Effects of dietary modifications on the tapeworm Hymenolepis diminuta

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EFFEFTS OF DIETARY MODIFICATIONS ON THE TAPEWORM

HYMENOLEPIS DIMINUTA

By

Anna Hager

A Thesis Submitted to the Graduate Faculty for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject Zoology

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>TABLE OF CONTENTS</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>5</td>
</tr>
<tr>
<td>REVIEW OF LITERATURE</td>
<td></td>
</tr>
<tr>
<td>Literature Concerning the Parasite</td>
<td>6</td>
</tr>
<tr>
<td>Literature Concerning Investigations on Effects of Dietary Modifications on Intestinal Parasites</td>
<td>14</td>
</tr>
<tr>
<td>THE INVESTIGATION</td>
<td></td>
</tr>
<tr>
<td>Materials</td>
<td>34</td>
</tr>
<tr>
<td>Procedure</td>
<td>35</td>
</tr>
<tr>
<td>Results</td>
<td></td>
</tr>
<tr>
<td>1. Effects of an Exclusive Milk Diet</td>
<td>38</td>
</tr>
<tr>
<td>Figure 1. Numbers of tapeworm eggs eliminated from rats K and L on an exclusive milk diet and on Steenbock's growing ration.</td>
<td>41</td>
</tr>
<tr>
<td>Figure 2. Variations in body weight and numbers of tapeworm eggs eliminated daily for rat C12, on Steenbock's growing ration, and rat C10 alternately on Steenbock's ration and milk.</td>
<td>44</td>
</tr>
<tr>
<td>Figure 3. Comparison of the total numbers of tapeworm eggs eliminated daily by rats C12, C13, and C14 on Steenbock's growing ration and by rats C9, C10 and C11, alternately on Steenbock's ration and milk.</td>
<td>46</td>
</tr>
<tr>
<td>2. Effects of a Diet Deficient in Vitamins B&lt;sub&gt;1&lt;/sub&gt; and G</td>
<td>47</td>
</tr>
<tr>
<td>Figure 4. Variations in the numbers of tapeworm eggs eliminated daily by rat A2 alternately on a control diet and one lacking in vitamins B&lt;sub&gt;1&lt;/sub&gt; and G.</td>
<td>50</td>
</tr>
</tbody>
</table>

**T6152**
3. Effects of a Diet Deficient in Vitamin B<sub>1</sub>. 51

Figure 5. Variations in body weight and numbers of tapeworm eggs eliminated daily by rat D16 on a control diet and by rat D20, alternately on a control and a vitamin B<sub>1</sub> deficient diet 54

Figure 6. Comparison of the total numbers of tapeworm eggs eliminated by rats D16, D17 and D18 maintained on a control diet and by rats D20, D21 and D22 maintained alternately on a control and a vitamin B<sub>1</sub> deficient diet 56

4. Effects of a Diet Deficient in Vitamin G. 57

Figure 7. Variations in body weight and number of tapeworm eggs eliminated daily for rats Cl, C4 and C7 on vitamin G deficient and control diets 60

Figure 8. Comparison of the total numbers of tapeworm eggs eliminated by rats C5, C6, C7 and C8 maintained on the control diet and by rats Cl, C2, C3 and C4 given alternately a control and a vitamin G deficient diet 62

5. Effects of Limiting the Amount of Food. 64

Figure 9. Variations in body weight and numbers of eggs eliminated for rats D12 and D15 with free and limited food intake 67

Figure 10. Comparison of the total numbers of tapeworm eggs eliminated daily by the group of rats D2, D3, D4, D8, D10 and D12, and the group D5, D6, D7, D13, D14 and D15 with free and limited food intake 69

6. Comparison of the Effects of Soy Bean Oil Meal and Wheat Middlings in the Diet. 65

Figure 11. Total numbers of tapeworm eggs eliminated daily by the group of
rats D2, D3 and D4; the group D5, D6 and D7; the group D8, D10 and D12 and the group D13, D14 and D15 maintained on diets containing soy bean oil meal or wheat middlings ........ 72

7. Relation of the Worm Burden to the Numbers of Eggs Eliminated .......... 73

   Figure 12. Mean numbers of tapeworm eggs eliminated per day by rats harboring various numbers of worms ... 77

   Figure 13. Mean numbers of eggs produced per worm per day by worms grouped according to the numbers of worms present ........ 77

8. Relation of the Worm Burden to the Lengths of Worms Harbored ........ 78

DISCUSSION ............ 81

CONCLUSIONS ........... 89

SUMMARY ............... 92

ACKNOWLEDGMENT .......... 95

LITERATURE CITED .......... 96
INTRODUCTION

There have been a number of investigations pursued with a view to determining the effects upon intestinal parasites of modifications in the diet of the host. Very few of these studies, however, have been made using cestode parasites. It is not to be expected that all parasites will be affected in the same way by dietary modifications, particularly because of the differences in the various life histories. A parasite such as the rat tapeworm *Hymenolepis diminuta*, which dwells in the lumen of the small intestine, might be expected to be affected more directly and rapidly by the diet of the host than one which obtains its nourishment from the host's tissues.

