 2X8 surfaced white pine planks, three feet in length. These planks were nailed together into the pattern of the maze and braced firmly. The surface of the maze was carefully sanded, and all cracks and joints were filled with plastic wood. The maze them received three coats of dull shellac, and was thoroughly sanded again after the last coat. Six inches from the end of each blind a transverse stripe was painted. Crossing this stripe was later to be our criterion of error. Symmetrical stripes were made on the true path. There were no gates or other impediments on the maze.

3. Rotating Food Table. In order that all animals might have similar food compartments, and to facilitate the running of a large number of animals, a rotating food table was constructed, patterned after the delivery table used in Tolman, Tryon and Jeffress' self-recording maze (70). This food table had twenty-five compartments, and was supported by ball and roller bearings.

4. Food. The food given the animals was a modified Steenbach diet prepared in the form of a wet mash. The method of administration used in this experiment was new, and consequently will be described in some detail.

Whenever it is necessary to control the amount of food given to an animal in an experiment of this kind, it has been necessary to carefully weigh each portion. Even when experimenters are exercising considerable care in the control of food, deviations of from 2 to 3 grams are not infrequent. Most of these deviations are the result of differences in weight between food pans used. In this experiment use was made of an ordinary pastry bag of the type used by bakers in decorating cakes. The bag was conical in form, and at the apex was a nozzle having a diameter of one-half inch. The mash was mixed to the proper consistency and transferred to the bag. The mash was then squeezed from the bag in the form of a long cylinder onto a table covered with a thin layer of dry food. The cylinders were dusted with dry food and cut to the desired length. In the present experiment twelve grams of food were fed to the female animals and fourteen grams to the males. The lengths cut were six and seven inches, respectively. The mash was then rolled into a ball. A large number of balls were weighed, and in no case was the deviation from the required weight greater than one gram. A sufficient number of balls were made at one time for the day's run, and they were kept in a closed container until needed.

Animals

The animals were from the colony maintained by the Department of Psychology at the University of California. This colony is not inbred. The animals were from 120 to 150 days old when removed from the colony. The original group (Group I) used was composed of 55 males and 55 females, and was run for 40 days on the maze. A second group (Group II), consisting of 55 males, was run for a period of 20 days under conditions similar to those which prevailed when the original group was run. While no attempt was made to run animals within definite age limits, all animals were between 180 and 200 days of age when killed and dissected.

Of the original 55 females and 110 males, but 38 females and 88 males remained in the final data. Of the 17 females and 22 males which were discarded, 15 were eliminated because of sickness, death, injury or refusal to run the maze. The remainder were eliminated because of unsatisfactory brain weight or measurements, or other technical difficulties. Eighteen unselected animals were among those whose brain weights were discarded because of difficulty experienced with the pyknometer. The effect of elimination of animals because of errors in weighing has been discussed in Section III. It is difficult to estimate how correlations may have been affected by elimination of sick animals or animals which refused to run the maze. The guess which we would hazard is that both body and brain corre-

lations with maze scores might have been slightly higher had these animals been included.

Enucleation and Numbering

The animals were anaesthesized before enucleation. At this time their ears were marked according to the numbering system used in the Psychological Laboratory of this University.

Preliminary Training

The animals were carefully gentled by handling for a period of three days after enucleation. Actual preliminary training may be said to have begun on the fourth day after enucleation, and will be designated in the following outline as Day 1.

Day 1. The animals were removed from their cages and placed in a compartment of the rotating food table in which a 15-gram pellet of food had previously been placed. The animals were left for a period of about 15 minutes in the compartment, and then removed. Regardless of whether they had eaten any of the food in the compartment or not, they were immediately given their regular ration in the cage. They were transferred to and from the cage in a metal waste basket, the floor of which was covered with shavings. This waste basket was used subsequently whenever animals were carried to or from their cages.

Day 2. The animals were again placed in the compartment with the food pellet, and were left for one hour. They were not given additional food when returned to their cages. On this and

all succeeding days, 14-gram pellets were given to the males and 12-gram pellets were given to the females.

Day 3. The same procedure was adopted as on Day 2, except that the animals were left but one-half hour in the food compartment. All but three animals had eaten at least some of their food in the compartment before removal to their cages. These three animals were eliminated.

Day 4. A plank, similar to those comprising the maze later to be used, was placed at the entrance of the rotating food table. The animals were removed from their cages and set on this board one inch from the opening into the compartments. They were then eased gently into the compartment, and the table was rotated until the next compartment was in front of the entrance.

Day 5. Procedure was similar to that followed on the preceding day, except that most of the animals stepped into the compartment from the plank without assistance. About thirty seconds was allowed before the experimenter assisted an animal into a compartment.

Day 6. Procedure was similar to that of Day 5.

Day 7. The animals were placed on the plank about six inches from the opening into the compartment. Almost all animals entered the compartments without assistance.

Day 8. Procedure was similar to that of Day 7, except that the animals were placed one foot from the opening into the compartment.

Day 9. Procedure was similar to that of Day 7, except that the animals were placed three feet from the opening into the compartment. When animals reversed their direction on the plank they were allowed to proceed to the end of it, which was three feet from the entrance into the compartment.

Day 10. The plank was extended in length to a total of 10 feet, and the animals were placed about 9 feet from the entrance of the compartment.

Day 11. The plank was extended in length to a total of 20 feet, and the animals were placed about 15 feet from the entrance of the compartment. When the animals reversed their direction, a piece of cardboard 18 inches square was quietly placed in front of them. This same cardboard was used to block all retracing during the rest of the preliminary training, and during the actual running of the maze.

Day 12. The animals were placed 19 feet from the entrance to the compartment, and facing away from it. In all cases they proceeded to the end of the plank and then reversed their direction.

Day 13. Procedure was the same as that on Day 12, except that the entire apparatus was reversed in the room, and the animals were required to run south instead of north (Figure 3).

Day 14. Procedure was the same as that on Day 13.

Day 15. The animals were actually run on the maze, and error scores were recorded. Since these scores were not included in the total error scores of the animals, Day 15 may properly be

considered the last day of preliminary training. Procedure was, however, identical with that followed during subsequent days of maze running. Four animals who refused to traverse the maze were eliminated on Day 15.

Maze Running Procedure.

The plan of the maze used is shown in Figures 3 and 4. An entire cage of animals (usually five) was removed from the shelves in the metal waste basket and carried to the start of the maze.

The animals were placed successively on the maze by hand and were allowed to run through to the food compartment. A few animals, during the first few days, attempted to retrace the maze. They were blocked as soon as possible with the cardboard. On a few occasions animals retraced into a blind before it was possible to block them. This was not scored as an error. One trial per day was given, and the animals received no food other than the 12 and 14-gram rations which were given in the food compartment. Approximately 15 minutes were allowed for eating.

Olfactory Cue Control.

Two measures were taken for the purpose of controlling or equating the effect of olfactory cues. The first of these measures consisted of washing the surface of the maze with a wet cloth. When, as was the case with Group 1, both males and females were being run at the same time, the males were run first. The

maze was then washed, and the females were run. This was followed by a second washing. While Group 2 was being run, the maze was washed once at the end of each day's run.

The second precaution taken was to rotate, from day to day, the order in which animals ran. If, for example, the animals from cage A were run first on a certain day, on the succeeding day they were run last, and cage B was run first. On the third day cage C would be first, B would be last, and A would be next-to-last, etc.

Error Scoring.

An attempt was made to define an error as objectively as possible. As has previously been stated, black lines crossed the maze at points six inches from the end of each blind. Errors were scored only when an animal entered the blind at least far enough for his nose to cross the black line. There were, during the entire course of the experiment, very few cases where there was even slight doubt with regard to whether an animal had made an error or not. In nearly all cases, when an animal entered a blind more than three inches, he proceeded to the end of the blind.

Choice of Measures of Learning Ability.

Early maze studies frequently selected the number of days required to reach a criterion, or the number of errors made before

reaching a criterion, as a measure of individual differences in learning. More recently, Tolman and Nyswander (69), and Tryon (75) and Leeper (39) have found that highest reliability co-efficients were obtained when animals were run for a constant number of trials, and when error scores on even days were corre-lated with error scores on odd days. There is, however, no certainty that a procedure which is highly reliable is also very valid. Since the writer was interested in obtaining the most valid measure of learning ability possible, Group 1 was run for a period of 40 days. It was hoped that most of the animals would learn the maze perfectly within this time. This, however, did not prove to be the case. Even when animals made errorless runs during the early part of training, they never maintained perfect scores for more than three or four days. The maze, apparently, was too difficult to be perfectly learned and retained by all animals. There were, however, wide in-dividual differences. After the first few days, several ani-mals averaged less than two errors per day for the entire period.

The intercorrelations and reliabilities of several of the scores calculated are given in Table I. Only 44 animals reached a criterion of one errorless run during the 40-day period. Total errors for 40 days correlated with 10 and 20-day error scores, +.70 and +.82, but the 20-day scores correlated with 10-day scores but +.63. In view of the relatively high r between error scores for shorter lengths of time and 40-day scores, it was deemed ad-

visable to run the animals of Group II for but 20 days. The error score for the animals, as a group, plateaued at about 12 days with an average of 5.2 errors per trial. During the remaining 28 days the curve did not go below 4.7 errors per day.

Moreover, the cases of six animals indicated that the inclusion of the last 20 days might not be desirable. All six of these animals learned rapidly and made zero scores before trial 25. Yet, at trial 30, they were making from five to nine errors per day. The fact that none of these animals was noticeably slower in running, and that none of them lost any undue amount of weight seemed a fairly good indication that the animals were in good health.

While similar behavior has doubtless been noticed by other experimenters, there seems to have been no attempt to explain it. The possibility occurred to the writer that there are actually two "good" learning responses which an animal may make to the maze situation. It is usually assumed that animal maze learning consists essentially of elimination of blinds. In this assumption is often implied that blind entrance, and the reversal of direction thereby necessitated, is an "unpleasant" experience. That this is true is supported by the fact that most animals actually do give evidence of learning in terms of blind elimination. It would seem equally possible, however, that some animals might learn to enter and leave blinds skillfully, and without "unpleasant" experience. This might be especially true in the case of a long and extremely complex maze. In other words, the writer suggests the possibility that some animals, after con-

siderable experiance on a maze, may learn that an easy method of negotiating the maze is to run almost at random. Particularly in the animal maze situation where no punishment is used, the reward, in terms of food, is the same regardless of the number of blinds entered. Moreover, the actual running time may not be greatly increased by the entrance into a half-dozen culs-de-sac.

Because of these considerations, two error scores were chosen as representative measures of learning ability. These error scores were from days 1 to 20, and from days 1 to 10. Group II was run but 20 days on the maze. The correlation between these scores and the anatomical variables are presented in Section V.

SECTION V.

The Association Between Brain Size and Maze Ability
in an Unselected Sample of Colony Rats

The preceding Section has presented the details of experimental procedure followed in running two groups of unselected animals on a 22-unit elevated maze. It will be remembered that Group I consisted originally of 55 normal males and 55 normal females. Sickness, failure of animals to run, errors in anatomical measurements, etc., reduced the number of animals to 38 females and 40 males. Neither of these sub-groups was large enough for separate correlation analysis, and sex differences in all anatomical measurements precluded their combination into a single group. Consequently 55 additional males (Group II) were run on the maze. Of this number, complete data were obtained on 48 animals. These animals from Group II were combined with Group I males to give a total of 88 male animals. It will be remembered that all animals were between 180 and 200 days of age when killed and dissected.

Intercorrelations were calculated between the following variables: total errors made for 10 trials, total errors for 20 trials, body weight, length from nose to tip of tail, length from nose to base of tail, brain weight, width of brain, length of brain, the index M (the product of 3 dimensions of the cerebrum), and tibia length. These intercorrelations are presented in Table 2.

Before the various correlations are compared it might be well to discuss the magnitude of a correlation which may be considered significant. A correlation whidh is greater than four times its probable error is usually thought to be significant, since it could occur by chance in a normal population less than once in a hundred times. In dealing with low correlations it is probably safer to use the probable error of a correlation of zero rather than the probable error of the found correlation. The probable error of a zero correlation with an N of 88 is $\pm.071$. A correlation of .284 is thus four times the probable error of a zero r. Somewhat less stringent limits would admit of the significance of an r 3 times its P.E. With our N, such a correlation would be .213.

It will be seen that the correlations of maze scores with brain weight are -.24 and -.15, while those of maze scores with M are -.29 and -27. A negative r indicates a positive relationship between brain size and maze ability.

Such correlations, taken alone, might lead one to suspect that there probably is an association between brain size and maze ability in an unselected population of rats. A number of analogous conclusions from investigations of human beings have been described in Section II. The correlations between certain measurements of body size and maze ability throw considerable doubt on the validity of such a conclusion. These correlations range from -.01 to -.24, and show a consistent tendency for body size to be related to maze ability.

While it is true that the correlations between brain measurements and maze scores are almost uniformly higher than the correlations between measures of body size and maze scores, yet it is quite possible that the slightly greater magnitude of the brain-size correlations may have arisen by chance. In other words, it is possible that the correlations found between brain size and maze scores may have been but a reflection of the small but consistent relationship found between general bodily development and maze ability. This is possible particularly in view of the relatively large magnitude of all the intercorrelations between anatomical measures.

Summary and Conclusions

Correlations between maze scores and measures of brain size indicate that there is probably a real association between the variables. The magnitude and consistency of the correlations between other anatomical variables and maze scores, together with the relatively high intercorrelations of all anatomical variables suggests that the correlations found might be attributable to a tendency for all desirable traits to correlate positively.

SECTION VI.

A Comparison of Bright and Dull Animals and Unselected Colony Animals with Regard to Brain and Body Measurements

It has previously been noted that the bright and dull animals were available for dissection at ages ranging from 90 to 350 days. Obviously anatomical measurements on these animals would be in part a function of the age at which they were dissected. The normal animals used were all between 180 and 200 days of age. However, for the purpose of preliminary examination of the data, age differences were disregarded, and means and standard deviations for a number of variables were calculated for the entire groups of bright, dull, and unselected animals. Table 3 presents these data and the critical ratios of the differences between the bright and dull animals. Variables so treated include brain weight (BW), M, length (of cerebral hemispheres), width (of cerebral hemispheres), length from nose to tip of tail (nose-to-tip), length from nose to base of tail (nose-to-base), body weight, tibia length, age, and maze scores. The units of measurements are grams, in the case of the weights; cubic centimeters, in the case of M; centimeters in the case of all dimensions; days in the case of age; and errors in the case of maze scores. Table 4 presents a comparison of bright and unselected animals for all the data except age and maze scores. A similar comparison of dull and normal animals is presented in Table 5.

With regard to the differences between brights and dulls in anatomical variables as presented in Tables 3, 4 and 5, it should be noted that animals varying greatly in age are grouped together. A large number of studies cited by Donaldson (18) indicate that there are marked differences in growth rates between different organs and measurements of the skeleton of the rat. It is thus conceivable that if age were allowed to vary indiscriminately, differences might appear between the strains which were due to growth factors. In order to preclude the possibility that such factors might lead to spurious results in the present experiment, the animals have been grouped into several age categories.

That the bright animals are far superior to the dull animals in maze ability is shown by the critical ratios of the differences between bright and dull maze scores. This but substantiates the great mass of evidence which has accumulated through the 12 filial generations of Tryon's experiment, to the effect that the animals bred for brightness are far superior in maze ability to the animals bred for dullness. During subsequent analysis of these data we will consider this fact established, and will not report on the maze scores of bright and dull animals. "Brightness" will subsequently be defined as descent from bright parents, and not as referring to individual performance.

All bright and dull animals were then divided into five subgroups on the basis of age. Those below 150 days of age were placed in Group P, 150-199 in Group Q, 200-249 in Group R, 250-299 in Group S, and all animals above 300 in Group T. The number of

cases in each of these Groups is shown in Table 6. The following variables were selected for intensive comparison: brain weight, M, body weight, nose-to-tip, nose-to-base and tibia. In order to further insure the comparability of the age-groups with respect to age, subsequent treatment of the data included a calculation of age means and differences between bright, unselected and dull groups within the same age category. Means and standard deviations were calculated for each variable within each age-group. Reference to Table 6 will indicate that, in several age-groups, the number of animals is quite small. For mathematical or interpretative purposes a standard deviation should be considered indeterminate when the N is less than 10. These standard deviations, however, were to be used solely for the purpose of graphical representations of the data, as will be seen below.

Figures 6 through 19 present the means of the seven variables for age-groups P, Q, R, S and T. Means for bright animals are designated by the solid black lines, and means for dull animals are designated by the solid green lines. Data for males and females are graphed separately. Units of measurements are grams for brain weight, cubic centimeters for M, centimeters for body weight, nose-tip, nose-base and tibia, and days for age. The variability of the individual data comprising each mean is indicated in terms of standard deviations above and below the means, and is shown by the dotted lines. Figure 14 may be taken as a case in point. It will be noted that the mean nose-to-base measurement for the dull males of age-group S rises to 21.3 cm., and falls to 19.8 for age-group T. The

greater magnitude of the standard deviation thus suggests that the mean at this point is influenced considerably by sampling errors, such as might be expected if the mean were determined by a small number of cases. This is substantiated by the fact (Table 6) that but 6 individuals are included in the data represented by the mean of 21.3.

The means from the normal groups are designated by black dots slightly to the left of an ordinate erected at Q, and the standard deviations of these means are designated by red dots above and below the means for the normal groups.

Examination of Figures 6-19 will reveal the following trends of the data:

1. For most of the variables there is a marked tendency for measurements to increase from P to Q, and a somewhat less marked tendency for measurements to increase from Q to R. This merely indicates that growth continues at a noticeable rate until the 200th day.

2. Such increase as exists from R through T is of such minor degree as to be almost completely obscured by sampling errors in the population.

3. For most variables the means of the dulls of both sexes seem to be somewhat smaller than the means of the brights.

4. The difference between the bright and dull strains seems to be more marked in the cases of brain weight and M than in the cases of other variables. It should be noted, however, that Figures 6 through 19 serve but to give a graphic picture of the dif-

ferences between the two strains. Before final conclusions are made with regard to the differences here presented, it will be necessary to reduce all of the variables to some comparable basis for comparison.

5. The sharp rise in most of the curves from P to Q indicated that growth was taking place at a rapid rate up to 150 days. In view of the small number of cases in the P category, these animals were not included in further analysis of the data.

6. The age range for Q animals included the age range of the unselected animals.

7. There is a tendency for most of the curves to rise from Q to R, but the R, S and T groups show little increase after the animals have reached the age of 200 days. (Most of the growth curves presented by Donaldson (18) substantiate the findings regarding the rates of growth from P through T).

In view of above considerations, the data were treated in the manner which is detailed in the following pages. Animals from Q groups were compared with unselected animals for differences between bright and unselected, and dull and unselected animals. The first step in this comparison consisted in the calculation of differences and critical ratios in the case of the several variables. The significance of the difference between bright and dull Q animals was not calculated, since this type of comparison was made for older animals. Subsequent correlational analysis will indicate that the comparison for Q animals would result in findings similar to those found with the older animals. Groups R, S and T

were combined and treated as a single group. This procedure was
followed for the purpose of securing a large enough number of cases
to make subsequent calculations statistically reliable. It is
justified on the basis of small change in the growth curves be-
tween R, S and T groups, as discussed in 7 (above).

Tables 7 and 8 present a comparison of Q animals with un-
selected colony animals, and Table 9 presents a comparison of
bright and dull animals for age-groups R, S and T. Before these
tables are discussed in detail we may profitably examine the dis-
tributions of the data by means of another method of graphic re-
presentation. This method is designed to indicate the actual
amount of overlap between the bright and dull strains in the case
of the several variables. The frequency distribution of each vari-
able for bright and dull animals is shown by a series of histograms
for age-groups Q, R, S and T, in Figures 20 through 31. As in pre-
vious figures, black represents bright animals and green represents
dull animals. As before, it will be seen that the actual over-
lapping of brights and dulls is less in the case of brain weight
and M than in the case of other variables.

Table 7 presents the means, differences and critical ratios
(C.R. = Diff./ Diff.) of differences between bright Q animals and
unselected animals. It will be seen that the bright Q animals are
significantly larger than unselected animals in brain weight, M,
and body weight. In the case of the females in brain weight the
critical ratio of the difference is 2.92. The only other measure-
ment in which the brights are significantly larger than the unse-
lected rats is the nose-to-tip measurement of the females. It

seems well established that the bright Q animals have larger brains and heavier bodies than the unselected animals. This should be borne in mind in considering Table 8.

Table 8 presents means, sigmas and critical ratios of differences between unselected animals and dull Q animals. Here it will be seen that the unselected animals have significantly heavier brains than the dull animals, and that this difference is reflected in the measurement M. When we consider body weight, however, we find that the unselected animals are as small as or smaller than the dull animals. Other variables in which significant differences appear are nose-to-tip for males, nose-to-base for males, and tibia for males. It will be remembered, however, that bright Q animals did not differ significantly from unselected rats in the case of these later variables.

Taken together, Tables 7 and 8 indicate that brain weight is the only variable in which bright animals are significantly and consistently greater than unselected animals, and in which dull animals are consistently and significantly smaller than normal animals.

These data alone constitute strong evidence for the conclusion that brain size is the sole anatomical variable which distinguishes, with consistent significance, bright from normal animals, and at the same time distinguishes dull from normal animals. While it is true that brights and dulls differ significantly in one respect or the other from normals, such differences do not form a continuous series of significant differences from bright through normal to

dull animals.

Table 8 presents a comparison of bright and dull animals for the combined R, S, and T age groups. A number of significant differences between the two strains are apparent. The magnitude of the critical ratios in the case of brain weight, M, body weight, nose-to-tip, and nose-to-base indicate with considerable certainty that bright animals of the combined R, S, and T group are larger than the dulls with respect to this variable. In order correctly to interpret the greater magnitude of the critical ratios in the case of brain weight it is necessary to remember that the critical ratio is a function of both the difference between the means and the variance of the variables in the bright and dull groups. The greater magnitude of the critical ratio in the case of brain weight would therefore indicate that the difference between the brights and dulls is greater than in the case of the other variables, in terms of the respective variances of the two strains.

In order quantitatively to compare the differences found between the bright and dull strains, use has been made of a correlational method developed independently by Tryon (unpublished ms.) and Zubin (81). This method is designed for the purpose of obtaining a product-moment correlation between a two-step variable and a continuous variable. In our case, brightness and dullness are treated as the two categories of the two-step variable, and are correlated with the several somatic variables.

Before proceeding with the details of this method we wish to present our rationale for treatment of brightness and dullness as

a single variable, as well as the limitations entailed in this
treatment. As has been described in Section I, the animals com-
prising the bright and dull strains are of common origin, and
have been differentiated by a gradual process of selective breed-
ing. The present generation is analagous to extreme cases se-
lected from the ends of a distribution. Unfortunately we have
no anatomical data on the F_{10} and preceding generations. At the
present time the bright and dull strains interbreed freely. There
is no evidence that either of the strains has achieved its present
characteristics through some sudden mutation. On the other hand,
maze scores for the early generations suggest that the process of
differentiation has been a gradual one. Probably then, the vari-
able "brightness and dullness" may be legitimately considered as
a continuum, despite the fact that intervening steps are absent.

On the other hand, we have no data and can make no assump-
tions regarding the shape of the distribution which would inter-
vene between our bright and dull groups. Consequently, the ab-
solute magnitude of correlations between the bright-dull variable
and the somatic variables are not necessarily identical with the
correlations which would be found if intervening steps were pre-
sent between brightness and dullness. The correlational technique
in this case is valid for prediction, and is equally valid for the
purpose of comparing the several somatic variables with regard to
their association with the bright-dull variable. The reader should
be cautioned against interpreting such correlations as representing
a relationship between maze ability and the somatic variables, but

rather as an unique association which is the direct result of selective breeding experiments. Moreover, since the correlations include only cases from the extremes of a theoretical distribution, they are doubtless much higher than those which would be found if it were possible to correct for truncation of the theoretical distribution.

The first step in the statistical procedure employed in obtaining the correlation between the variable of selection (bright-dull variable) and the somatic variable was the calculation of the composite sigma of the somatic variable. This sigma is identical with that which would be found if brights and dulls were thrown into a single distribution. The composite weighted mean of each somatic variable (M_x) is calculated from the mean of the brights (M_b) and the mean of the dulls (M_d), and the respective Ns, by the formula:

$$M_x = \frac{N_b\,M_b + N_d\,M_d}{N_b + N_d}$$

Let the difference between M_x and M_b be called D_b, and the difference between M_x and M_d be called D_d. From D_b, D_d, N_b, N_d, the variance of the brights σ_b^2, and the variance of the dulls σ_d^2, we may calculate the composite variance for the combined bright and dull groups by the formula given by Yule (80) on page 142:

$$N\,\sigma_\gamma^2 = N_b\,(\sigma_b^2 + D_b^2) + N_d\,(\sigma_d^2 + D_d^2)$$

where N is the total number of cases in the bright and dull groups.

We will now let p equal the proportion of brights and q

equal the proportion of dulls. The Pearsonian $\underline{r}$ between the two-step variable of selection and the continuous somatic variable, after Tryon (unpublished ms.) and Zubin (81) is:

$$\underline{r} = \frac{p\,q}{\sigma_x}\,(\underline{M}_b - \underline{M}_d)$$

These correlations are presented in Table 10. As has previously been indicated, the magnitude of the $\underline{r}$'s is not to be interpreted as representing the correlation between maze ability and the respective somatic variables. Neither are the correlations those which would be necessarily found if intervening stages between "brightness" and "dullness" were present. The procedure commonly followed in determining the significance of differences between $\underline{r}$'s involves the calculation of the standard errors of the coefficients. Since the correlations found are probably higher than those which might be expected if all the cases in the theoretical distribution were present, it is not legitimate to interpret differences between the correlations in terms of the standard errors of the $\underline{r}$'s and the differences between them.

It will be noted that the correlations presented in Table 10 are based on data from four independent experimental groups. Fisher (21) on page 110 has suggested that replication of experiments is of great importance in determining the confidence which should be placed in a result. Moreover, he states that results are particularly dependable when the magnitude as well as the direction of differences are similar in parallel experiments. Examination of Table 10 will reveal that the highest correla-

tions in all four groups are between the variable of selection and brain weight. These correlations range from +.7769 to +.8399. Next in order of magnitude are the correlations with M, but in one instance the nose-to-tip measurement correlates slightly higher than M with the variable of selection. The remaining three correlations with nose-to-tip are slightly lower than the lowest M correlation. Body weight, nose-to-base, and tibia length correlations follow the nose-to-tip correlations, in fairly regular descending order. There is but one major irregularity in the entire correlation table,--the correlation between the variable of selection and body weight in the case of RST females. Reference to Figure 11 will show that the 26 dull females of age-groups R, S and T were smaller than might have been anticipated from the size of the dull Q females. If this finding is not due to sampling errors, it would seem probable that some genetic factor is at work in the females of the dull strain which tends to inhibit growth after 200 days.

The body measurement which correlates most highly with the variable of selection is the nose-to-tip length of the animals. If these correlations are compared with the correlations between the variable of selection and the nose-to-base measurement, it will be seen that the latter are uniformly and materially lower. Since these two skeletal measurements are identical except for the inclusion of the tail in the nose-to-tip measurement, it is clear that the two strains differ to a greater extent in tail length

than they do in body length. Unfortunately calculations were not made for length of tail alone.

Summary

When bright and dull animals of age-group Q were compared with unselected colony animals, brain weight was found to be the sole anatomical variable which distinguished, consistently and significantly, bright from unselected animals, and at the same time distinguished dull from unselected animals. While it was true that brights and dulls differed significantly in one respect or another from unselected rats, such differences did not form a continuous series of significant differences from bright through unselected to dull animals.

A comparison of bright and dull animals of age-groups RST indicated that the critical ratios of differences in brain weight were of considerably greater magnitude than other critical ratios. In order to express these findings in a fashion which could be more readily interpreted, a correlational method developed independently by Tryon (ms.) and Zubin (81) was used. "Brightness" and "dullness" were taken as the two categories of a two-step variable, and were correlated with the several somatic variables. The inclusion of Q males and females with RST males and females in this analysis provided four independent but paralled experimental groups. On the basis of the magnitude of the correlations found and the agreement between the four groups it can be concluded

with reasonable certainty that the difference between the bright
and dull strains is greater in the case of brain weight and its
reflection in M than in the case of any of the other variables
considered.

SECTION VII.

Interpretations

A. Normal Colony Animals

The findings of this experiment concerning the association between brain size and maze ability in normal colony rats indicate that there is a small but consistent correlation of the order of about -.25 between brain size and errors made on a large and complex maze during the course of 10 or 20 trials. Insofar as maze errors constitute a valid measure of maze ability this means that the correlation between maze ability and brain size is of the order of +.25 in a normal population.

Were brain size unique in its association with maze ability, such a correlation might be of considerable theoretical interest. While other anatomical measures failed to correlate as highly with maze scores as did measures of brain size, yet there was a marked tendency for all anatomical variables to correlate with the maze scores. Although none of the later correlations were reliable, yet their consistency is strong evidence that the relationships are real. It is quite conceivable that the greater magnitude of the brain size correlations, as compared with body weight or body length, for example, might have risen by chance. In fact, in the case of the correlation between body weight and

20-day maze scores, the correlation was almost significant.

Such findings, while new in the field of animal research, are not particularly striking when compared with a great mass of experimental evidence on human beings. In an excellent critical summary of this latter field, Paterson (47) has cited over two hundred studies in which aspects of physique are studied in relation to intelligence. Many of these studies used correlational methods and had adequate experimental controls. The concensus of the findings is that there is a small but relatively consistent tendency for all measures of physical excellence or size to correlate with measures of mental ability. A rough summary of the best studies would indicate that this relationship is of the order of from +.05 to +.10.

An examination of Table 2 will reveal a tendency for almost all the anatomical measures used in this study to be rather highly correlated. Conceivably, then, the correlations between brain size and measures of maze ability might be a reflection of a general tendency for all desirable traits to correlate positively. Only when further studies confirm the finding that the correlations between maze scores and brain size are larger than the correlations between maze scores and other measurements can we conclude that the former relationship is greater than the latter.

B. Bright and Dull Animals

The findings in the case of bright and dull animals are more positive. It will be remembered that the sole differential in the

process of selective breeding was the maze ability of the animals as determined by their maze scores. An attempt was made, in the case of both strains, to choose healthy and fertile animals as parents for each succeeding generation.

As shown by the data presented in Section VI, this selective process has resulted in two strains of animals which differ in a number of anatomical characteristics. All the measures of physical size indicate that the bright animals, as a group, are larger than the dull animals. The normal colony animals used as controls are about midway between the bright and dull strains, and tend to resemble the dull somewhat more than the bright animals.

When the various anatomical characteristics of the two strains are compared with respect to variability, however, much more striking differences are apparent. While there is considerable overlapping between the three groups with respect to measures of gross body size, this overlapping is much less apparent in the case of measures of brain size. The bright animals have brains which are almost uniformly larger than the normal animals, and the brains of the latter, in turn, are larger than those of the dull animals.

Before we present conclusions with regard to the experimental findings of this study, it seems advisable to consider a number of possible explanations of the large difference between the size of the brain of bright and dull animals. Most of the remainder of this section will be devoted to a presentation and evaluation of number of such possibilities.

1. One possible explanation would take account of the low

but consistent correlations found between brain size and maze ability in the case of normal colony animals. Let us assume that there were some such relationship in the parental generation from which both bright and dull strains were developed. When animals were selected from the extremes of the distribution as parents for the bright and dull strains, they may have differed to some extent in brain size. If differences in brain size were inheritable, one would expect the F_1 bright animals to differ somewhat from F_1 dulls with respect to this trait. One of the factors which might have contributed to the difference between the maze scores of F_1 bright and dull animals was possibly gross brain size. As selection on the basis of maze scores in the case of the two strains continued, there may have been an increasing difference between the brain size of bright and dull animals in succeeding generations. Such a process would result in the extreme differences found between the size of the brains of the bright and dull animals in the F_{11} and F_{12} generations.

Such an explanation would not preclude the possibility that other inherited anatomical traits also contribute to the brightness and dullness of later generations, but it does postulate a causal nexus between brain size and maze ability.

2. A second type of explanation would take account of the difference between the size of the brain of the Albino and the Norway Rat. Donaldson (18) has presented evidence that the two varieties are of the same species, and suggests that the Albino

rat was originally derived from mutants of the Norway species.
Sugita compared the brains of Albino rats with brains of Norway
rats with respect to gross size (67) and number of cortical cells
(68). He reported that the brain of the Norway rat is 15 per cent
heavier than that of the Albino rat for animals of comparable body
size, but that the number of cortical cells is the same for both
species. Unfortunately there is no data available on the relative
maze ability of Albino and Norway animals. Stone (64) reports
that the Norway animals studied by him were so wild as to preclude
their use on the maze. Offspring of trapped animals were equally
wild. A possible explanation of the difference found between the
brains of bright and dull animals reported in this study might be
that the genetic factors which determine the larger brain size in
the case of Norway rats has been recovered in the course of the in-
breeding of the bright animals, and is not related directly to maze
ability. Against this hypothesis is the fact that the animals from
the dull strain have brains which are quite uniformly smaller than
the brains of unselected animals. Any explanation of the findings
must take account of the small brains of the dull animals as well
as the large brains of the bright animals.

3. In attempting to develop strains which are homozygous for
traits related to maze ability, Tryon has for the past few gener-
ations consistently inbred animals of both the bright and dull
strains. It is conceivable that this inbreeding in itself has de-
veloped strains which are homozygous for brain size. If this were
true, the brain size differential might be independent of maze

ability, and equally unrelated to the selective breeding which has resulted in the difference in maze ability between the two strains.

It should be pointed out that this type of argument can also be advanced against all assumptions of causality. Whenever two events or complexes of events are associated, it is always possible that this association is accidental, or that it is the result of other factors than those under consideration. In the present instance, therefore, we can do no more than attempt to estimate the probability that the selective breeding of animals for maze ability is causally related to the found differences in brain size.

It has been repeatedly demonstrated that inbreeding does tend to produce animals which are homozygous for many traits. Regardless of the number of genes which affect brain size, it is quite possible that animals which have been inbred for many generations might become homozygous for many or all of the genes affecting brain size. If, for example, Tryon had confined himself to the development of a bright strain of rats, any peculiarity of genetic constitution in this strain might with equal validity be attributed to selective breeding or to inbreeding. Fortunately, however, animals have also been selectively bred for lack of maze ability. Moreover, they have been found to differ as markedly from unselected animals as do the animals bred for maze ability. There is thus evidence not only that the difference between the brights and dulls is greater in the case of brain size than in the case of any other variable considered, but that the association found is systematically related to selective breeding. Insofar as our

evidence reveals, the association is not systematically related to inbreeding. In view of this fact, it may be considered more probable that the causal nexus involves selective breeding than that it involves inbreeding alone.

4. Nutritional factors constitute another possible differential which might cause the observed differences between the bright and dull animals. It is possible that dull animals have inherited a tendency to be lethargic, which results in ingestion of less food than normal or bright animals. The smaller amount of food taken by the dulls would conceivably stunt them in all aspects of their anatomical make-up.

Two lines of evidence tend to refute this argument. Paterson (47) quotes unpublished studies of R. Scammon which indicate that even when gross malnutrition exists to a degree which retards or halts physical growth, the nervous system continues to grow. Hoefer and Hardy (30) report data which indicate that nutritional deficiency does not retard the intelligence of children.

The other evidence is from the studies of Anderson and Smith (1, 2). These investigators found that diets insufficient in caloric content had no effect on maze scores, although the regimens were so strict that they permanently stunted the experimental animals.

From these data it would seem reasonable to conclude that dietary deficiency induced by lethargy on the part of the dulls would probably result in a more marked difference between the bright and dull strains with respect to body size than with respect to brain size. As has been demonstrated in Section VI, the reverse holds true in the case of the bright and dull animals.

5. From data presented in Section V it is apparent that there is probably a consistent but not significant correlation between measures of gross body size and brain size.

It is conceivable that the selective process acted to produce strains of animals which differed essentially in gross body size and weight. The greater brain size in the case of the bright animals would thus be merely a reflection of their greater body size.

Against this argument are again the findings with regard to the relative homogeneity of the brain and body variables. If the selective process had specifically tended to produce differences in gross body size, it would seem that such differences would be more marked than their reflections in brain size differences.

Actually, however, it is impossible to estimate the extent of the effect of gross body size differences on brain size differences from data which are now available. If the genetic determiners of body size and brain size are relatively independent, it might be possible to study this phenomenon by breeding bright animals with dull animals, and comparing the maze scores of the progeny with brain and body measurements. Such a study is being conducted at the present time.

6. A number of investigators have studied the relationships between measures of ability in the rat. These investigations have been summarized by Tryon (77,44). In the earlier study he reports that the correlation between scores on two mazes of similar construction but differing in pattern is +.77 ±.02. More recently, Commins, McNemar, and Stone (14) have reported an elaborate study in which intercorrelations were calculated between scores on three

mazes, a brightness discrimination problem, and a triple platform problem box. The correlations between the three mazes ranged from +.56 to +.66, while all other correlations were of zero order.

Such findings tend to indicate that maze ability is a trait which is relatively unique with respect to other measures of learning ability, and that the latter in turn are quite specific. If this be true we are confronted with two possible interpretations with regard to the specificity of maze ability. We may infer that all abilities, including that of maze learning, are very specific kinds of endowment. Neurologically this would mean that excellence in maze performance would be related to special qualities of nervous tissue or function. Genetically it would mean that the inherited traits conducive to maze superiority are of a very specific nature, and not conducive to excellence in other learning functions. Such an interpretation would lead us to question the existence of a causal nexus between mass of brain tissue available and maze ability.

There is, however, another possible interpretation of the findings with regard to the lack of association between maze learning problems for the rat. Lashley (37) has recently reviewed findings of studies of cortical localization which are pertinent to the present problem. All investigations of the localization of simple sensory habits indicate that these habits are confined to the respective sensory areas concerned. The problem box habit is confined to the frontal (motor) and occipital cortex. Removal of a part of the occipital area results in a loss of visual habits in proportion to the extent of the lesion. The maze habit, however,

does not seem to be localized in any particular cortical area.

That the occipital area has a function in maze learning which is independent of vision is shown by the experiment of Lashley (36,p.111). Blind rats were taught a maze, and portions of the occipital area were removed. Maze habits were lost roughly in proportion to the extent of the lesions. It should be pointed out that in this case the occipital area could not have contributed to the maze habit as a visual projection area, since vision did not play any part in original maze learning or performance. It should be noted that this argument, insofar as it applies to the present experiment, involves no assumptions regarding the mechanism of the cortex in the maze-learning function. If, for example, the cortex operates as a complex of relatively specific sensory projection areas, the maze habit may involve so many of these areas that for present purposes the whole brain may be considered as a unit.

In addition to the evidence from experiments on the effect of destruction of cortical areas, there is another possible explanation of the correlations between measures of ability in the rat. This ex- planation is not necessarily unrelated to the evidence presented above. A consideration of the various problems which have been ex- perimentally presented to the rat will reveal that most of these problems are quite dissimilar to the environmental situations which are likely to confront the rat in his normal habitat. Adaptation to many of these situations is not necessarily a good biological adap- tation. The maze is perhaps unique among the experimental situations which have been used in the laboratory, in its similarity to the nat-

ural environment of the rat. It is possible that the selective breeding of animals for maze ability has been selective breeding for general biological superiority. If this be true the results would indicate that size of brain is a more important factor in individual differences in the rat's biological adaptability than body size.

7. A number of investigators have suggested the possibility that learned responses can be transmitted to progeny by an hereditary mechanism. A summary and evaluation of the experimental data relevant to this theory have been made by Morgan (44a). Among the more recent supporters of the theory have been William McDougall and I. P. Pavlov. McDougall has found that a strain of animals trained to make a brightness discrimination improved considerably during the course of some 30 generations. This improvement took place in spite of the fact that no attempt was made to breed selectively for the ability to make the discrimination. Pavlov found that the progeny of mice which had been conditioned to a sound were more rapidly conditioned than control animals. Morgan states, however, that Pavlov has recently repeated his experiment and repudiated his original conclusion. Morgan suggests that the results of Pavlov and McDougall, as well as other findings which suggest the inheritance of acquired characteristics, are likely to have been caused by uncontrolled factors in the experimental situations. He further states that the whole weight of genetic evidence is against the Lamarckian hypothesis.

Summary

The experimental findings presented in this dissertation indi-

cate that there is a low but positive correlation between maze ability and brain size in an unselected sample of colony rats. During the course of an experiment on the inheritance of maze ability in the rat, Tryon (74) has selectively bred animals for maze ability, in the case of the bright strain, and for lack of maze ability, in the case of the dull strain. A comparison of bright and dull animals from the eleventh and twelfth generations indicates that the most marked anatomical difference between the two strains is in the gross size of the brains of the animals.