This study was undertaken with a view to determining the effects of partial starvation, of an exclusive milk diet, of diets containing soy bean oil meal and wheat middlings and of diets deficient in both vitamins B₁ and G and in each vitamin alone, on the rat tapeworm *Hymenolepis diminuta*. 
REVIEW OF LITERATURE

The Parasite

The original description of the species Hymenolepis diminuta was given by Rudolphi in 1819 (95). He described the parasite, from specimens obtained from a rat, as six to nine inches or more in length, possessing an obconical head with four rather large suckers, a slender neck and segments always wider than long. To this tapeworm he applied the name Taenia diminuta.

In 1825 Creplin (35) described as a new species a rat tapeworm to which he gave the name Taenia leptocephala, but Dujardin (36) pointed out the similarity between this species and that of Rudolphi.

The first to report Hymenolepis diminuta as a human parasite was Weinland (107), who described it as the new species Hymenolepis flavopunctata.

The identity of Taenia diminuta Rudolphi, Taenia leptocephala Creplin and Hymenolepis flavopunctata Weinland was established by Grassi (48).

Ransom (89) gave a detailed account of the anatomy of Hymenolepis diminuta based upon descriptions by preceding authors, particularly Zschokke (110), supplemented by original observations. Unless otherwise noted, the figures in the fol-
lowing descriptions are those given by Ransom.

_Hymenolepis diminuta_ may normally vary in length from ten to sixty centimeters, although Sturdevant (105) described an unusual specimen which measured ninety-nine centimeters aside from the loose proglottids found in the large intestine. The maximum width usually lies between two and a half and four millimeters, or perhaps as much as seven millimeters (Packard, 87). The head, although variable, is almost round, 200 to 600 microns in width, and equipped with a rudimentary, unarmed rostellum and four suckers.

The neck is short, only one-half of a millimeter in length according to Grassi (48), and may equal or exceed the scolex in width but most frequently is narrower (Sturdevant, 105).

There are usually 800 to 1000 segments according to Zschokke (110). Magalhaes (78) reported a maximum of 1300, but Sturdevant (105) described his unusual specimen mentioned above as possessing over 2850. The proglottids are always wider than long. In young segments the width may be twenty times the length; in mature segments, two to twenty times.

The nervous system has been described by Zschokke (110). It consists of a longitudinal nerve trunk and two accessory longitudinal nerves on either side. The nerve trunks unite near the rostellum and from this region four nerves extend anteriad. Two branches arise in each proglottid from ganglionic enlargements on the lateral trunks.
Along either side, mediad to the nerve trunks, lie two excretory canals of which the ventral is the larger except in the anterior part of the strobila and in the scolex. The four excretory canals anastomose just behind the rostellarium.

Frequently there are proglottids which are sterile because the female reproductive organs have failed to develop. These are said to be more numerous in specimens from man than in those from the more common rat host.

The eggs exhibit three-layered shells, the outer, thick and striated; the intermediate, thick, granular and albuminous; the inner, delicate, rather oval and closely applied to the onchosphere. The inner layer frequently shows polar extensions but not filaments. Three pairs of hooks can usually be distinguished in the embryo. Nearly clear when first shed from the parasite, the eggs become yellowish by staining with the bile (Narihara, 83). The size of the eggs may vary considerably, and slightly different measurements are given by different authors (Dujardin (36), Weinland (107), Grassi (48), Magalhaes (78), Sonsino and Zschokke (100), Ransom (89), Fülleborn (45), Kamalow (71)) but the majority fall between 54 and 86 microns for the outer envelope, between 24 and 40 microns for the embryo.

When ingested by a suitable invertebrate intermediate host, the eggs hatch in the digestive tract and the hexacanth embryos migrate through the walls of the digestive tube and lie in the
body cavity or in the adipose tissue. The earliest stages in the development of the cysticercoid have not been observed. According to Joyeux (70) it may occur free or in a capsule apparently derived from the host. The body of the cysticercoid is a gastrula-like structure with an anterior opening and a secondary cavity within which the scolex is attached by a peduncle. When, in the digestive tract of a definitive host, mature cysticercoids are liberated by digestion of the invertebrate host, the scolex evaginates and the strobila begins to develop, reaching maturity in 17 to 21 days.