In consideration of a number of possible explanations, we suggest that the following is the most likely interpretation of the experimental findings:

1. In the original parental generation from which the two selected strains were developed, as well as in succeeding filial generations, there was an association between brain size and maze ability.

2. The process of selective breeding for maze ability resulted in a simultaneous selection for brain size.

3. The difference between the maze ability of bright and dull animals is in part a function of the difference in brain size between the animals of the two strains. There is no evidence regarding the extent to which differences in maze scores between the two strains are determined by brain size. Methods are available, however, for approaching a solution to this problem.

4. Individual differences in the acquisition and retention of a complex habit are in part a function of the mass of brain tissue available.

A P P E N D I X   I.

A Comparison of Bright and Dull Animals with Regard to Measurements of the Cerebellum and Cranium

Section III has described in detail the measurements of the cerebellum and cranium which were taken on bright and dull animals. An attempt was made to choose measurements which were clearly delimited by definite anatomical landmarkds. Length of the cranium was measured from the center of the coronal suture to the lambdoidal ridge, and width was taken as the greatest width of the paired parietal bones. Length of the cerebellum was defined as the length of the median vermis, and width was the greatest width of the cerebellum after the removal of the paraflocculi. All measurements were taken with metal dividers similar to those used for the measurements of length and width of the cerebrum.

It will be remembered that Series R consisted of fifty normal colony animals which were used solely for the purpose of determining the reliability of measurements used. Coefficients of reliability and their probable errors for measurements of the cerebellum and cranium are presented in Section III. These coefficients ranged from +.92 ±.015 to +.97 ±.005. The bright and dull animals were divided into two age-groups for comparison of the variables to be studied. These age-groups were (150-200 days) and R-S-T (200-350 days). Since the animals were also separated according to sex, there are four independent comparisons of bright and dull animals for each variable. Table 11 presents these comparisons

for both measurements of the cranium and cerebellum.

RESULTS

A. Measurements of the Cranium

The differences and critical ratios presented in Table 11 indicate that bright animals have longer and wider crania than dull animals, in the case of four independent groups of animals. Four of the eight critical ratios calculated are larger than 3.00, and all differences between the two strains are in the same direction. When these critical ratios are compared with those presented in Table 9 for the difference in brain weight between the bright and dull strains, it is apparent that neither of the cranial measurements serves to differentiate the bright and dull strains as well as does brain weight. This suggests the possibility that the greater size of the brains of the bright animals may be reflected in other dimensions than those measured in this experiment.

B. Measurements of the Cerebellum

When the findings with regard to the magnitude of the difference between cerebellar measurements of the two strains are compared with the critical ratios for M as presented in Table 9, it will be seen that the differences, in terms of critical ratios, are of magnitude comparable to those found in the case of the measurement M. It is thus apparent that the greater weight of the brains of bright animals is a function of the size of cerebellum as well as the cerebrum.

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brain of the Norway rat (Mus Norvegicus), compared with the
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Figure 1. Dorsal Aspect of the Rat Brain, with Measurements of Width (WW') and Length (LL'll').

Figure 2. Lateral Aspect of the Rat Brain, with Measurement of Height (HH').

Figure 3. Plan of the Room in which Maze Experiments were Conducted.
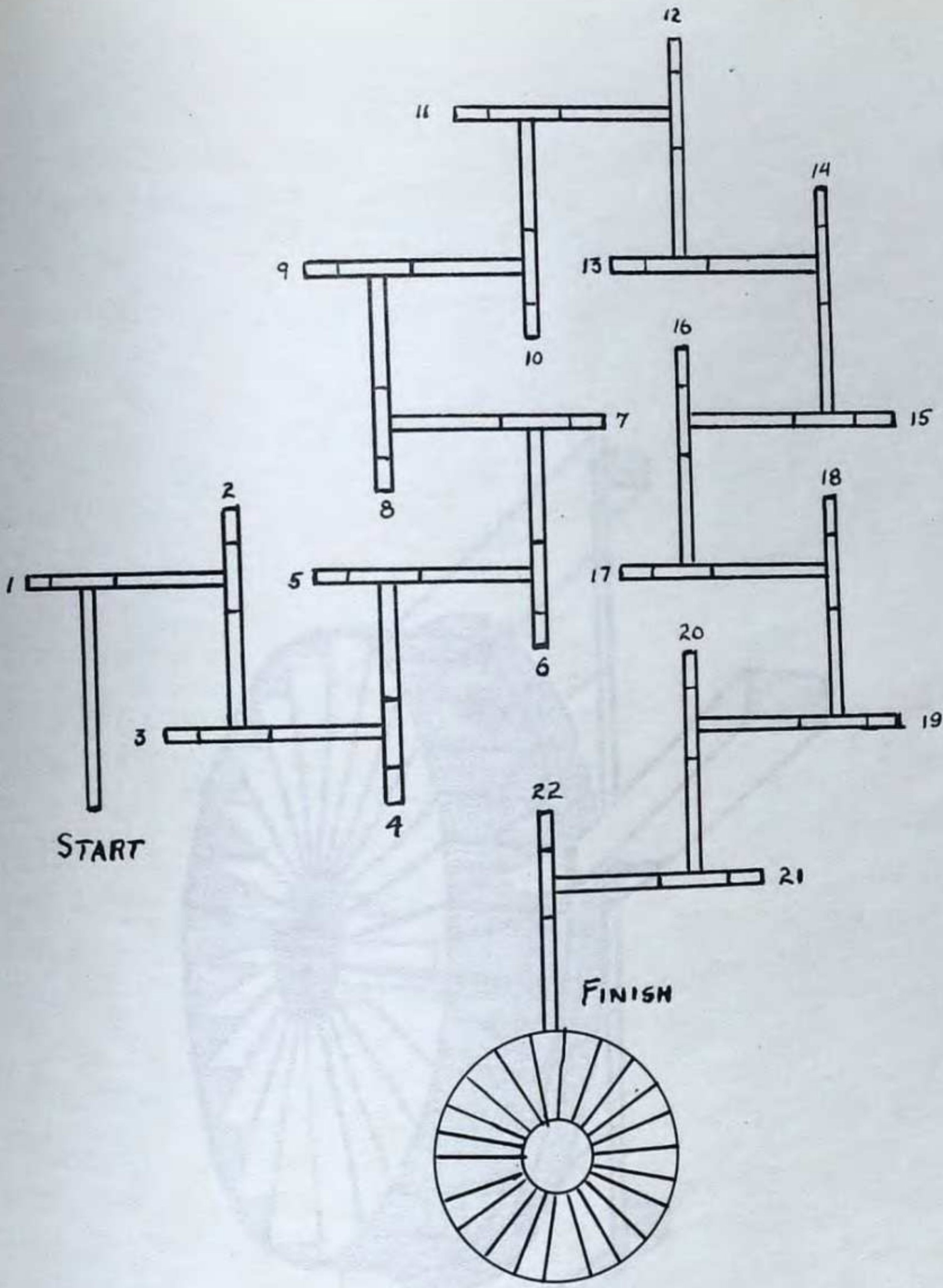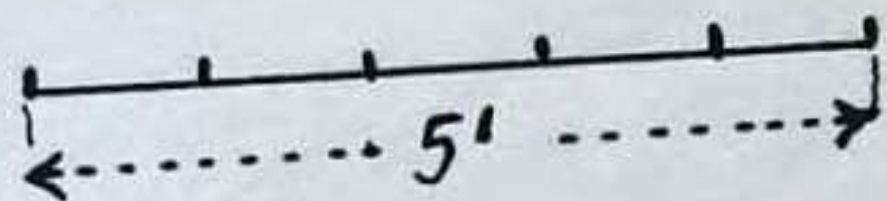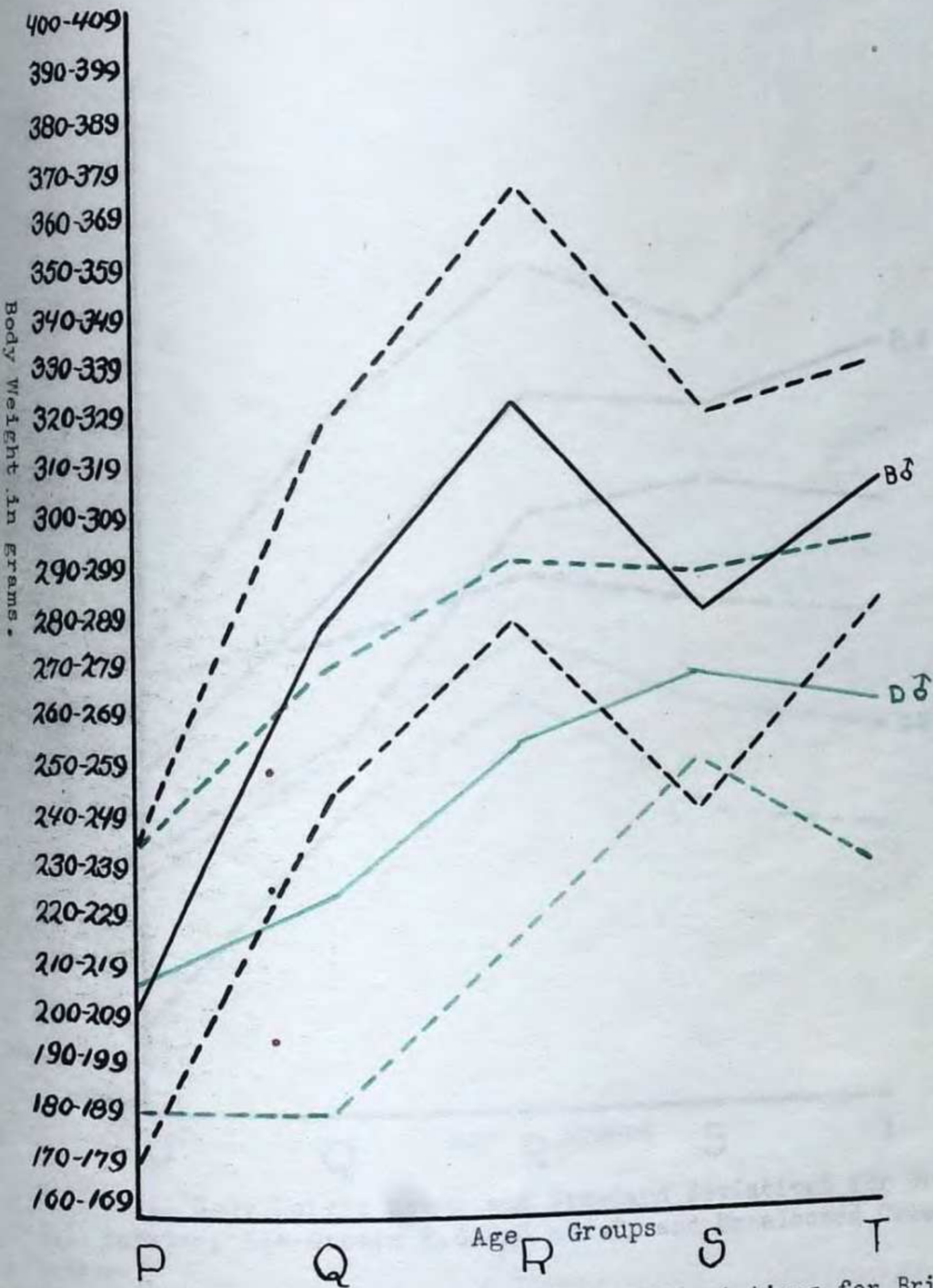
Figure 4. Pattern of the Maze.
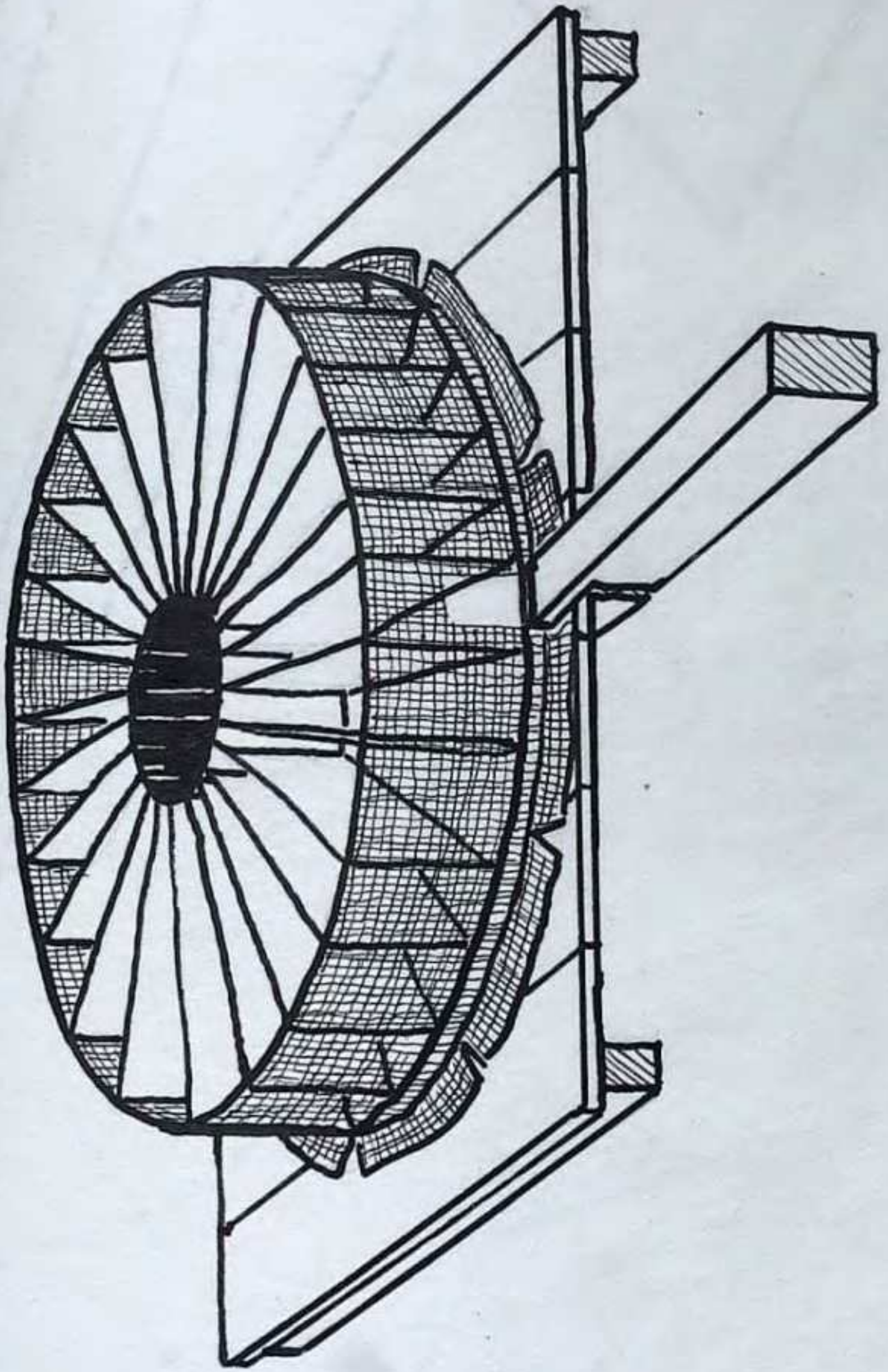
Figure 5. Rotating Food Table.
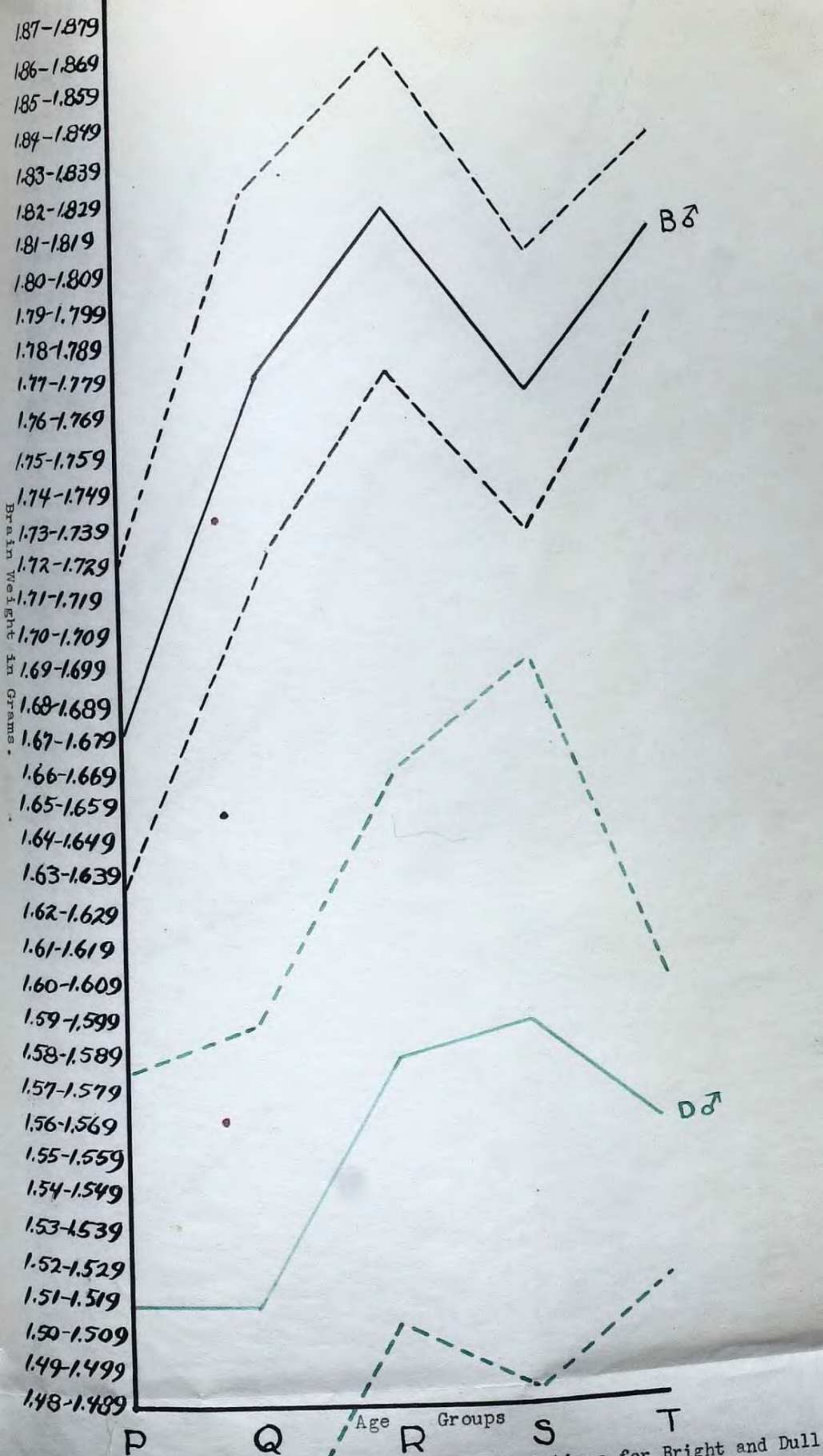
Figure 6. Brain Weight Means and Standard Deviations for Bright and Dull Males, Age-Groups P,Q,R,S, and T, and Unselected Colony Males.

Brain Weight in Grams.

1.80-1.809
1.79-1.799
1.78-1.789
1.77-1.779
1.76-1.769
1.75-1.759
1.74-1.749
1.73-1.739
1.72-1.729
1.71-1.719
1.70-1.709
1.69-1.699
1.68-1.689
1.67-1.679
1.66-1.669
1.65-1.659
1.64-1.649
1.63-1.639
1.62-1.629
1.61-1.619
1.60-1.609
1.59-1.599
1.58-1.589
1.57-1.579
1.56-1.569
1.55-1.559
1.54-1.549
1.53-1.539
1.52-1.529
1.51-1.519
1.50-1.509
1.49-1.499
1.48-1.489
1.47-1.479
1.46-1.469
1.45-1.459
1.44-1.449
1.43-1.439
1.42-1.429
1.41-1.419
1.40-1.409

B ♀

D ♀

P   Q   Age R Groups   S   T
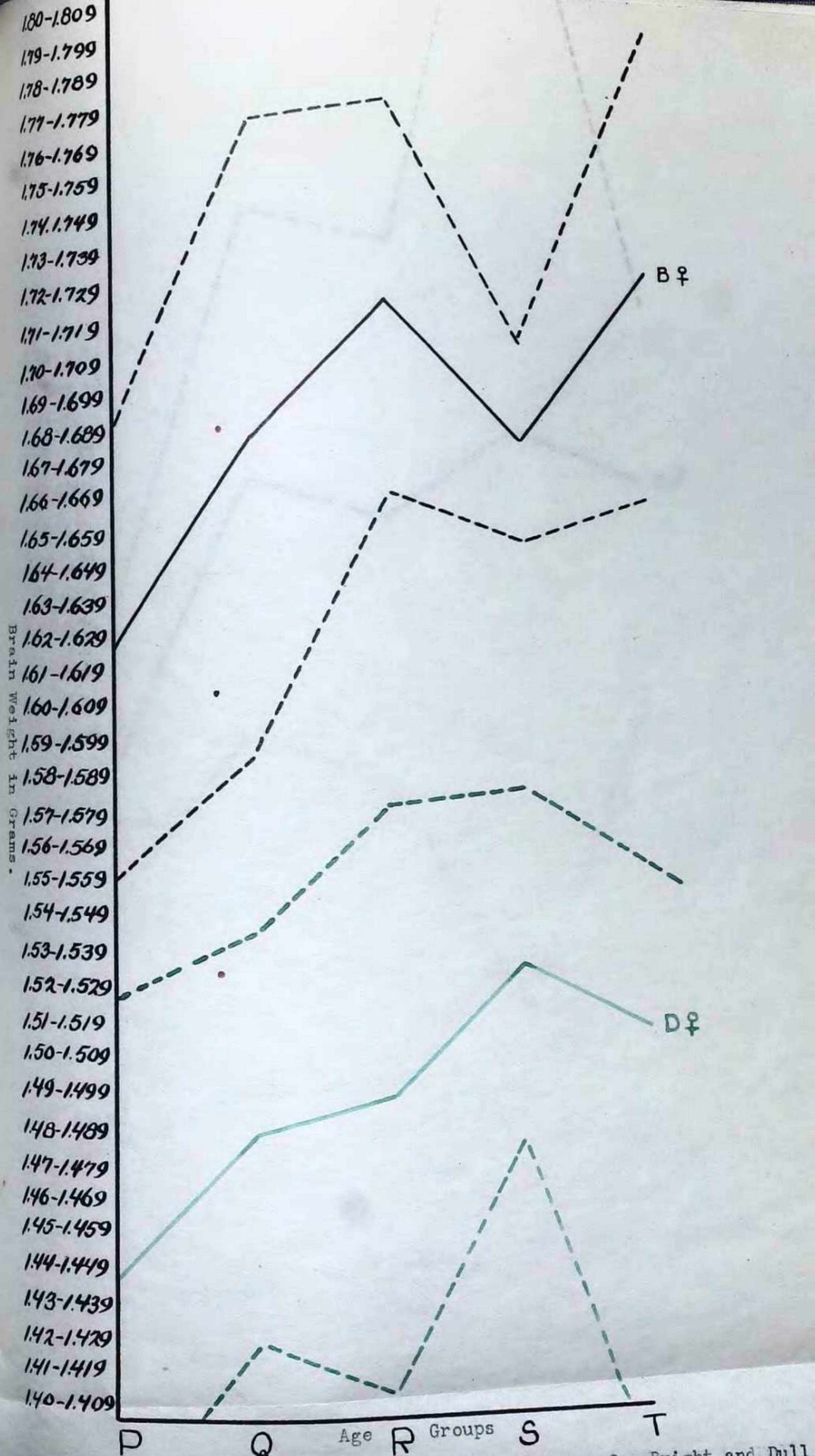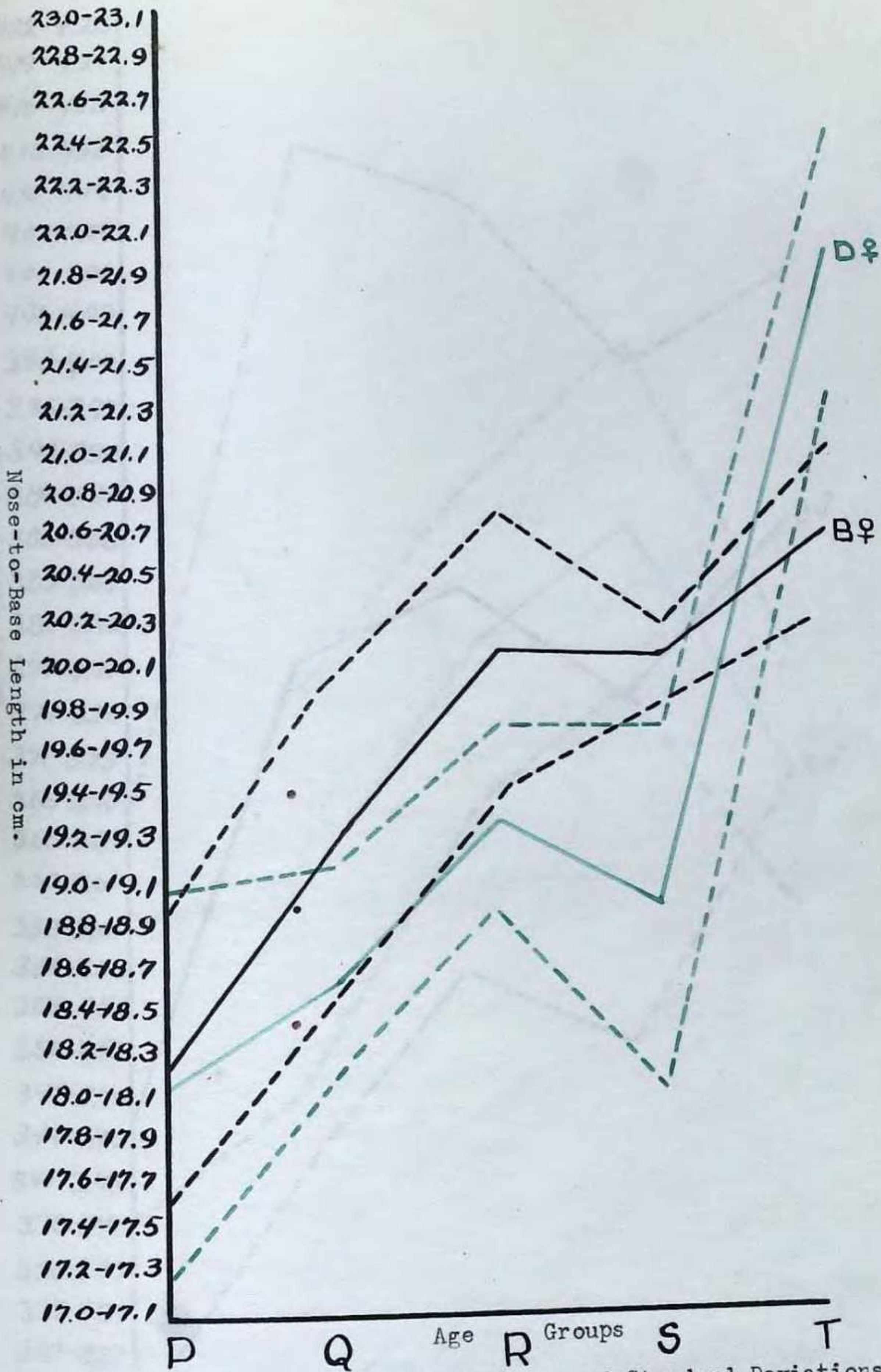
Figure 7. Brain Weight Means and Standard Deviations for Bright and Dull
Females, Age-Groups P, Q, R, S and T, and Unselected Colony Females.
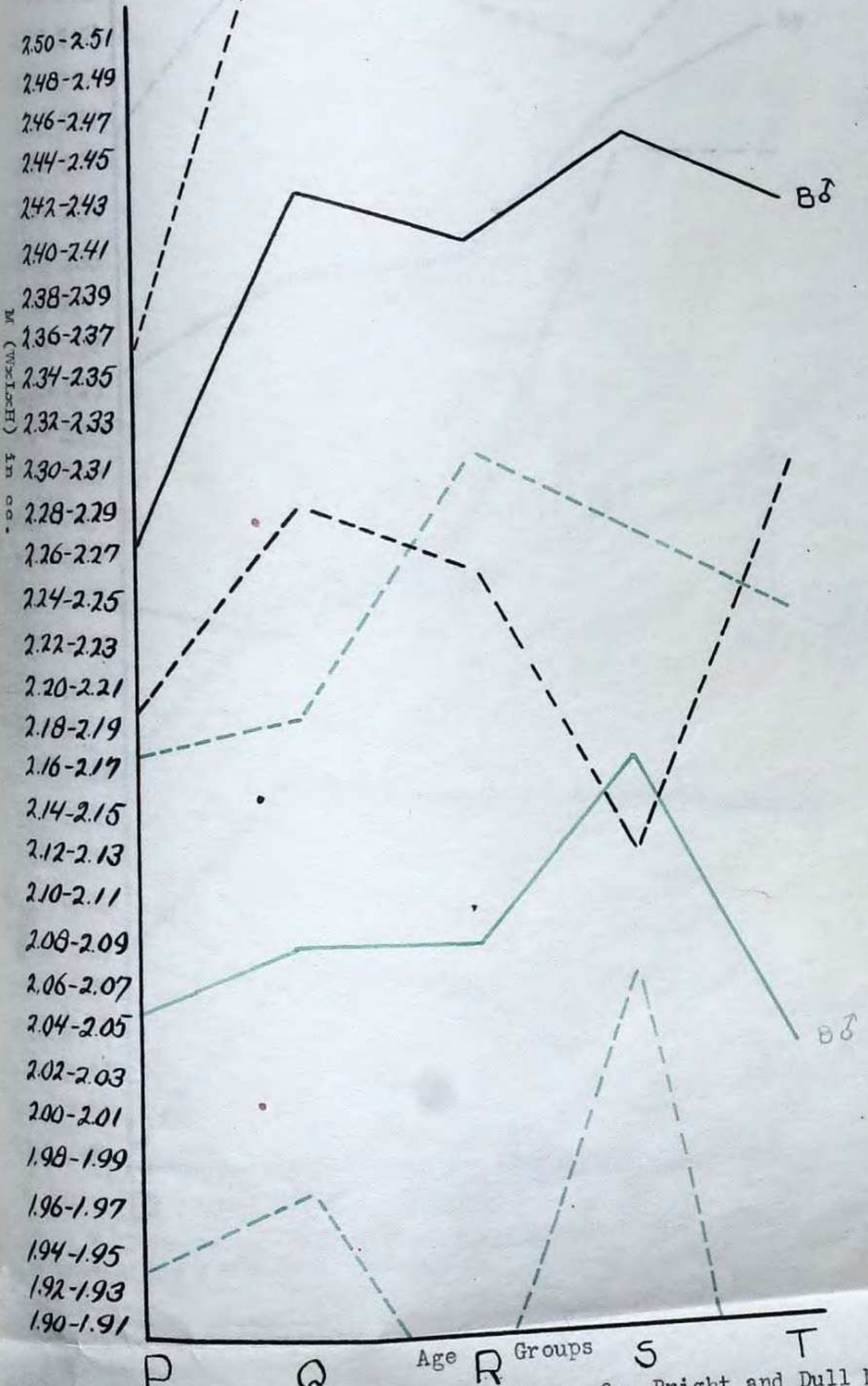
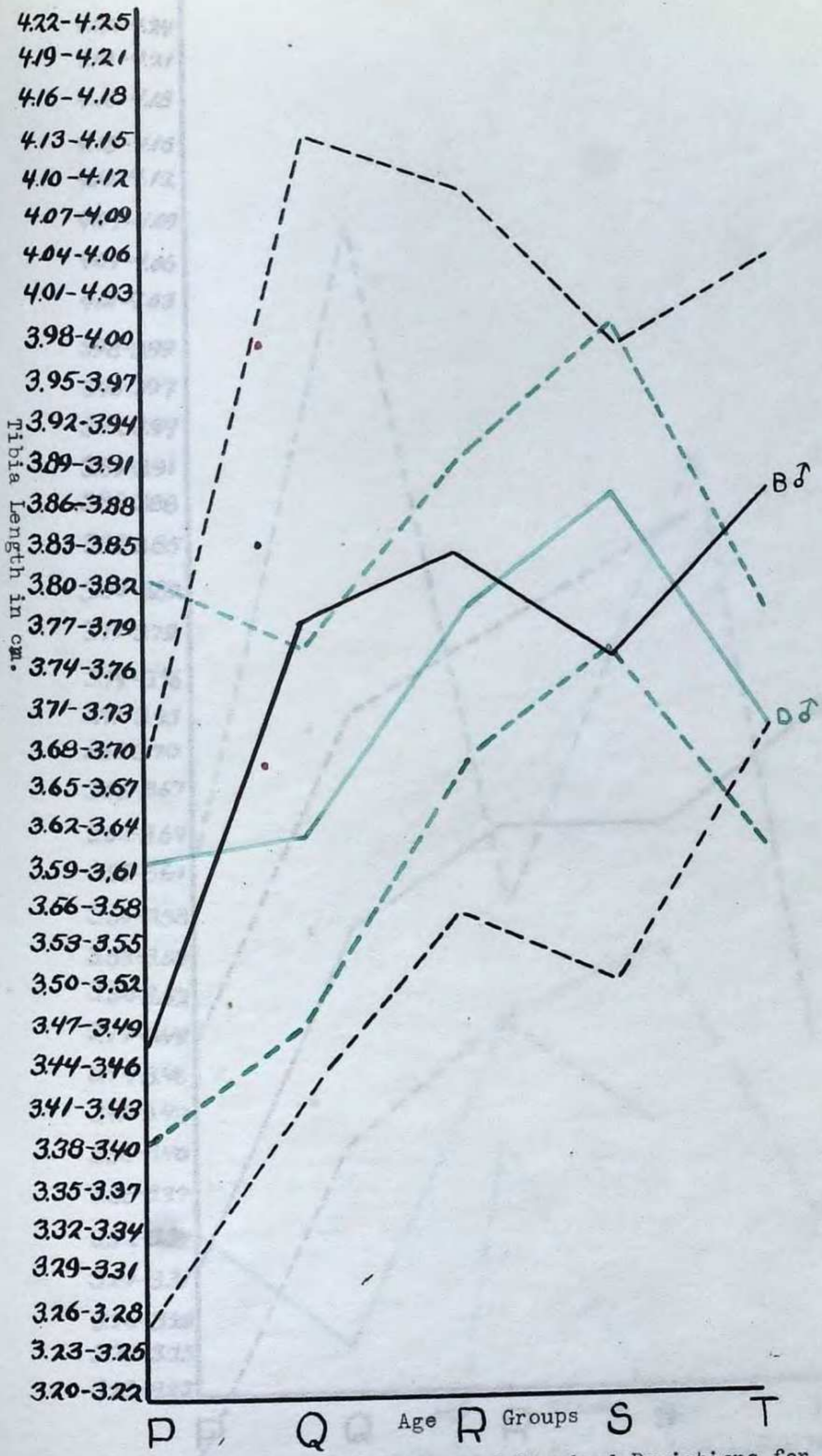Figure 8. M Means and Standard Deviations for Bright and Dull Males, Age-Groups P,Q,R,S and T, and Unselected Colony Males.

Y-axis labels (top to bottom):
2.50-2.51
2.48-2.49
2.46-2.47
2.44-2.45
2.42-2.43
2.40-2.41
2.38-2.39
2.36-2.37
2.34-2.35
2.32-2.33
2.30-2.31
2.28-2.29
2.26-2.27
2.24-2.25
2.22-2.23
2.20-2.21
2.18-2.19
2.16-2.17
2.14-2.15
2.12-2.13
2.10-2.11
2.08-2.09
2.06-2.07
2.04-2.05
2.02-2.03
2.00-2.01
1.98-1.99
1.96-1.97
1.94-1.95
1.92-1.93
1.90-1.91