Two testes are normally present on the right and one on the left in each proglottid, but the number and position are somewhat variable (Sturdevant, (105), Ransom, (89), Bacigalupo, (10)). Occasionally there are one, two, four, five or six instead of three. Sometimes they are reversed in position or all on one side.

Vasa efferentia leading from the testes converge to form the vas deferens extending toward the left side and enlarging as the seminal vesicle of which the distal end forms the slender cirrus lying within the cirrus pouch. The genital pore is nearly always on the left side of the proglottid, but sometimes on the right (Bacigalupo, (10), Faust, (37)).

Opening from the genital pore, and ventral in position with relation to the cirrus pouch, is the vagina which dilates to form the seminal receptacle extending to the center of the
proglottid and emptying into the oviduct. Situated in the median part of the proglottid is the bilobed ovary. The oviduct extends anteriorly from the ovary, is joined by the seminal receptacle, then turns back and, within the small shell gland, is joined by the duct from the yolk gland, which is posterior in position with respect to the shell gland. Both the shell gland and the yolk gland are located caudal to the ovary. After being joined by the duct from the yolk gland, the oviduct again turns forward and empties into the uterus which overlies the anterior part of the ovary. The uterus, at first a transverse mass of cells, enlarges rapidly with later development and shows many lobes which increase in size and become pressed together as they become filled with eggs. With the growth of the uterus, the ovary atrophies.

Rats are considered the normal hosts of the strobilat worm. Fourteen per cent of the rats examined in Minneapolis and St. Paul by Riley and Shannon (93) were found to harbor this parasite; Moll (81) reported it in twenty-five per cent of the examinations of rats made in Madison; and Chandler (30), in a third of two hundred rats caught in Houston. *Hymenolepis diminuta* may also develop in mice (Meggitt, (80), and Gedoelst (47)) reported a case of infestation in a monkey. Ransom (89) listed and described twenty cases of human infestation noted in the literature before 1904. Forty-nine cases occurring between that date and 1922 were reviewed by Riley and Shannon
Since 1922 at least fifty-four cases of parasitism of man by this cestode have received mention in the literature (Butka (29), Chandler (31), Momma (82), Spindler (101), Clark (34), Keller (72), Fisher (38), Keller and Leathers (73), Keller, Leathers and Knox (74)). Thus there are known over a hundred cases of human infestation, and Riley and Shannon (93) suggested that probably some cases have not been recognized because of confusion in routine examinations between the eggs of Hymenolepis diminuta and those of Hymenolepis nana.

The comparative rarity of human infestation as well as the relatively easy expulsion of the parasite from the human host by anthelminthics or even by cathartics (Hansom, 89; Chandler, 30) suggest that Hymenolepis diminuta should be considered as an abnormal or accidental human parasite. The great majority of the human cases were reported as occurring in children and were probably due to the accidental ingestion of infected intermediate hosts.

The early knowledge of the life history of Hymenolepis diminuta was due largely to the observations of Grassi and Rovelli (49, 50, 51, 52). They reported failure in attempting to infect rats by feeding the eggs of the parasite directly, but success in finding appropriate intermediate hosts. The cysticercoids were found in the body cavities or in the adipose tissue of the larval and adult meal moth Asopia farinalis, the young and adult earwig Anisolabis annulipes and in the adult
beetles *Acis spinosa* and *Scaurus striatus*. When cysticercoids from these hosts were fed to white rats free from tapeworms, adult worms corresponding in all respects to *Hymenolepis diminuta* were found in the intestine after fifteen days or longer.

As a result of later investigations, *Hymenolepis diminuta* has been found to develop in a number of arthropods. Other Lepidoptera which may serve as hosts in addition to the meal moth mentioned above were cited by Hongo (66, 67). They are *Aphornia gularis*, *Aglossa dimidiata*, *Tinea pellionella* and *Tinea granella*.

Additional intermediate hosts have also been found among the Coleoptera. Joyeux (70) found the adult of *Tenebrio molitor* capable of acting as an intermediate host, but the larva incapable of infection, and Riley and Shannon (93) reported similar findings. Nickerson (84) and Oldham (86), too, attempted to develop cysticercoids in *Tenebrio molitor* larvae but with negative results. *Tribolium castaneum* was cited as a vector by Hongo (66, 67) and *Ulosonia pervicornis* in the adult stage by Bacigalupo (11), who also listed the larva of *Dermestes peruvianus* (12). Joyeux (70) experimentally infected the adult *Geotrupes sylvaticus*.