B♀

D♀

Age   Groups

P   Q   R   S   T

Figure 9. M Means and Standard Deviations for Bright and Dull Males, ♀
Age-Groups P,Q,R,S and T, and Unselected Colony Males.
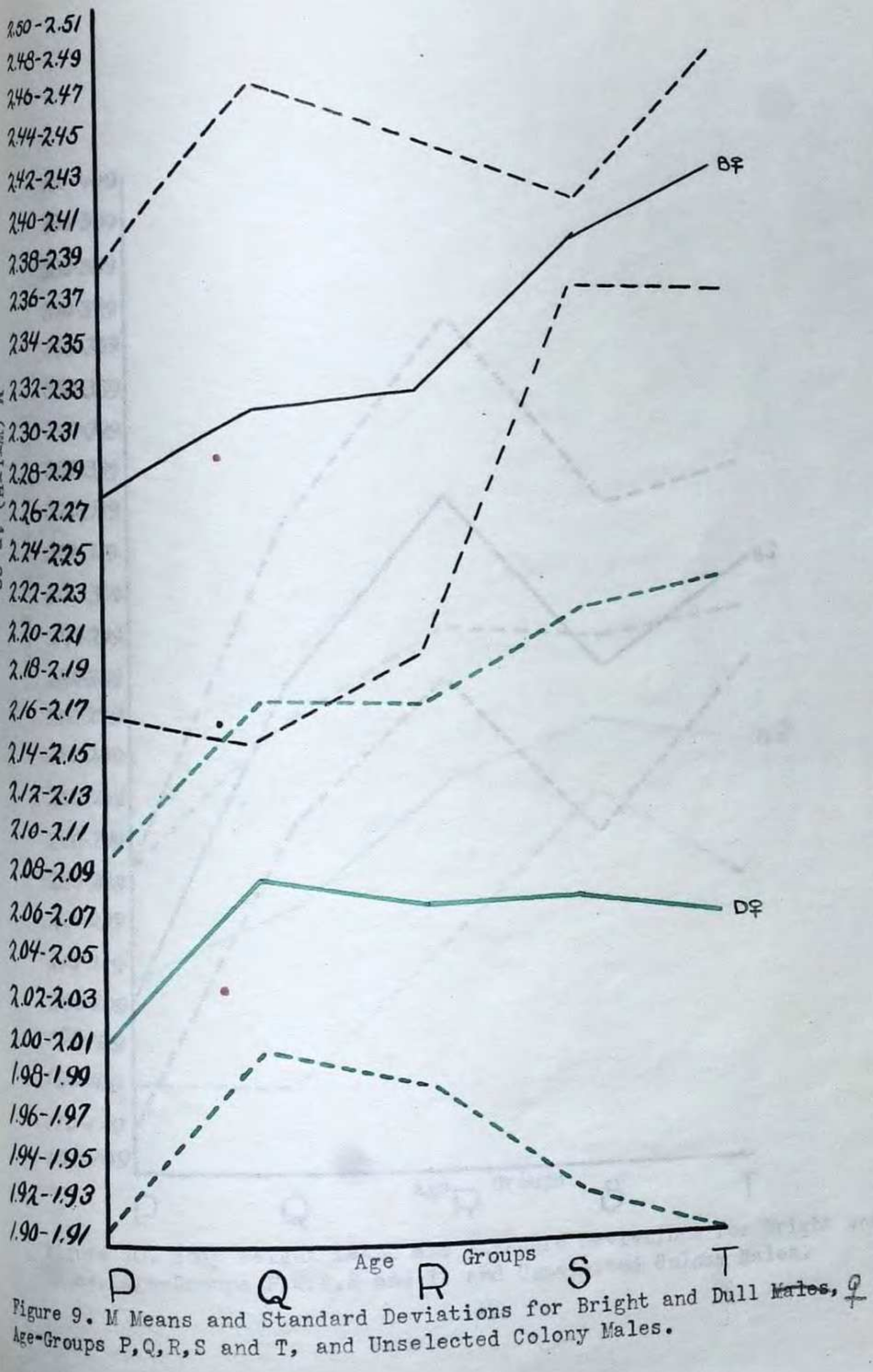
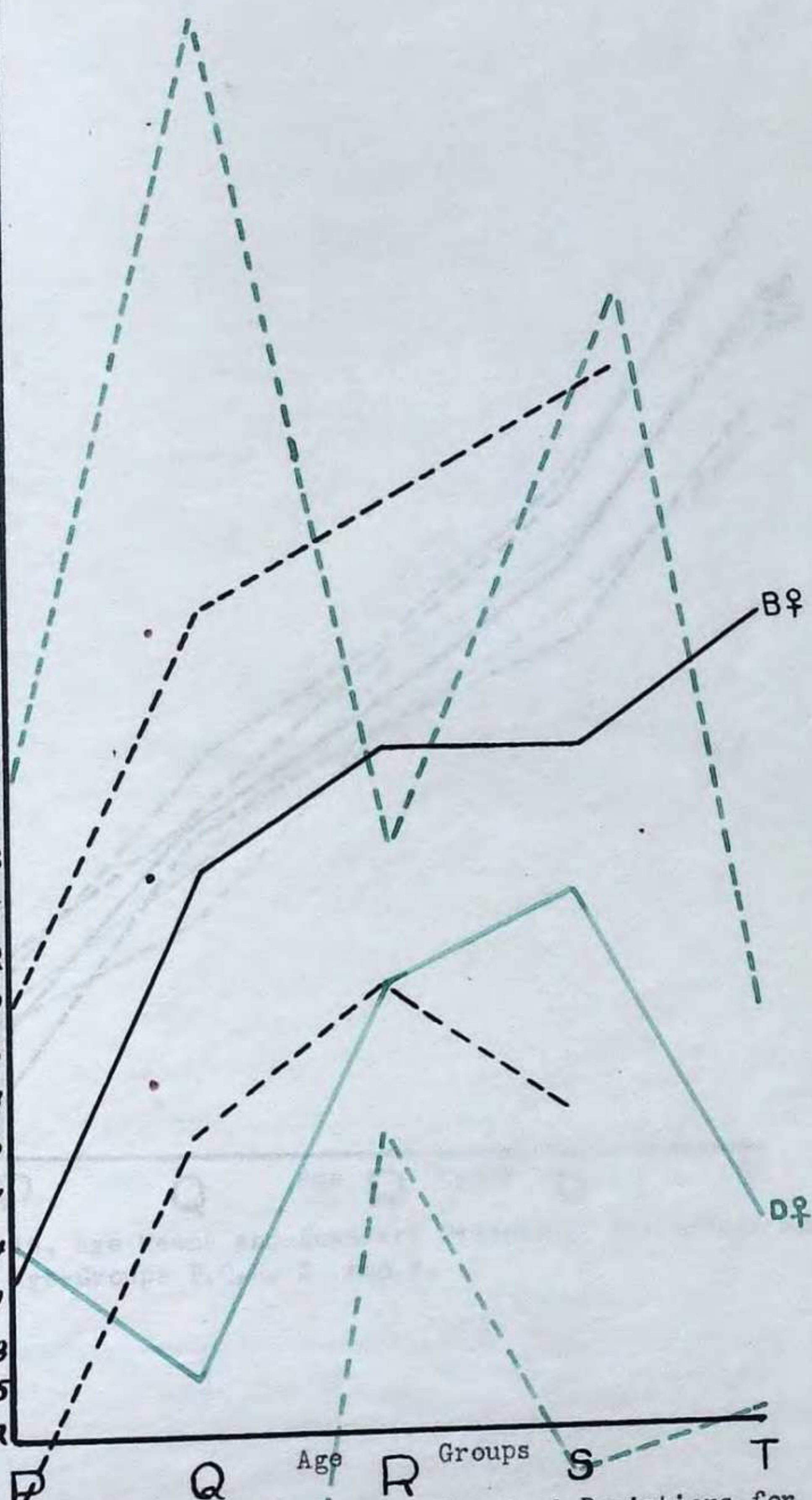Figure 10. Body Weight Means and Standard Deviations for Bright and Dull Males, Age-Groups P, Q, R, S and T, and Unselected Colony Males.
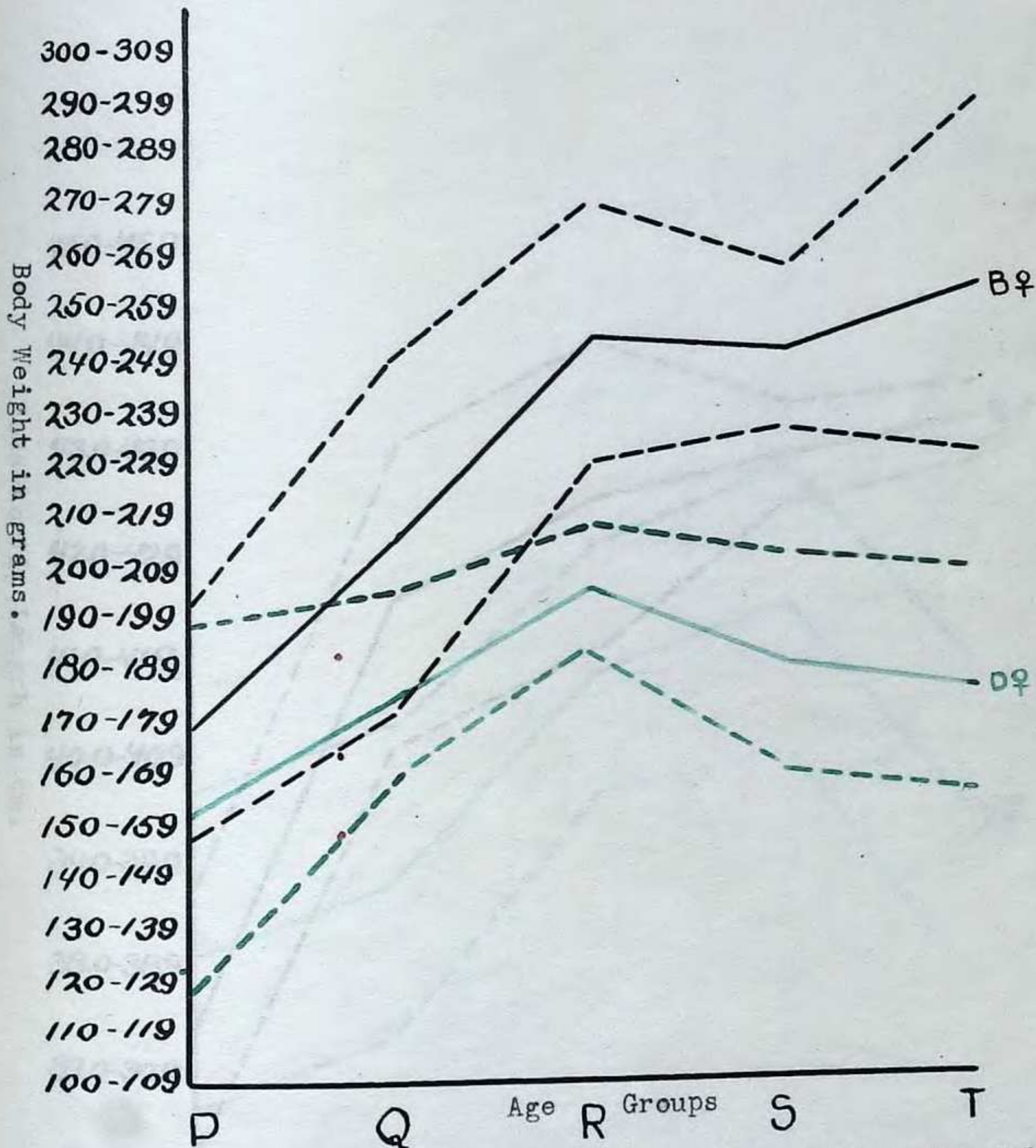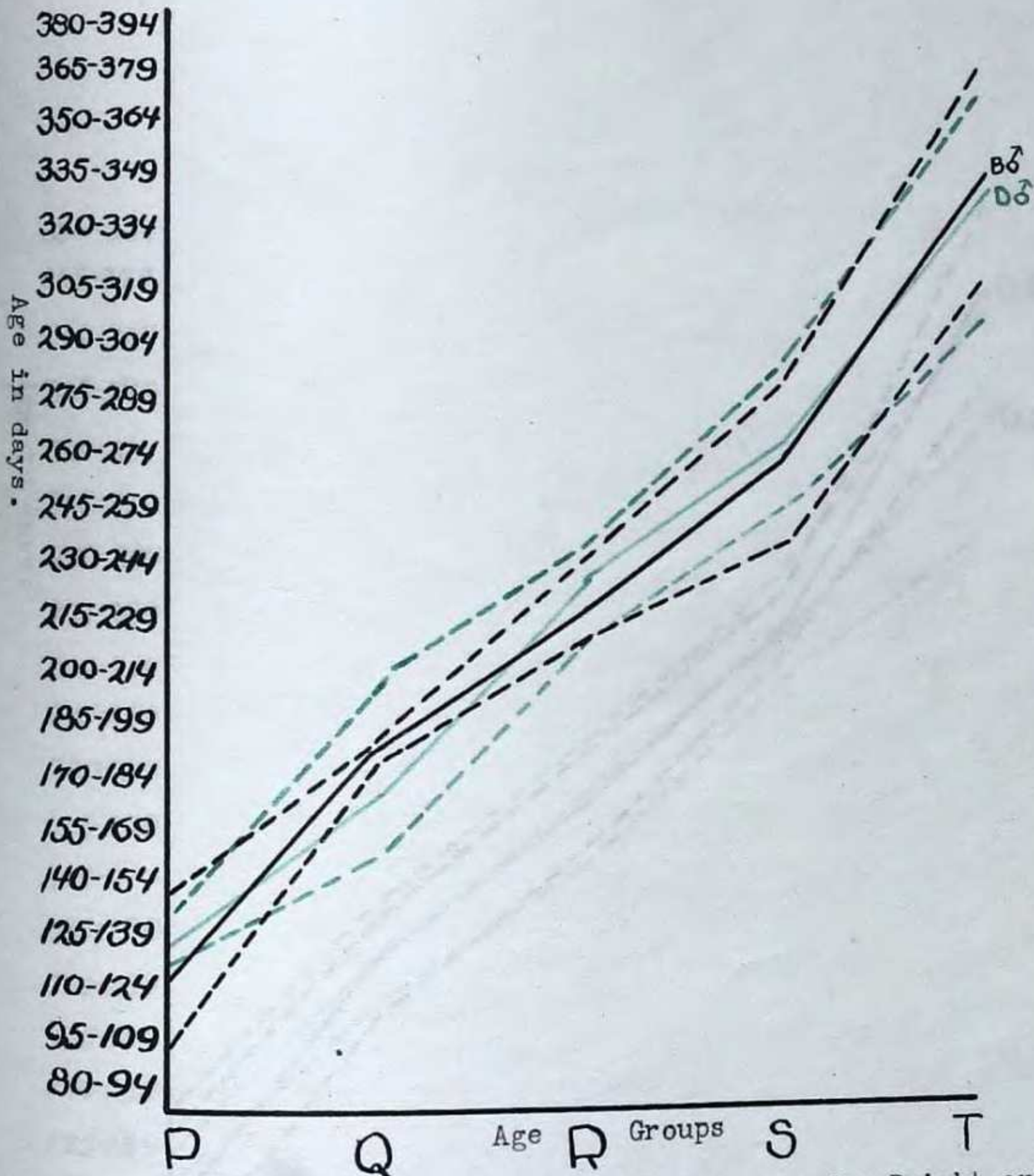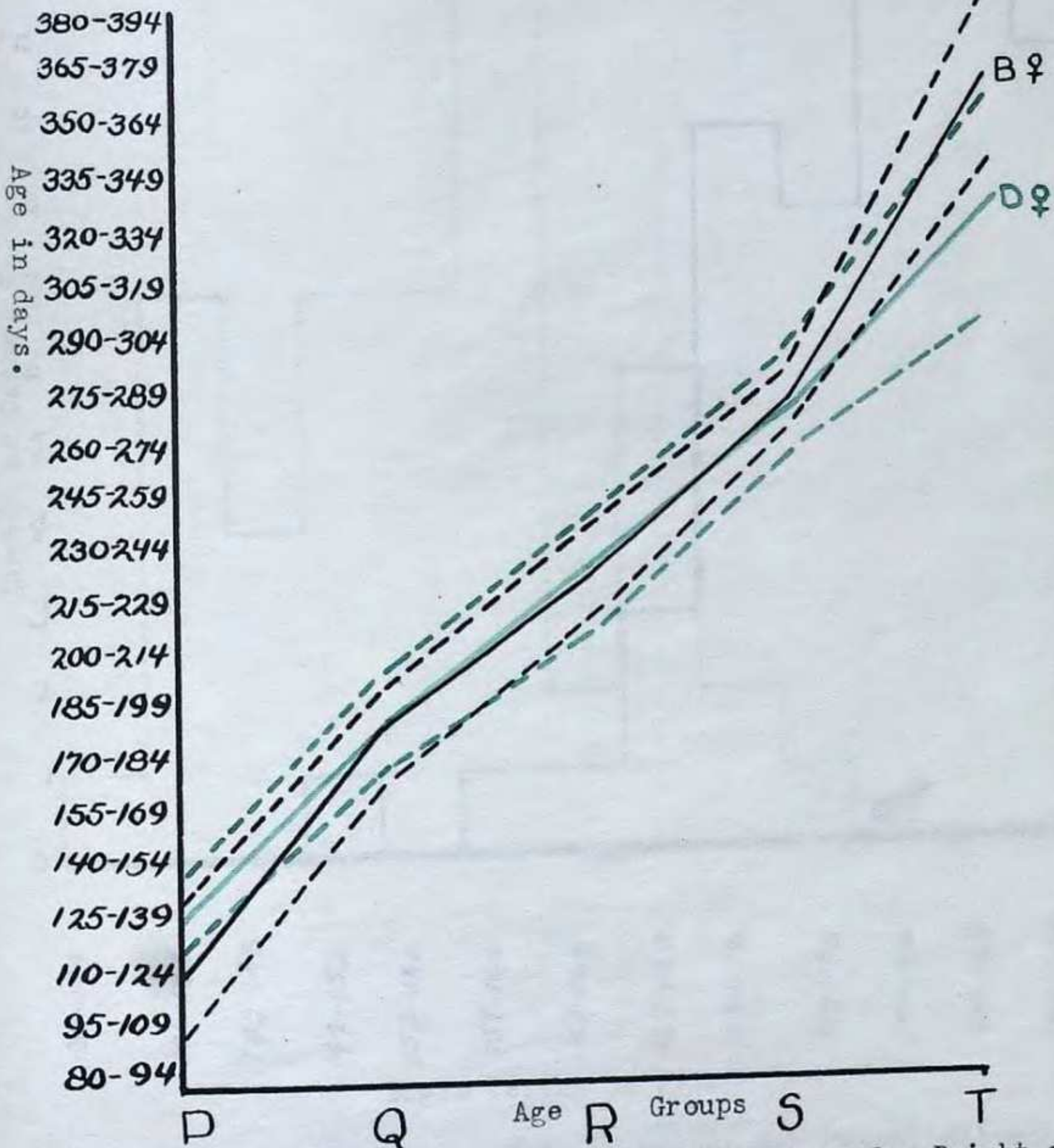
Figure 11. Body Weight Means and Standard Deviations for Bright and Dull Females, Age-Groups P,Q,R,S and T, and Unselected Colony Females.
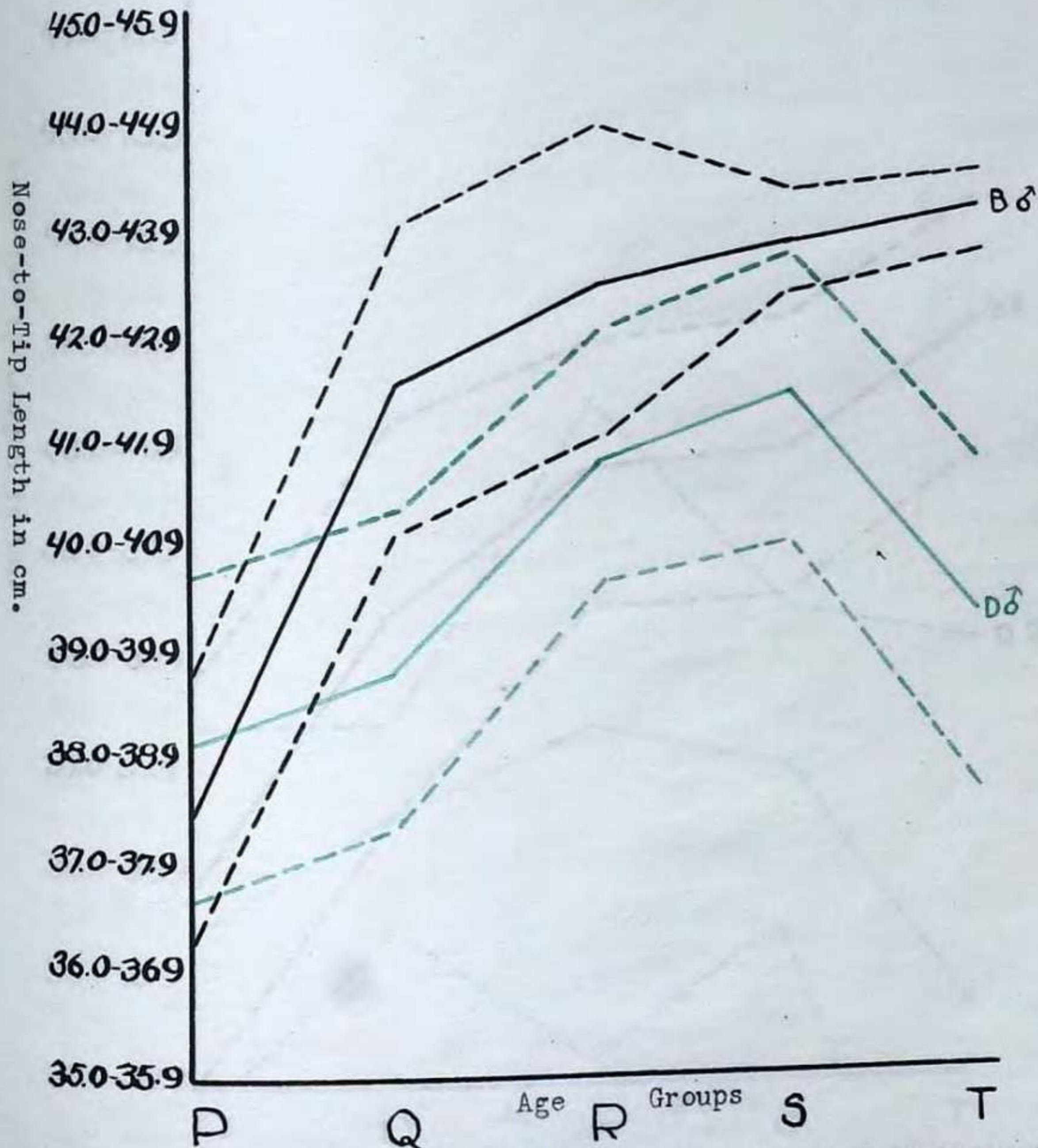
Figure 12. Nose-to-Tip Length Means and Standard Deviations for Bright and Dull Males, Age-Groups P,Q,R,S and T, and Unselected Colony Males.
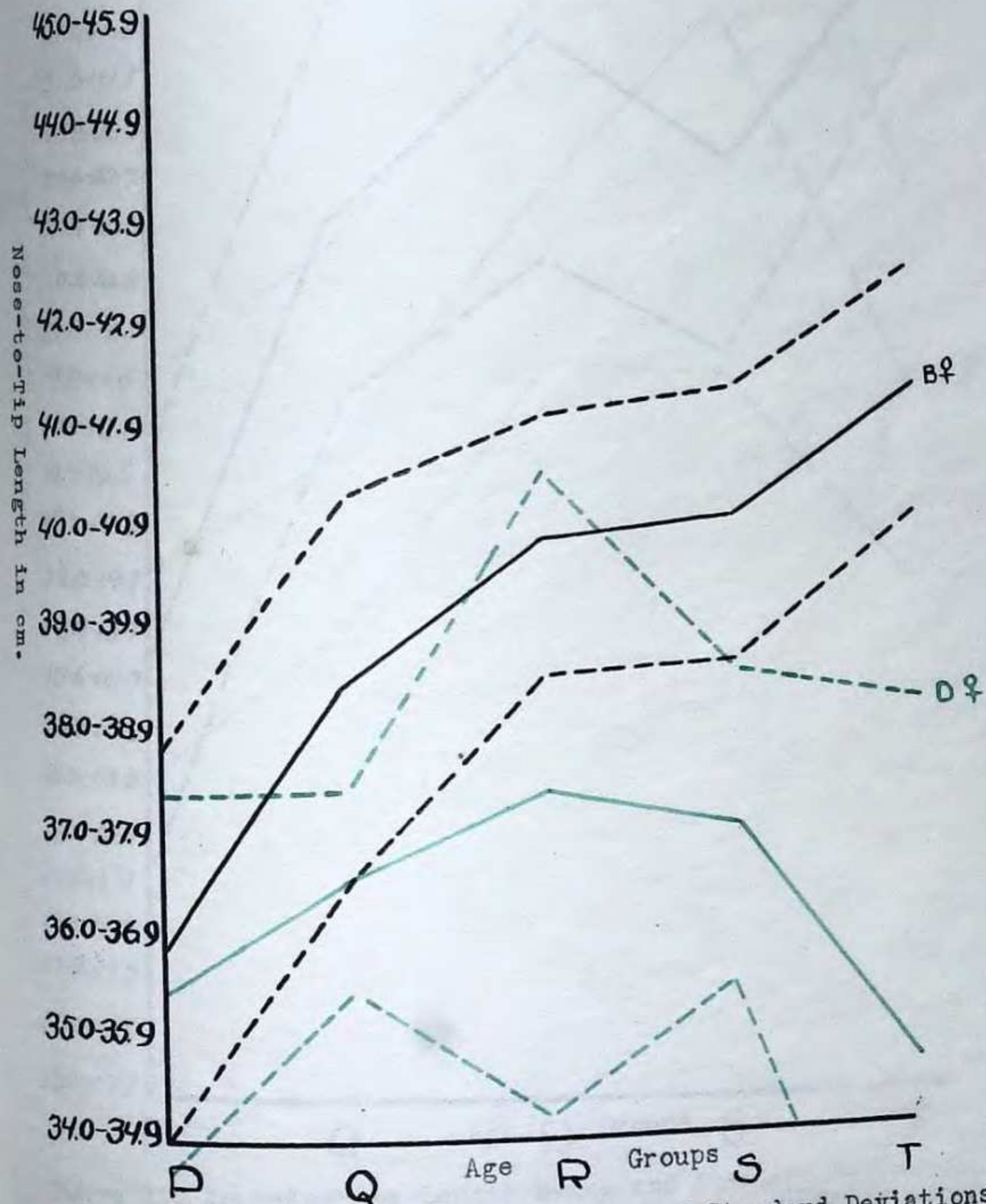
Figure 13. Nose-to-Tip Length Means and Standard Deviations for Bright and Dull Females, Age-Groups P, Q, R, S and T, and Unselected Colony Females.
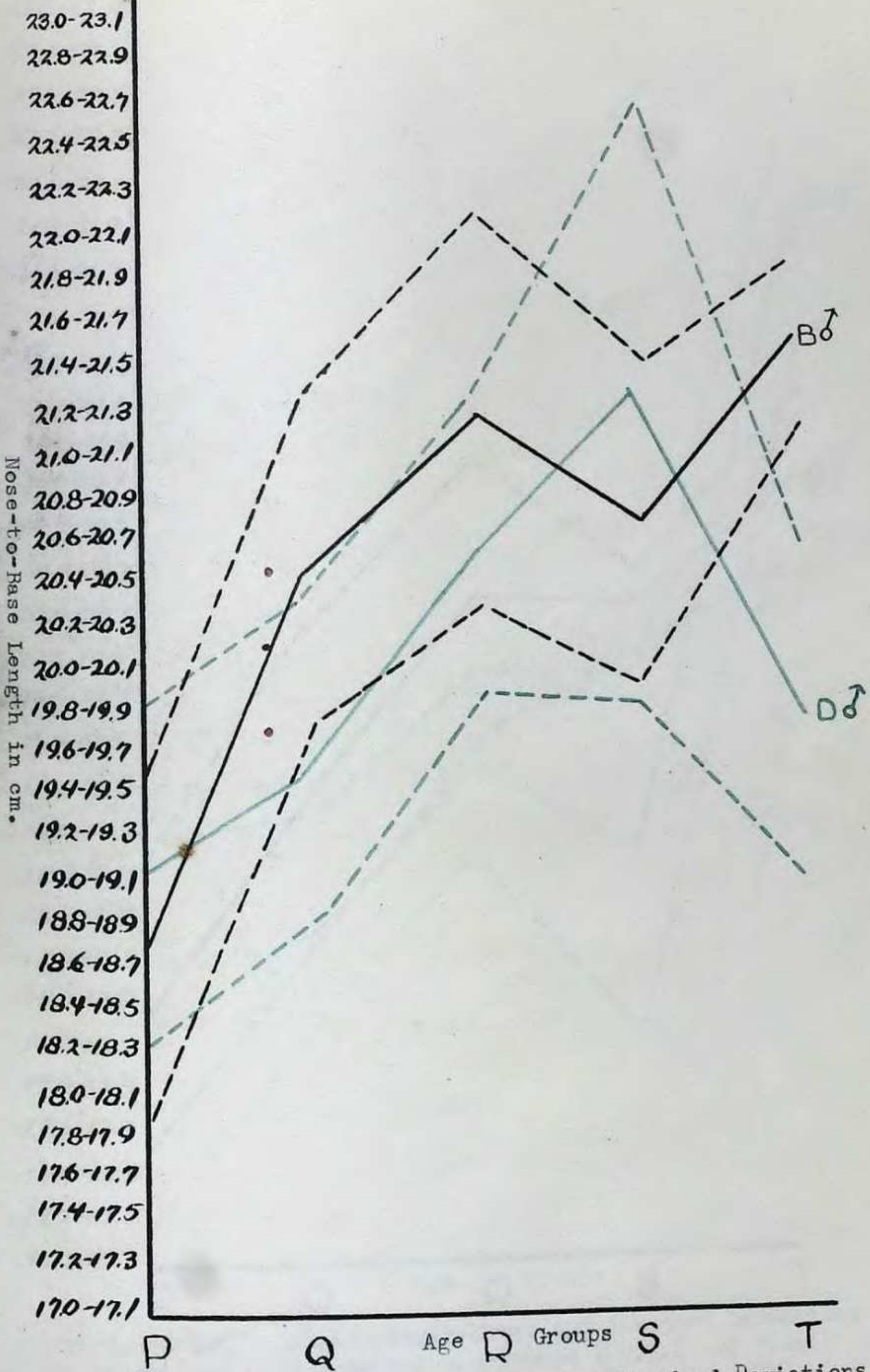
Figure 14. Nose-to-Base Length Means and Standard Deviations for Bright and Dull Males, Age-Groups P, Q, R, S and T, and Unselected Colony Males.