A number of fleas have been found to be naturally infected or susceptible to experimental infection. Joyeux listed the larvae of *Pulex irritans*, the larvae of *Ctenocephalus canis* and *Lentopsylla musculi* (70) as capable of being experimentally in-
fected, but Johnston (68) was not able, in the case of the last, to demonstrate the cysticercoids. He did find developmental stages in Xenopsylla cheopsis, but Joyeux (70) considered only the larvae of this flea susceptible to infection. *Ceratophyllus fasciatus* was reported as an intermediate host by Nicoll and Minchin (85) and by Johnston (68) and was experimentally infected by Joyeux (70). Oldham (86) fed gravid proglottids of the rat tapeworm to young larvae of *Ceratophyllus wickhami* and upon dissection three weeks later found cysticercoids in the body cavity.

There appears to be some doubt about the ability of cockroaches to serve as intermediate hosts for this cestode. Stiles and Hassall cited *Blatta orientalis* as a vector in one publication (103) but failed to mention it in a later one (104), and Kamalow (71) and Joyeux (70) were not able to infect any stage of this insect. Stiles and Hassall (103) likewise reported the susceptibility of *Blattella germanica*, as did Faust (37), but Kamalow (71), Joyeux (70) and Chandler (30) tried unsuccessfully to use the German roach as an intermediate host. Chandler's attempt to infect the American roach was unsuccessful (30), but Faust (37) cited *Periplaneta americana* as a vector. Hall (53) did not include any roaches in his list of vectors.

Other arthropods which may harbor cysticercoids of the rat tapeworm are the myriapods *Fontaria virginiensis* and *Julus* sp.
Hinman and Faust (64) consider *Tenebrio molitor* to be the intermediate host most frequently responsible for human infection. They reported two cases of ingestion of the larvae of this beetle by man and include references to twenty such cases. The fact that meal worms are known to be at least occasionally eaten by man, their frequent occurrence in human foods and the association of rats and mice with cereals suggest a train of circumstances which might at times lead to human infection with the rat tapeworm. Joyeux (70) considered *Tenebrio molitor* and the two rat fleas *Ceratophyllus fasciatus* and *Xenopsylla cheopsis* to be the usual sources of infestation in rats.

**Previous Investigations on the Effects of Dietary Modifications on Intestinal Parasites**

The majority of the observations which have been made on the influence of changes in host diet upon parasites harbored, concern intestinal protozoa. In 1923 Hegner (54) reported that different protozoa respond in different ways to dietary modifications. In rats fed an exclusive animal protein ("carnivorous") diet the numbers of *Giardia muris* and of *Trichomonas muris* were decreased. To the same diet the response of *Hexamitum muris* was a shift in location from duodenum and jejunum
to ileum. An exclusive milk diet was associated with a decrease in the incidence of all three forms, but a diet high in yeast appeared to produce a differential effect, decreasing the numbers of Trichomonas muris and Hexamitus muris but resulting in an increase in the numbers of Giardia muris.

The same author (55) further investigated this subject by feeding three rats throughout their entire lives on a "carnivorous" diet adequate for good growth and reproduction and found them to be free from Giardia muris and Trichomonas muris. Two had a few specimens of Hexamitus muris. When rats heavily infected with these three types of protozoa were fed an animal protein diet for one week, the last form increased in numbers and the first two fell off greatly. At the same time the bacterial content changed to a predominantly putrefactive type. A possible relationship was suggested between the influence of such a diet as indicated by these observations and the fact that intestinal protozoa are rarely reported from carnivorous mammals. Hegner (56) also recorded three cases of human flagellate diarrhea in which conditions were improved by an animal protein diet over a period of several weeks. Two were giardia infections; the other, a trichomonas infection.

The numbers of trichomonads in the ceca of rats were found by Ratcliffe (90) to vary inversely with the number of proteolytic anaerobes. The reduction in the numbers of trichomonads in rats fed a high protein diet was considered by this author
to be chiefly attributable to the influence of the protein used on the development of these bacteria in the rats' intestines. Of the proteins used, casein was the most effective, beef steak somewhat less so and beef liver ineffective in reducing the numbers of trichomonads. Ratcliffe noted also (91) that numbers of Endamoeba muris and of Chilomastix bettencourtii were decreased when the host rats were maintained on a diet favorable to the growth of proteolytic anaerobes. The same author stated, too (92), that infections of rats with Trichomonas hominis and Pentatrichomonas ardini delteili became lighter when the hosts were given a diet which increased intestinal acidity and still lighter on a high protein diet containing 56 per cent unpurified casein, possibly because of the greater number of proteolytic anaerobes present among the intestinal flora. The organisms, however, were not eliminated by the use of the high protein diet. Infections in the control animals did not vary to any great extent during the same period.

The numbers of trophozoites of Giardia canis found by Tsuchiya (106) in puppies on a high protein diet were considerably less than those found in young dogs given a high carbohydrate diet.

An abundance of starch in the diet of chicks, according to Hegner (57), appeared to enable Endamoeba histolytica to maintain itself for a longer period in the ceca than was otherwise possible. Hegner and Eskbridge (59) stated that a diet rich in
animal proteins produced conditions in the ceca of rats unfavorable for the growth and multiplication of *Trichomonas hominis*, as evidenced by great reduction in numbers or loss of the parasites from rats fed such a diet, as compared with rats on a control diet. Using the same parasite, these investigators (60) found that the number of rats which remained infected and the numbers of parasites present were consistently greater when liver in any form (raw or dried beef liver, liver extract or powder) was fed or injected. The effects of this treatment were compared with the results of feeding a normal stock diet, a high carbohydrate diet containing 85 per cent whole wheat flour or a high protein diet in which casein was used as the source of protein.

In rats and in monkeys, Kessel reported (75) that an exclusive milk diet or neutral diets with lactic acid or large amounts of lactose added, produced a lowering of the pH of the colon contents and a decrease in the amoebae and trichomonads present. Kessel and K'E-Kang (76) fed an exclusive raw milk diet to monkeys and to children and observed that during that period there was almost always a reduction in the numbers of intestinal amoebae, and in some cases the intestine was cleared of *Endamoeba dysenteriae* and other forms.

Infections of *Balantidium coli* from the pig were established in rats by Schumaker (97). Within a week the infection was greatly reduced or eliminated from rats on a diet of whole
milk. Diets high in casein prevented infection and eliminated heavy infections within eight days, but a high carbohydrate diet containing no casein was favorable for the development of the parasite. Examinations by Schumaker (98) of the cecal contents of 79 pigs killed at an abattoir indicated that heavy infections with Balantidium coli were generally accompanied by larger amounts of starch in the ceca and by diets heavier in carbohydrates in the form of grain, than in the case of light infections.

In rats, the population of Balantidium coli was not affected significantly, according to Gabaldon (46), by increasing the viscosity of the intestinal contents by the use of agar-agar, linseed or psyllium seed, nor by increasing the crystalloid content with barium sulphate or bismuth subcarbonate.

Hegner and Eskbridge (61) maintained three groups of ten rats infected with amoebae, on a high carbohydrate diet, a high casein diet and a high liver diet, respectively. After two weeks, no amoebae were found in the ceca of rats in the last two groups, but every rat given the carbohydrate diet was still infected. They concluded that the carbohydrate diet created in the cecum a condition favorable to the development of the amoebae, but that a high protein diet, consisting chiefly of casein or of liver, produced one so unfavorable that the parasites were no longer able to live there.

The same investigators (62) kept six rats showing good in-
fections with intestinal trichomonads without food for eight days. At the end of this period of starvation, the hosts were all still infected. One infection was considered light; one, fair; three, heavy and one, very heavy. It would appear that trichomonads are not easily eliminated from rats by starvation.

In an attempt to determine some of the factors responsible for host-parasite specificity among protozoa, Hegner (58) investigated the reactions of natural and foreign parasites to modifications in the host. A high carbohydrate diet rendered the intestinal contents of rats more favorable to the development of trichomonads natural to these hosts, and a high protein diet was correspondingly unfavorable. The colonization of Balantidium coli in a foreign host, the rat, appeared to be due solely to a change in diet to one abnormally high in carbohydrate content for this host. Hegner urged the desirability of further investigations directed toward rendering hosts more favorable for parasites since data might be obtained by this procedure that would possibly not be evidenced if efforts were directed solely at control.

Frye and Meleney (44) reported that neither the lack of vitamin A in the diet nor the condition of vitamin-A deficiency in rats seemed to render the lumen of the cecum unsuitable for the development of Endamoeba muris.

A considerable number of papers have appeared recently reporting investigations on coccidiosis and the effects of
dietary modifications on coccidia. Beach and Davis (15) stated that chicks were given an appreciable protection against the effects of coccidiosis by being fed mash containing 40 per cent dry skim-milk or 20 per cent lactose. The authors attribute the protective effects to the greater acidity of the cecal contents. Their conclusions were drawn only from observations of the birds and no counts of the numbers of oocysts in the droppings were made.