Figure 15. Nose-to-Base Length Means and Standard Deviations for Bright and Dull Females, Age-Groups P, Q, R, S and T, and Unselected Colony Females.

Figure 16. Tibia Length Means and Standard Deviations for Bright and Dull Males, Age-Groups P,Q,R,S and T and Unselected Colony Males.

Figure 17. Tibia Length Means and Standard Deviations for Bright and Dull Females, Age-Groups P,Q,R,S and T, and Unselected Colony Females.

Figure 18. Age Means and Standard Deviations for Bright and Dull Males, Age-Groups P, Q, R, S and T.

Figure 19. Age Means and Standard Deviations for Bright and Dull Females, Age-Groups P, Q, R, S and T.

Figure 20. Distribution of Brain Weight for Bright and Dull Males, Age-Groups Q, R, S and T.
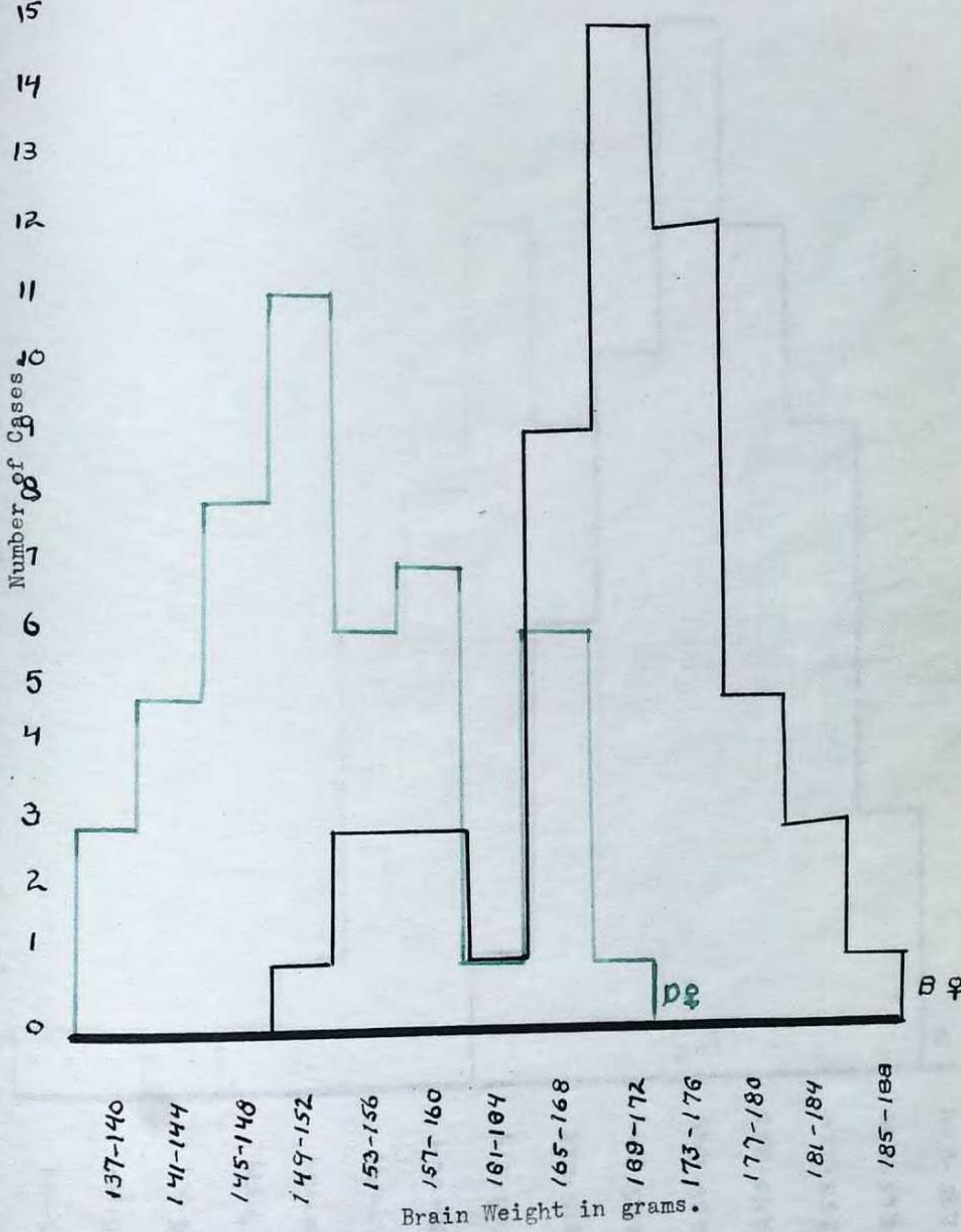
Figure 21. Distribution of Brain Weight for Bright and Dull Females, Age-Groups Q, R, S and T.
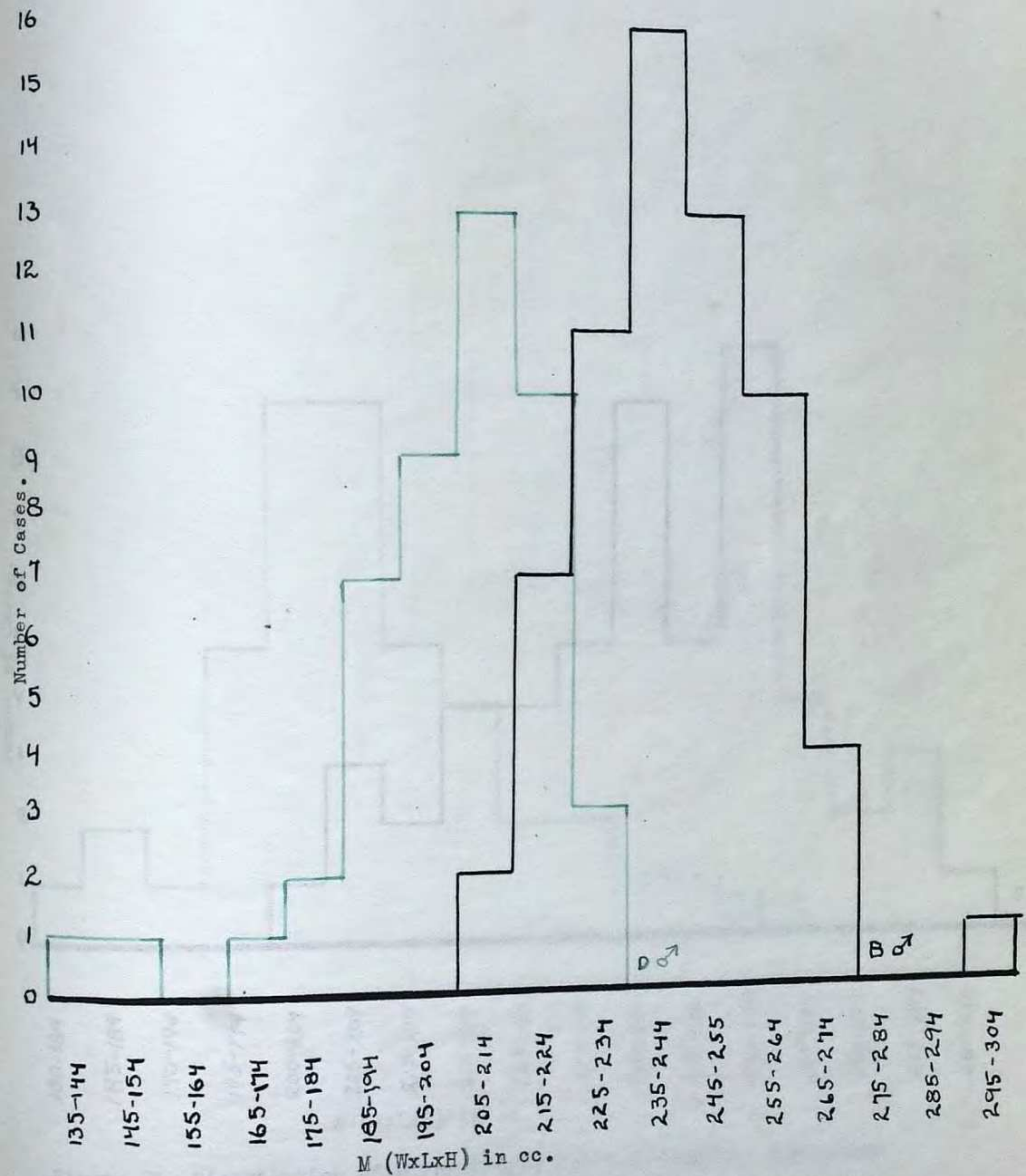
Figure 22. Distribution of M for Bright and Dull Males, Age-Groups
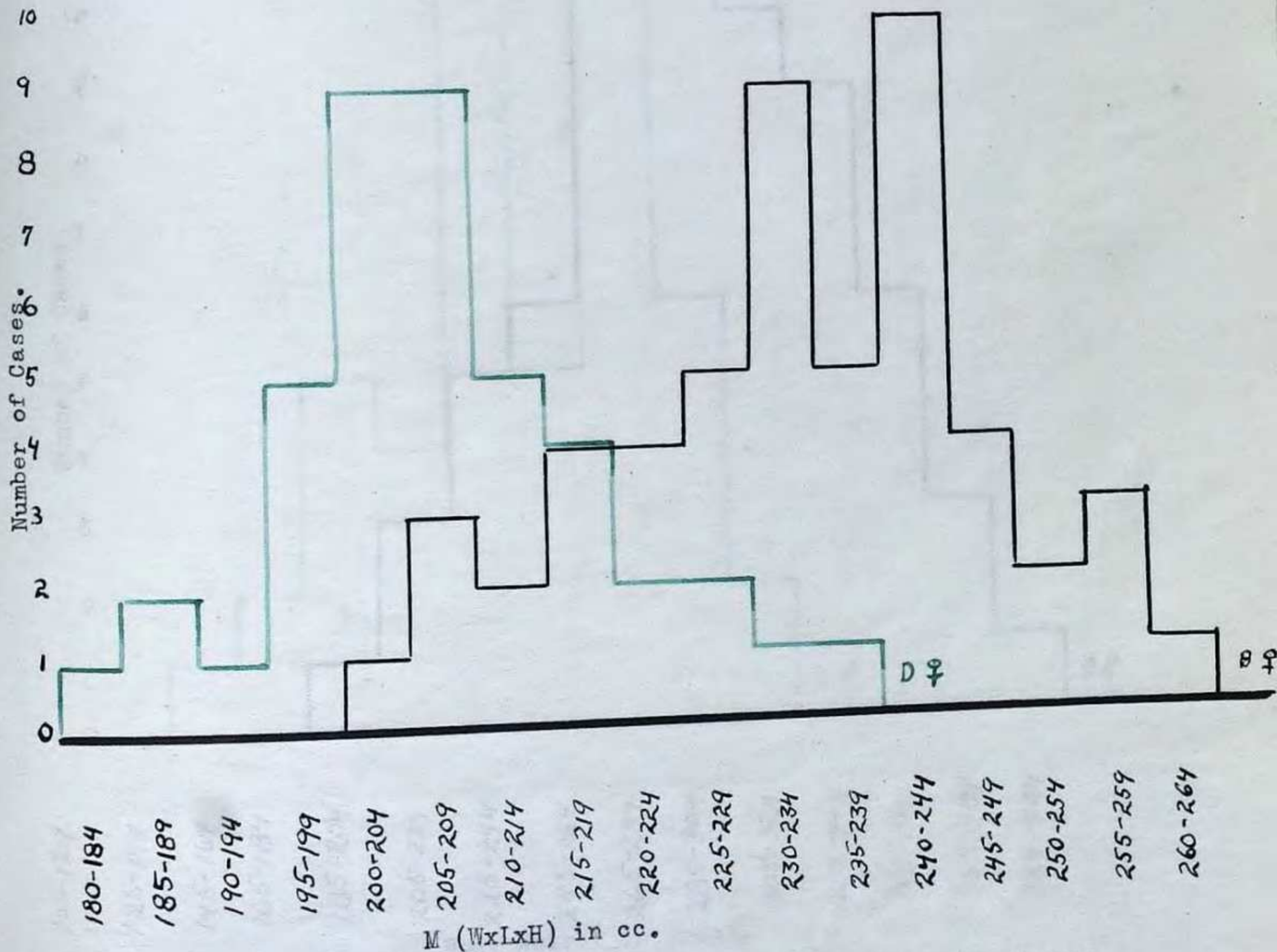Q, R, S and T.

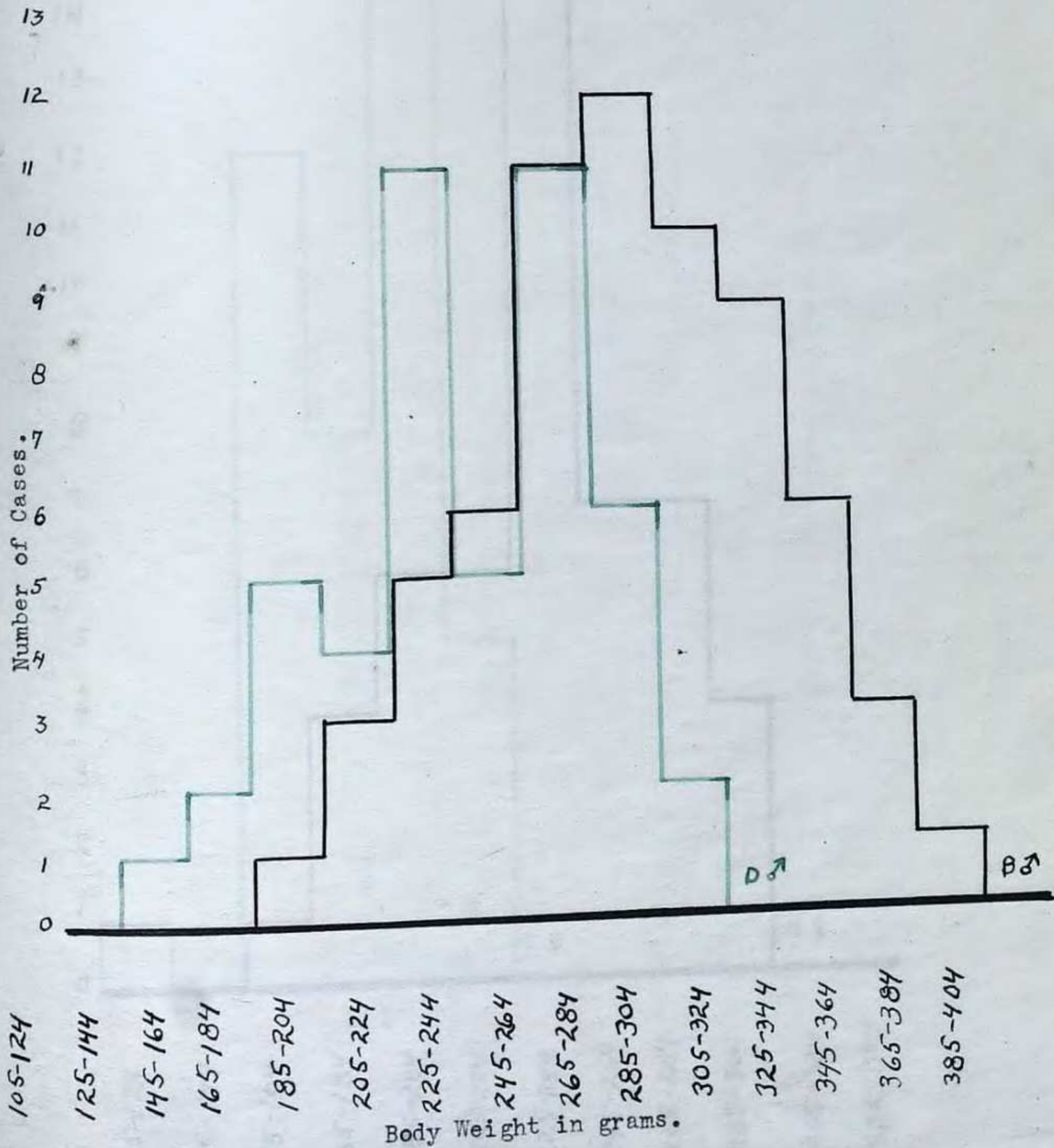Figure 23. Distribution of M for Bright and Dull Females, Age-Groups Q, R, S and T.