Chickens were given approximately equal numbers of the oocysts of *Eimeria tenella* by Allen (8), and then maintained under similar conditions except for diet. Those given a high protein, high vitamin diet eliminated fewer oocysts for the first five days of the patent period than did chickens on a low protein, low vitamin diet. After the fifth day, however, the numbers became and remained relatively higher and there was subacute or chronic coccidiosis. The reverse conditions were associated with a low protein, low vitamin diet.

Somewhat similar results were reported by Jones (69), who studied *Eimeria tenella* infections in chicks on diets different in protein and in vitamin-A content. No differences attributable to vitamin-A deficiency were noted. Oocyst production was greater and immunity developed more slowly in those birds on a high protein diet than on those given a diet low in protein, but the latter group failed to maintain weight as well.

Becker and Spencer (28) found nicotine worm powder, pyre-
thrum, calomel, sodium bicarbonate, calcium carbonate, calcium chloride, disodium phosphate and creatin to be ineffective in retarding the development of coccidia in the rat. Nor, according to Becker and Morehouse (20), did skim-milk, lactose, vinegar or iodine added to the diet of rats exert a restraining influence upon the numerical increase of *Eimeria miyairii*. On the other hand, they did find that yeast appears to contain a factor favorable to the growth of this parasite (21). Rats receiving a diet deficient in vitamins B₁ and G (casein, starch, butter, salts and cod liver oil) were given sporulated oocysts of *Eimeria miyairii*: rats given a ration made adequate for vitamins B₁ and G by the addition of yeast were also infected. The hosts in the latter group eliminated four to five times as many oocysts as did those maintained on the deficient diet. They reported, also, (25) that the quantitative character of *Eimeria miyairii* infections in the rat was not significantly reduced by vitamin A deficient diet, vitamin D deficient diet, a diet of liver only, low- or high-salt diets, alfalfa or tobacco supplements, yeast or irradiated yeast supplements added to a normal diet, or desiccation. The numbers of oocysts were somewhat reduced when the diet was high in casein and greatly reduced when there was a deficiency of vitamins B₁ and G. A diet generally deficient in proteins, vitamins and salts did not lower the hosts' resistance to the coccidian infection.

In order to test the effects of vitamins B₁ and G sepa-
rately, Becker and Morehouse (22) made up a diet consisting of
casein, salts, butter, cod liver oil, agar and beet sugar,
which was deficient in both vitamins. To one group of rats
they fed this diet plus wheat germ oil to add vitamin B₁; to a
second group, as a control for the first, the basic diet plus
wheat germ oil and autoclaved yeast; to a third, the basic
diet without wheat germ oil but with a part of the sugar re-
placed by autoclaved yeast for vitamin G; to the fourth, as a
control for the vitamin B₁ deficient rats, the basic diet with
the same amount of sugar replaced by unautoclaved yeast to add
both vitamins. All the rats were infected with approximately
equal numbers of oocysts of *Eimeria* miyairii. Vitamin B₁ de-
iciency did not alter the numbers of oocysts developed in the
infection. The vitamin G deficient rats eliminated signifi-
cantly fewer oocysts than their controls, but there was not so
great a reduction as in those receiving neither B₁ nor G. It
was suggested that the alcoholic extract of wheat germ used
as a source of vitamin B₁ may also have contained a slight
amount of vitamin G.

The same authors (23) stated that the factor which promotes
growth in coccidia appears to be linked with the vitamin G com-
plex since wheat germ and other substances furnish it as well
as yeast. Liver as a source of the vitamin did not favor the
parasite. When powdered dried liver was used instead of yeast,
the numbers of oocysts eliminated by rats were much smaller
Chickens receiving a ration with liver as the source of the vitamin also eliminated fewer oocysts than those receiving Steenbock's growing ration. Host growth was normal in all cases. The conclusion of these authors was that liver lacks the coccidium growth promoting substance or else has a definite retarding effect. Later (26) they reported that rats eliminated fewer oocysts of *Eimeria miyairii* when rice polishings, powdered liver or skim milk, in that order, were use as a source of vitamin G, than when the vitamin was supplied by yeast. According to these investigations, there would seem to be associated with vitamin G from some sources a factor which stimulates coccidium growth; it appears that the effect of this factor is on the parasite directly and not that the growth of the parasite is merely a function of that of the host.

Certain constituents of diets for chicks, particularly skim milk, buttermilk and wheat middlings in certain amounts or combinations, were reported by Becker (17) to increase greatly the severity of *Eimeria tenella* infections in chicks.