Figure 24. Distribution of Body Weight for Bright and Dull Males,
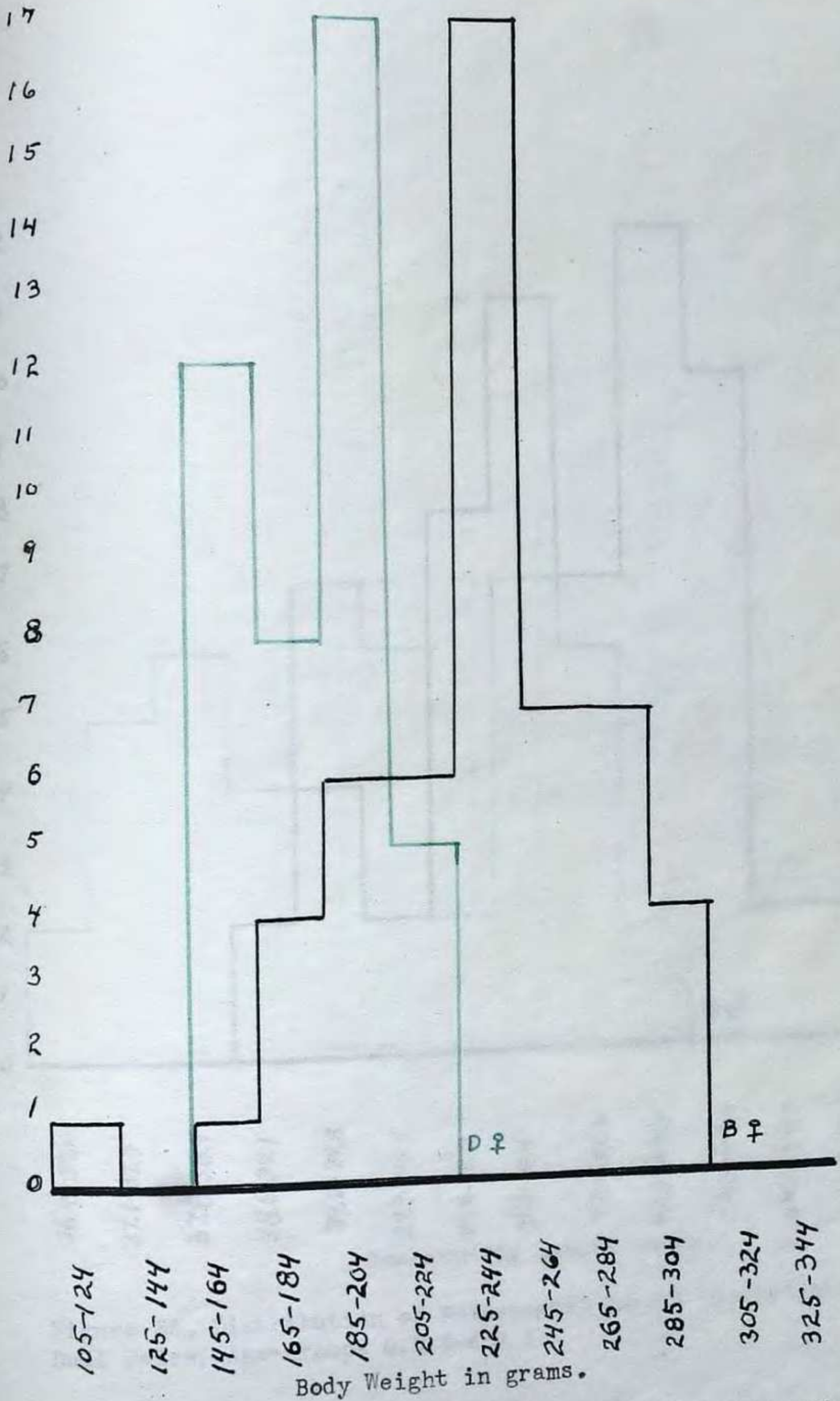Age-Groups Q, R, S and T.

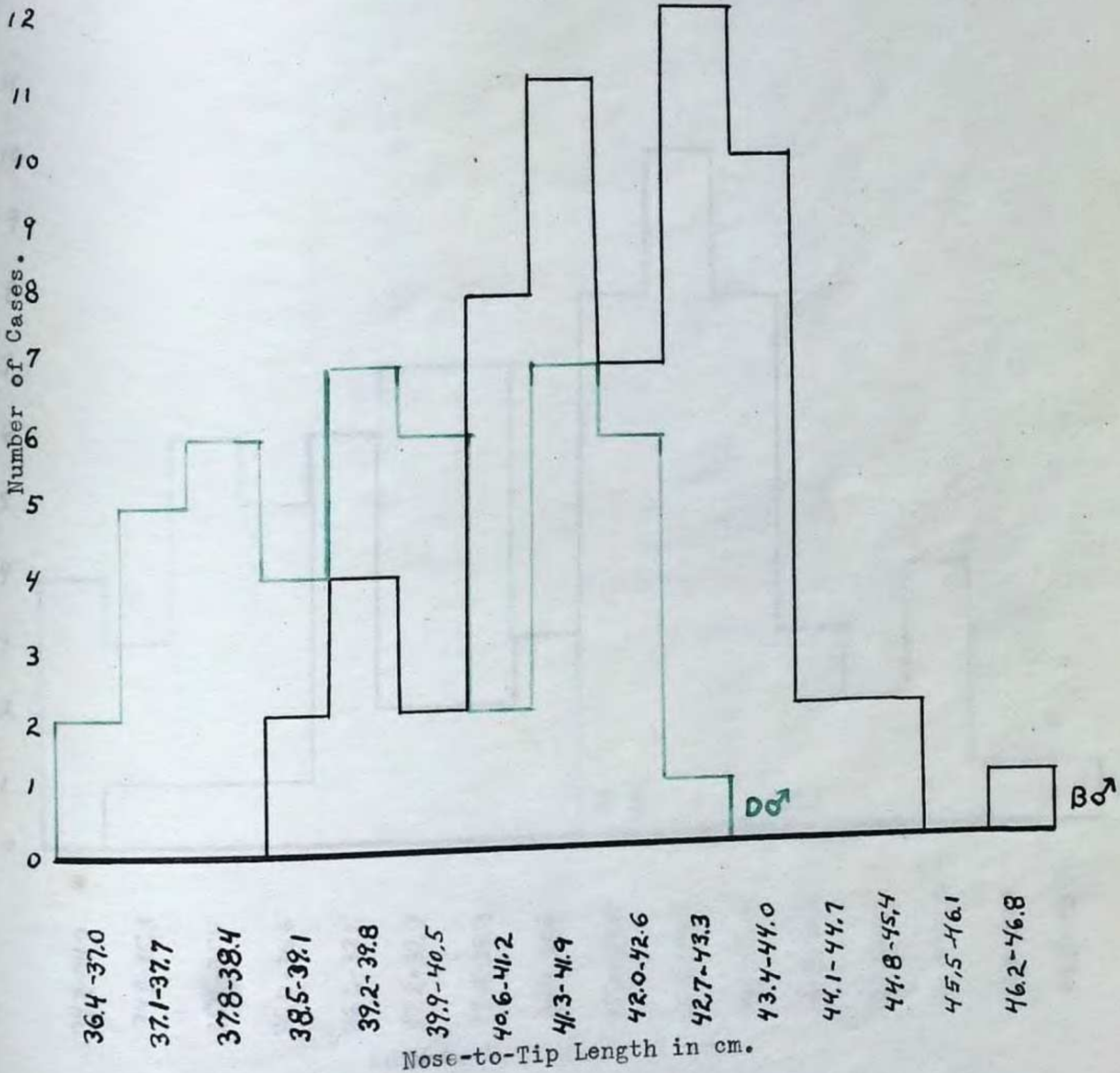Figure 25. Distribution of Body Weight for Bright and Dull Females, Age-Groups Q, R, S and T.

Figure 26. Distribution of Nose-to-Tip Length for Bright and Dull Males, Age-Groups Q,R,S and T.
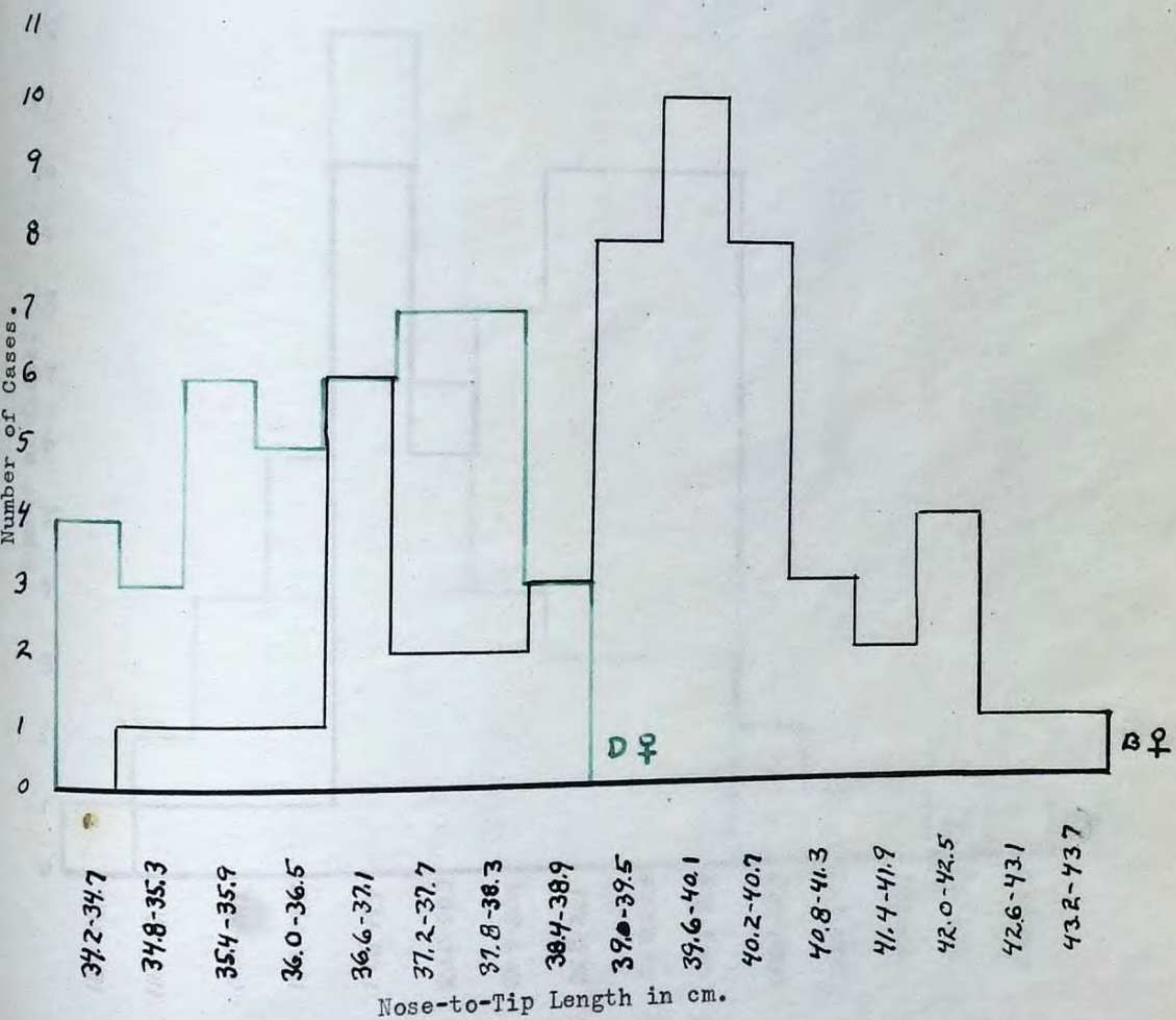
Figure 27. Distribution of Nose-to-Tip Length for Bright and Dull
Females, Age-Groups Q, R, S and T.

Figure 28. Distribution of Nose-to-Base Length for Bright and
Dull Males, Age-Groups Q, R, S and T.

Figure 29. Distribution of Nose-to-Base Length for Bright and Dull
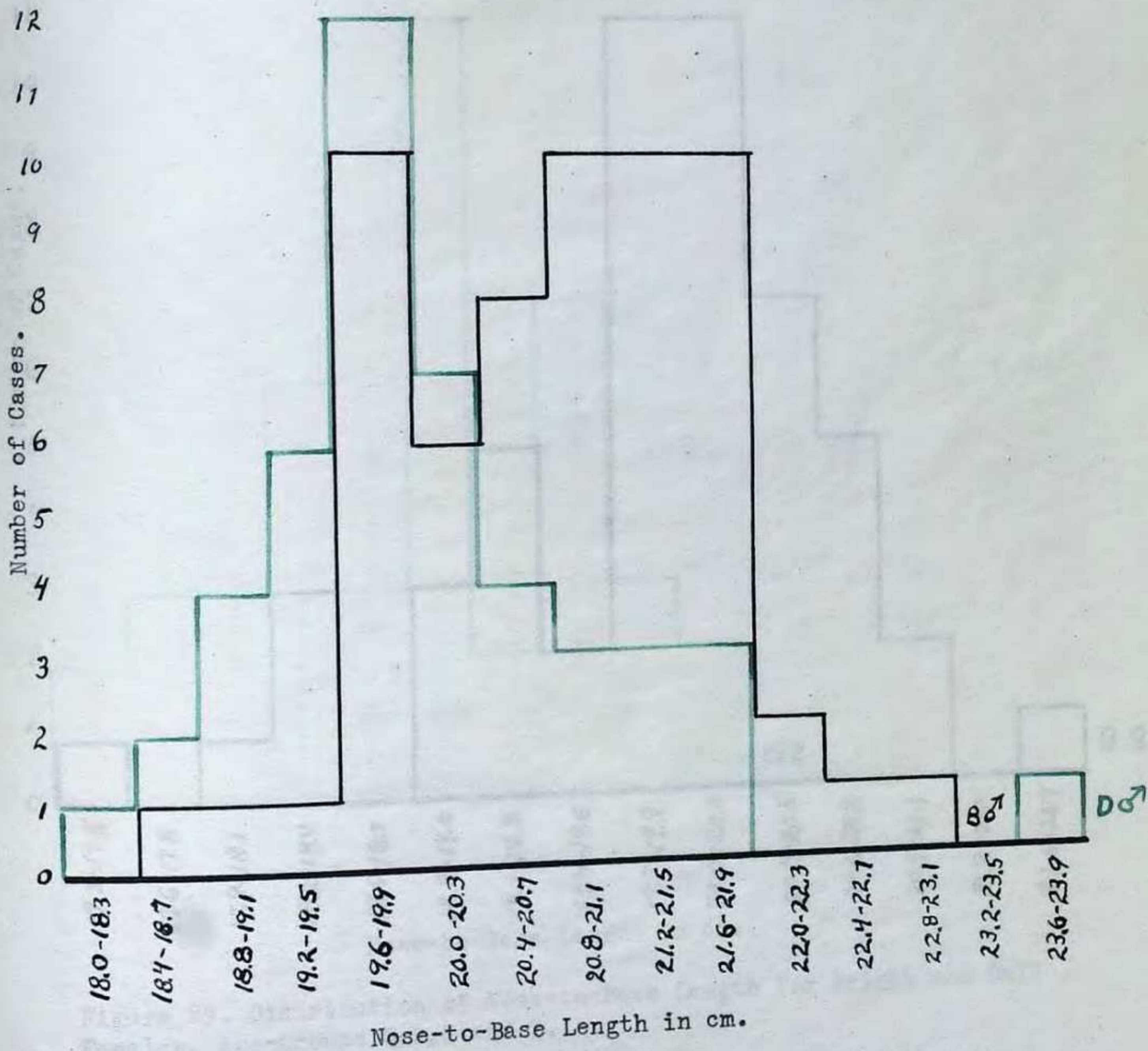Females, Age-Groups Q, R, S and T.
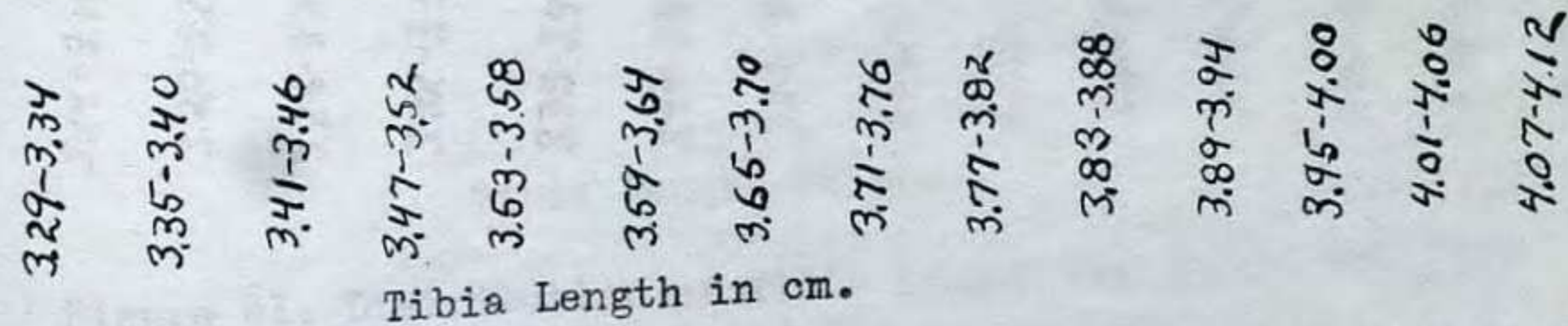
Figure 30. Distribution of Tibia Length for Bright and Dull Males, Age-Groups Q, R, S and T.
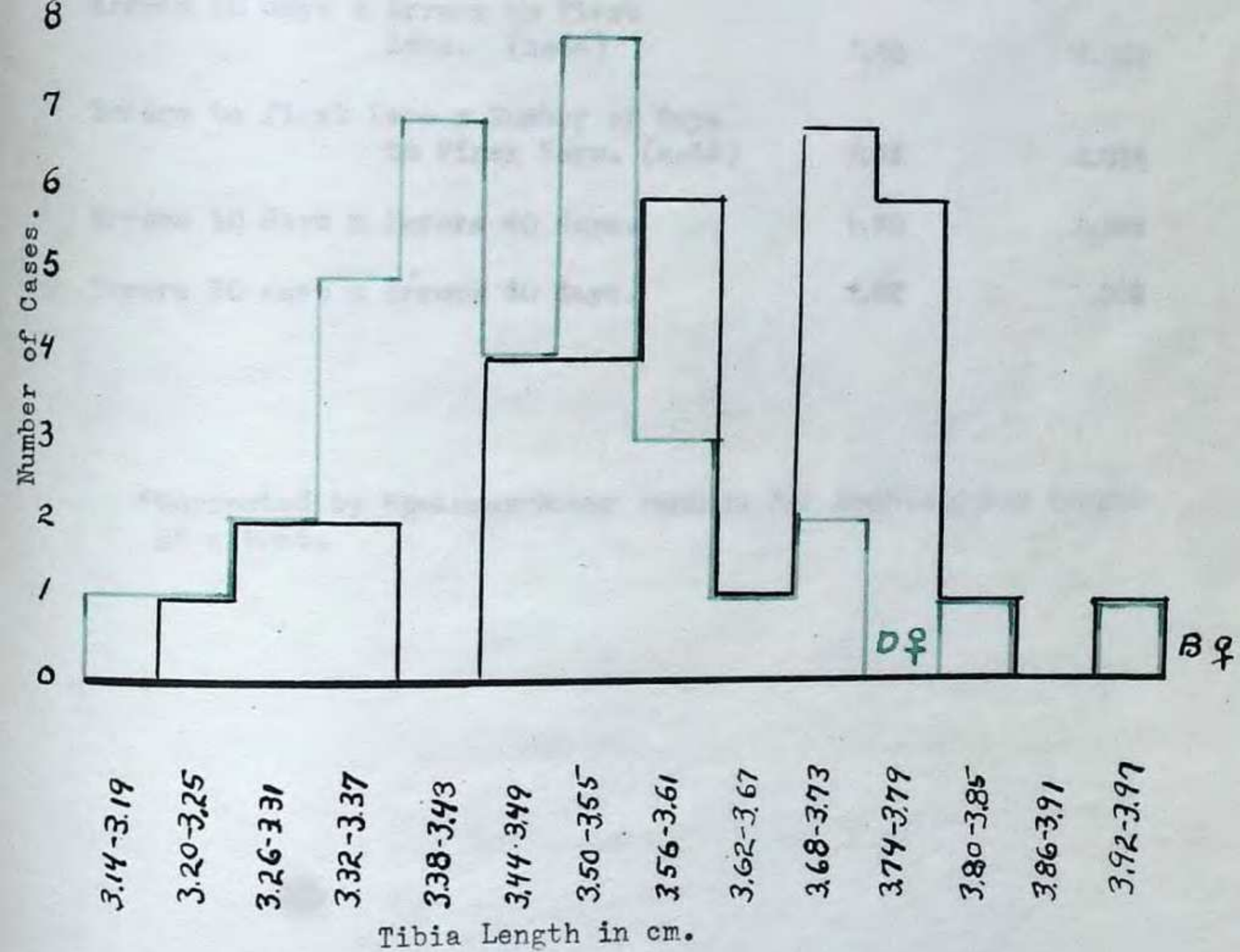
Figure 31. Distribution of Tibia Length for Bright and Dull Females, Age-Groups Q, R, S and T.