Becker and Derbyshire (18) found no correlation between the bulkiness of the ration and the number of oocysts of *Eimeria miyairii* eliminated by rats nor between growth of host and parasite development. As compared to yeast, the ratios of the numbers of oocysts eliminated by rats given various dietary supplements replacing the sugar of the basic diet were: for linseed meal, 0.94; for whole wheat, 0.922; for hulled oats,
0.591; for oat hulls, 0.494; for yellow corn meal, 0.474; for meat and bone meal, 0.311. In a similar study (19) they found the ratios of the coccidium-growth-promoting substance in other feeding stuffs as compared to yeast in the same way, to be: for soy bean oil meal, 0.51; for barley, 0.98; for rye, 1.63; for wheat bran, 1.91; for wheat flour middlings, 2.65. The ratios of the weight gains of the experimental hosts on the various diets in this experiment to the weight gains of the controls receiving yeast were: for soy bean oil meal, 1.00; for barley, 0.92; for rye, 1.5; for wheat bran, 1.73; for wheat flour middlings, 1.72.

As a very brief summary of the investigations mentioned above concerning the effects of diet on intestinal protozoa, it might be pointed out that different parasites responded differently to dietary modifications. A diet rich in protein appeared to be associated with greater growth in coccidia and a slower development of immunity on the part of the host (69) but to be unfavorable to amoebae (61, 91), giardias (54, 55, 56, 106) and trichomonads (54, 55, 56, 58, 59, 90, 92). A diet high in carbohydrates was reported as favorable to amoebae (57, 61), trichomonads (58) and Balantidium coli (97, 98, 58). Milk, lactose or lactic acid were said to be unfavorable to the growth of amoebae and trichomonads (75, 76) and also to that of Balantidium coli (97). Milk was reported to impart a certain protection against the undesirable effects of coccid-
iosis (15) but to exert no restraining influence on the growth of the parasites (17, 20, 26), although the feeding of large amounts of casein was associated with a slight decrease (25). Liver was ineffective in reducing the numbers of coccidia (23, 24, 25, 26) and was without a restraining effect on (90) or actually favorable to (60) trichomonads. Changes in bulkiness (18) or in viscosity (46) were without effect. Deficiency of the vitamins A (69, 25), B₁ (22), or D (25) had no restraining effect on coccidia, nor did a lack of vitamin A produce any appreciable effect on amoebae (44). Starvation was ineffective in reducing the numbers of trichomonads (62). Yeast appeared to decrease the numbers of trichomonads but to be favorable to giardias (54) and to stimulate the growth of coccidia if added to a diet deficient in vitamins B₁ and G (21). If additional yeast was added to a diet already adequate, however, there was no extra stimulating effect (25). Vitamin G or, more probably some factor associated but not identical with the vitamin G complex, had the effect of promoting growth of coccidia (18, 19, 22, 23, 25, 26).

Some of these same dietary modifications as well as others have been investigated with regard to the effects produced on helminth parasites. In 1926 vitamin B₁ was reported by Zimmerman, Vincent and Ackert (109) to be a factor in the resistance of chickens to *Ascaridia lineata*. The worms in the intestines of the chickens on a diet deficient in vitamin B₁ but adequate
in other respects were significantly larger and more numerous than those in chicks of the same age receiving an adequate diet.

Ackert and Nolf (5) gave to chickens the same numbers of embryonated eggs of *Ascaridea lineata*. To one group of these hosts they fed a diet deficient in vitamin B₁; and to the second group, a diet in which Baker's yeast was used to supply the vitamin. Those in the first group were found to harbor a greater number of parasites than those in the control group. These findings were attributed in part to weaker peristalsis. Larger parasites, however, were found in the chickens whose diets contained yeast. It was suggested that yeast may contain a factor favoring the growth of *Ascaridia lineata*.

The relationship of vitamin A and resistance of chickens to the same parasite was investigated by Ackert, Fisher and Zimmerman (3) who placed young chickens from the same hatches in three groups. To one was given a synthetic diet adequate for proteins, carbohydrates, fats, minerals and vitamins B₁ and D but lacking in vitamin A; to the second, a diet similar to the first except for the addition of vitamin A, and to the third, a natural diet furnishing an adequate amount of vitamin A. After three weeks, all of the chickens were parasitized with approximately equal numbers of embryonated eggs of *Ascaridea lineata*. Three weeks later at autopsy the deficient chicks had significantly more and larger parasites. The same
investigators (Ackert, McIlvaine and Crawford, 4) stated that the results may be attributable in part to the weakened peristalsis in the deficient chicks and, if bacteria are food for Ascaridia lineata, to their greater number. Cod liver oil was used as the source of vitamin A. Ackert (1) did not indicate that there is any evidence that this nematode requires either vitamin A or vitamin B₁. He did suggest that the greater lengths of the worms harbored in chickens receiving yeast as compared to the lengths of those in hosts on any of the other diets suggest a special growth factor for this parasite in yeast. However, an experiment designed by Beach and Ackert (14) to test for the presence of such a growth factor resulted negatively. Groups of chickens were maintained on diets including, in addition to the normal ration, twenty per cent Baker's yeast, six per cent Brewer's yeast or six per cent dry Baker's yeast, before and after being experimentally parasitized. In no case were there significant differences between the numbers or lengths of worms in these chickens and in the controls. It was concluded that yeast has no special growth factor for Ascaridia lineata nor does it alter its infectivity.