TABLE 1

Reliability Coefficients and Correlations between Maze Scores of Un-
selected Animals from Group I. One Hundred Males and Females.

*Odd-even Reliability, 10 days.	+.83	±.021
*Odd-even Reliability, 20 days.	+.93	±.009
*Odd-even Reliability, 40 days.	+.96	±.005
Errors 10 days x Errors 20 days.	+.63	±.041
Errors 20 days x Errors to First Zero. (n=44)	+.60	±.065
Errors to first Zero x Number of Days to First Zero. (n=44)	+.93	±.014
Errors 10 days x Errors 40 days.	+.70	±.034
Errors 20 days x Errors 40 days.	+.82	±.022

*Corrected by Spearman-Brown formula for doubling the length
of a test.

TABLE 2

Intercorrelations Between Maze Scores and Anatomical Variables.
Eighty-eight Males from Groups I and II

Variable	1	2	3	4	5	6	7	8	9	10
1 Errors: 20 Days	+.93 ±.009									
2 Errors: 10 Days	+.63 ±.041	+.83 ±.021								
3 Body Weight	-.24 ±.068	-.18 ±.070								
4 Nose-to-Tip Length	-.19 ±.069	-.19 ±.069	+.67 ±.040	+.94 ±.008						
5 Nose-to-Base Length	-.20 ±.069	-.17 ±.070	+.72 ±.035	+.92 ±.001	+.90 ±.014					
6 Brain Weight	-.24 ±.068	-.15 ±.070	+.43 ±.059	+.40 ±.060	+.49 ±.055					
7 Brain Width	-.19 ±.069	-.16 ±.070	+.38 ±.062	+.35 ±.063	+.32 ±.065	+.64 ±.042				
8 Brain Length	-.07 ±.072	+.03 ±.072	+.28 ±.066	+.52 ±.053	+.40 ±.060	+.49 ±.055	+.29 ±.066			
9 M	-.29 ±.066	-.27 ±.067	+.32 ±.065	+.24 ±.068	+.27 ±.068	+.76 ±.030	+.54 ±.051	+.56 ±.049		
10 Tibia Length	-.10 ±.071	-.01 ±.072	+.59 ±.047	+.81 ±.025	+.78 ±.028	+.41 ±.060	+.35 ±.063	+.29 ±.066	+.24 ±.068	+.92 ±.011

TABLE 3

Comparison of Bright and Dull Animals

Genera- Var. tion	Sex	Bright Animals			Dull Animals				
		N	Mean	σ	N	Mean	σ	Diff.	C.R.
Brain Weight									
F_{11}	♂	39	1.791	.091	30	1.553	.092	.238	10.48
F_{12}	♂	35	1.752	.092	38	1.531	.071	.221	11.05
$F_{11}\,F_{12}$	♂	74	1.772	.003	68	1.541	.083	.231	15.50
F_{11}	♀	30	1.731	.066	25	1.510	.077	.221	11.51
F_{12}	♀	29	1.656	.074	27	1.471	.076	.185	9.02
$F_{11}\,F_{12}$	♀	59	1.694	.079	52	1.490	.079	.204	13.69
M									
F_{11}	♂	39	2.430	.148	30	2.041	.187	.389	9.35
F_{12}	♂	35	2.381	.180	38	2.098	.114	.283	7.97
$F_{11}\,F_{12}$	♂	74	2.407	.166	68	2.073	.170	.334	14.15
F_{11}	♀	30	2.378	.133	25	2.066	.135	.312	8.64
F_{12}	♀	29	2.270	.115	27	2.053	.095	.217	7.86
$F_{11}\,F_{12}$	♀	59	2.325	.136	52	2.059	.117	.266	11.04
Length of Brain									
F_{11}	♂	39	1.612	.035	30	1.570	.078	.042	2.76
F_{12}	♂	35	1.593	.052	38	1.576	.057	.017	1.34
$F_{11}\,F_{12}$	♂	74	1.603	.044	68	1.573	.067	.030	3.19
F_{11}	♀	30	1.588	.061	25	1.560	.042	.028	2.06
F_{12}	♀	29	1.574	.046	27	1.552	.041	.022	1.83
$F_{11}\,F_{12}$	♀	59	1.581	.053	52	1.556	.042	.025	2.72

TABLE 3 Contd.

Var.	Genera-tion	Sex	Bright Animals			Dull Animals			Diff.	C.R.
			N	Mean	σ	N	Mean	σ		

Width of Brain

F_{11}		♂	39	1.673	.116	30	1.565	.057	.108	4.91
F_{12}		♂	35	1.679	.076	38	1.580	.090	.099	5.00
F_{11} F_{12}		♂	74	1.680	.092	68	1.573	.046	.107	8.56
F_{11}		♀	30	1.668	.036	25	1.557	.042	.111	10.47
F_{12}		♀	29	1.638	.034	27	1.554	.038	.084	9.13
F_{11} F_{12}		♀	59	1.654	.055	52	1.556	.039	.098	10.89

Body Weight

F_{11}		♂	39	293.67	44.79	30	251.50	40.39	42.17	4.12
F_{12}		♂	35	269.49	58.40	38	223.68	35.64	45.81	4.02
F_{11} F_{12}		♂	74	282.23	53.08	68	235.96	40.22	46.27	5.92
F_{11}		♀	30	238.20	33.87	25	182.16	21.02	56.04	7.50
F_{12}		♀	29	210.83	41.34	27	172.19	30.28	38.64	4.01
F_{11} F_{12}		♀	59	224.75	40.11	52	176.98	26.72	47.77	7.46

Nose-to-tip Length

F_{11}		♂	37	42.08	1.679	30	39.96	1.852	2.121	4.86
F_{12}		♂	34	40.947	2.677	37	38.786	1.640	2.161	4.06
F_{11} F_{12}		♂	71	41.538	2.85	67	39.312	1.825	2.226	5.50
F_{11}		♀	30	39.66	1.902	25	36.372	2.090	3.288	6.05
F_{12}		♀	29	38.579	2.209	27	36.248	1.473	2.331	4.68
F_{11} F_{12}		♀	59	39.129	2.123	52	36.308	1.739	2.821	9.27

TABLE 3 Contd.

Genera-Var. tion	Sex	Bright Animals			Dull Animals			Diff.	C.R.
		N	Mean	σ	N	Mean	σ		

Maze Score

Generation	Sex	N	Mean	σ	N	Mean	σ	Diff.	C.R.
F_{11}	♂	39	32.59	16.49	28	135.04	28.02	102.45	-17.32
F_{12}	♂	26	35.615	32.74	16	137.90	29.92	-101.58	10.31
$F_{11} F_{12}$	♂	65	33.80	24.37	44	135.82	28.75	-102.02	19.63
F_{11}	♀	31	36.194	18.89	25	147.160	20.71	-110.97	-18.72
F_{12}	♀	24	52.375	33.27	14	123.710	30.81	71.34	6.68
$F_{11} F_{12}$	♀	55	43.255	27.37	39	138.74	27.22	-94.49	-16.72

TABLE 4

Comparison of Bright and Unselected Animals

Genera- Var. tion	Sex	Bright Animals			Unselected Animals				
		N	Mean	σ	N	Mean	σ	Diff.	C.R.
Brain Weight									
$F_{11} F_{12}$	♂	74	1.772	.093	88	1.655	.084	.117	8.24
$F_{11} F_{12}$	♀	59	1.694	.079	38	1.615	.081	.079	4.82
M									
$F_{11} F_{12}$	♂	74	2.407	.116	88	2.154	.147	.253	11.90
$F_{11} F_{12}$	♀	59	2.326	.136	38	2.161	.046	.164	8.50
Length of Brain									
$F_{11} F_{12}$	♂	74	1.603	.044	88	1.561	.052	.042	5.38
$F_{11} F12$	♀	59	1.581	.053	38	1.531	.039	.050	5.43
Width of Brain									
$F_{11} F_{12}$	♂	74	1.680	.092	88	1.602	.047	.078	6.45
$F_{11} F_{12}$	♀	59	1.654	.060	38	1.606	.045	.048	4.53
Body Weight									
$F_{11} F_{12}$	♂	74	282.23	53.08	88	229.13	28.48	53.10	7.75
$F_{11} F_{12}$	♀	59	224.75	40.11	38	163.79	18.84	60.96	9.07

TABLE 4 Contd.

Var.	Genera-tion	Sex	Bright Animals			Unselected Animals				
			N	Mean	σ	N	Mean	σ	Diff.	C.R.

Nose-to-Tip Length

F_{11} F_{12}		♂	71	41.538	2.85	85	40.768	1.752	.770	1.99
$F_{11}F_{12}$		♀	59	39.129	2.12	37	36.454	1.292	2.675	7.67

Nose-to-Base Length

F_{11} F_{12}		♂	71	20.506	1.16	85	20.511	.46	-.005	-.034
F_{11} F_{12}		♀	59	19.664	.95	37	18.914	.563	.750	4.84

Tibia Length

F_{11} F_{12}		♂	58	3.763	.244	63	3.840	.159	-.077	-2.04
F_{11} F_{12}		♀	41	3.557	.199	32	3.549	.148	.008	.198

TABLE 5

Comparison of Dull and Unselected Animals

Genera- Var. tion	Sex	Unselected Animals			Dull Animals				
		N	Mean	σ	N	Mean	σ	Diff.	C.R.
Brain Weight									
$F_{11}\ F_{12}$	♂	88	1.650	.084	68	1.541	.083	.109	8.07
$F_{11}\ F_{12}$	♀	38	1.615	.081	52	1.490	.079	.125	7.35
M									
$F_{11}\ F_{12}$	♂	88	2.154	.147	68	2.073	.154	.081	3.26
$F_{11}\ F_{12}$	♀	38	2.161	.046	52	2.059	.117	.102	5.83
Length of Brain									
$F_{11}\ F_{12}$	♂	88	1.561	.052	68	1.573	.067	-.012	-1.2
$F_{11}\ F_{12}$	♀	38	1.531	.039	52	1.556	.042	-.025	-2.94
Width of Brain									
$F_{11}\ F_{12}$	♂	88	1.600	.047	68	1.573	.046	.027	3.46
$F_{11}\ F_{12}$	♀	38	1.606	.045	52	1.566	.039	.050	5.75
Body Weight									
$F_{11}\ F_{12}$	♂	88	229.13	28.48	68	235.96	40.22	-6.83	-1.19
$F_{11}\ F_{12}$	♀	38	163.79	18.84	52	176.98	26.72	-13.19	-2.74
Nose-to-Tip Length									
$F_{11}\ F_{12}$	♂	85	40.77	1.75	67	39.31	1.83	1.46	4.98
$F_{11}\ F_{12}$	♀	37	36.45	1.29	52	36.31	1.79	.14	.45

TABLE 5 Cont.

Genera-			Unselected Animals			Dull Animals				
Var. tion	Sex	N	Mean	σ	N	Mean	σ	Diff.	C.R.

Nose-to-Base Length

F_{11} F_{12}	♂	85	20.51	.46	67	19.76	1.10	.75	5.24
F_{11} F_{12}	♀	37	18.91	.56	52	18.66	.78	.25	1.80

Tibia Length

F_{11} F_{12}	♂	63	3.840	.159	51	3.680	.142	.160	5.63
F_{11} F_{12}	♀	32	3.549	.148	46	3.445	.174	.104	2.82

TABLE 6

Number of Bright, Dull and Unselected Animals

Included in Age Groups

♂

♀

Unselected Animals 88

Unselected Animals 38

Age Group	Bright ♂	Dull ♂		Age Group	Bright ♀	Dull ♀
P	10	21		P	6	10
Q	38	20		Q	21	16
R	14	10		R	24	7
S	4	6		S	3	14
T	8	11		T	5	5
Total -	74	68			59	52

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TABLE 7

Comparison of Unselected Animals with Bright Q Animals

| | Sex | Bright Animals | | | Unselected Animals | | | | |
		N	σ	Mean	N	σ	Mean	Diff.	C.R.
Brain Weight									
	♂	38	.110	1.77	88	.084	1.65	.12	6.00
	♀	21	.090	1.68	38	.081	1.61	.07	2.92
M									
	♂	38	.150	2.43	88	.143	2.15	.28	9.75
	♀	21	.160	2.31	38	.146	2.16	.15	3.57
Body Weight									
	♂	38	39.99	280.3	88	28.48	229.1	51. 2	7.14
	♀	21	33.88	208.3	38	18.87	163.8.	41.5	5.18
Nose-to-Tip Length									
	♂	37	1.59	41.7	85	1.75	40.77	.93	2.87
	♀	21	1.90	38.46	37	1.67	36.45	2.01	4.04
Nose-to-Base Length									
	♂	37	.80	20.50	85	.46	20.51	-.01	-.07
	♀	21	.75	19.21	37	.56	18.91	.30	1.60
Tibia Length									
	♂	29	.36	3.78	63	.16	3.84	-.06	-.60
	♀	15	.16	3.55	32	.15	3.55	0	0

TABLE 8

Comparison of Unselected Animals with Dull Q Animals

	Sex	Unselected Animals			Dull Animals			$D_{iff.}$	C.R.
		N	σ	Mean	N	σ	Mean		
Brain Weight									
	♂	88	.084	1.65	20	.079	1.51	.14	7.07
	♀	38	.081	1.61	16	.06	1.48	.13	6.07
M									
	♂	88	.143	2.15	20	.110	2.08	.07	2.42
	♀	38	.146	2.16	16	.083	2.08	.08	2.54
Body Weight									
	♂	88	28.48	229.1	20	45.84	227.5	1.6	.150
	♀	38	18.87	163.8	16	18.67	177.2	-13 .4	-2.41
Nose-to-Tip Length									
	♂	85	1.75	40.77	19	1.47	38.94	1.83	4.73
	♀	37	1.67	36.45	16	.99	36.53	-.08	-.22
Nose-to-Base Length									
	♂	85	.46	20.51	19	.75	19.59	.92	5.14
	♀	37	.56	18.91	16	.47	18.57	.34	2.28
Tibia									
	♂	63	.16	3.84	19	.14	3.62	.22	5.37
	♀	32	.15	3.55	16	.84	3.24	.31	1.46

TABLE 9

Comparison of Bright and Dull Animals
Age Groups R, S, T

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
		Bright Animals			**Dull Animals**				

Brain Weight

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
	♂	26	.084	1.81	27	.080	1.58	.23	10.31
	♀	32	.059	1.72	26	.073	1.51	.21	11.86

M

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
	♂	26	.183	2.428	27	.207	2.079	.349	6.51
	♀	32	.122	2.340	26	.136	2.070	.270	7.86

Body Weight

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
	♂	26	41.95	315.4	27	54.45	263.0	52.4	3.93
	♀	32	28.00	247.7	26	19.90	185.9	61.8	9.81

Nose-to-Tip Length

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
	♂	24	1.20	42.98	27	1.70	40.44	2.54	6.22
	♀	32	1.46	40.16	26	2.07	36.50	3.66	7.61

Nose-to-Base Length

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
	♂	24	.787	21.28	27	1.109	20.44	.84	3.15
	♀	32	.636	20.18	26	.804	18.93	1.25	6.48

Tibia Length

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
	♂	22	.240	3.84	22	.122	3.76	.08	1.39
	♀	20	.166	3.64	21	.189	3.49	.15	2.68

Age

	Sex	N	σ	Mean	N	σ	Mean	Diff.	C.R.
	♂	26	58.46	262.8	22	57.43	281.2	-18.4	-1.16
	♀	32	56.20	250.9	26	40.44	271.5	-20.6	-1.62

TABLE 10

Correlations between Variable of Selection and Somatic Variables, for Q Males, Q Females, RST Males and RST Females

Q Animals

Brain Weight	+ .7769	+.7834
M	+.7707	+.6523
Nose-to-Tip Length	+.6406	+.5193
Nose-to-Base Length	+.4820	+.4418
Tibia Length	+.2527	+.3273
Body Weight	+.4858	+.4405
Age	+.2971	+.2372

RST Animals

Brain Weight	+.8214	+.8399
M	+.6662	+.7277
Nose-to-Tip Length	+.6501	+.7174
Nose-to-Base Length	+.4532	+.6554
Tibia Length	+.1836	+.4953
Body Weight	+.4735	+.7847
Age	−.1568	+.2017

TABLE III

Comparison of Bright and Dull Animals with Regard to Measurements of the Cranium and Cerebellum

Var.	Age-Group	Sex	Bright Animals			Dull Animals			Diff.	C.R.
			N		Mean	N		Mean		
Cranium Length										
	Q	♂	35	.032	1.479	19	.057	1.403	.076	5.35
	RST	♂	24	.060	1.494	23	.066	1.437	.057	3.10
	Q	♀	19	.056	1.395	16	.070	1.369	.026	1.20
	RST	♀	32	.048	1.426	24	.077	1.394	.032	1.79
Cranium Width										
	Q	♂	35	.046	1.125	19	.032	1.086	.039	3.64
	RST	♂	24	.055	1.123	23	.048	1.098	..025	1.67
	Q	♀	19	.085	1.128	16	.043	1.093	.035	1.57
	RST	♀	32	.037	1.127	23	.041	1.091	.036	3.36
Cerebellum Length										
	Q	♂	38	.058	.7940	20	.058	.7200	.0740	4.63
	RST	♂	26	.055	.7777	27	.045	.7456	.0321	2.31
	Q	♀	21	.032	.7886	16	.036	.7000	.0886	7.77
	RST	♀	31	.086	.7719	26	.064	.7142	.0577	2.91
Cerebellum Width										
	Q	♂	38	.028	1.267	20	.061	1.177	.090	7.38
	RST	♂	26	.045	1.270	27	.034	1.195	.075	6.82
	Q	♀	21	.042	1.254	16	.037	1.176	.078	5.95
	RST	♀	32	.031	1.256	26	.033	1.174	.082	9.65