No difference was found by Ackert and Spindler (6, 7) in the number or length of these intestinal nematodes in chickens receiving an adequate amount of vitamin D through irradiation or the use of cod liver oil and in those whose diet was so lacking in vitamin D that leg weakness appeared. The chickens in both groups had been fed approximately equal numbers of
embryonated eggs of *Ascaridia lineata*. The deficient chickens did not show a normal weight again.

Certain other dietary supplements tried by Ackert and Beach (2) did appear to affect the resistance of chickens to this nematode. Chickens on an ordinary cereal ration adequate for vitamins and minerals made slower growth than those receiving meat meal also, or both meat meal and skim milk as supplements. The parasites in the first group were significantly larger and more numerous. Those hosts receiving both supplements harbored smaller, though not significantly fewer, parasites than those receiving only meat meal as a supplement.

Foster and Cort have carried on a number of investigations concerning the relationship of diet to the susceptibility of various hosts to the hookworm *Ancylostoma caninum*. Dogs on a generally deficient diet lost resistance to hookworm infestation and showed an increased elimination of eggs (43). Restored to a generally good diet, the dogs' recovery of resistance was shown by reduced egg production and a spontaneous loss of worms together with a development of resistance to further infection (39, 41). The same authors (40, 42) report that dogs on a poor diet were more susceptible to a cat strain of *Ancylostoma caninum* than were dogs fed an adequate diet. Cats on a similarly inadequate diet were somewhat more susceptible to the dog strain of the parasite than were the controls. Such results suggest undernourishment as a possible contribu-
tory cause of incidental parasitism and indicate the importance of quantitative work in normal and abnormal hosts.

Hiraishi (65) found young swine to be more easily infected with ascarids, either the swine or the human strain, when maintained on a vitamin A poor diet.

Spindler (102) reported that a lack of vitamin A in the diet lowered the resistance of experimental rats to superinfections with the intestinal nematode Hippostrongylus muris, whereas control animals fed a balanced diet developed a marked resistance to superinfection.

It was noted by Wright (108) that two dogs failed to become parasitized although fed two doses each of five thousand embryonated eggs of Toxocara canis while on a normal diet. Subsequently, when on a diet deficient in vitamin A, they became infected by two much smaller doses.

Vitamin A appears to bear some relation to resistance to Trichinella infections also. McCoy (79) noted that young rats on a vitamin A deficient diet showed, within two to three weeks, markedly lowered resistance to infection with Trichinella spiralis, as evinced by abnormally long persistence of adult worms in the intestine and by abnormally large numbers of larvae in the tissues. The deficient rats did not develop immunity to a second inoculation, whereas the controls became completely immune. Results were not so marked with half-grown rats as was the case when the hosts were slightly less than
a month old at the beginning of the experiment.

In Heterakis parasitism in chickens, according to Clapham (32), the vitamin A content of the diet seemed not to affect the course of the infestation. However, in rats experimentally infected with *Parascaris equorum*, vitamin A deficiency was associated with larger numbers and greater size of the parasites. The reasons for this difference may lie in the life histories. *Heterakis gallinacea* is always an occupant of the lumen and cecum and is not a tissue parasite. Clapham (33) also reported significantly larger numbers of *Heterakis* in the ceca of experimentally infected chickens fed on a ration deficient in calcium and phosphorus than in the ceca of those given an adequate diet. There was no significant difference in the sizes of the worms harbored by the two host groups.

It was stated by Ross and Gordon (94) that the usual resistance to parasitism by *Haemonchus contortus* which follows infection by this helminth in sheep or which accompanies old age, was broken down in the case of two animals by a diet markedly deficient in proteins and minerals, as compared to the situation in the one control animal given an adequate ration.

Reports of relations of diet to cestode parasites are not numerous. Shorb (99) pointed out that tapeworms present a different problem than do nematodes in this respect. Most cestodes do not receive nourishment directly from the host at
any time but only from the intestinal contents. _Hymenolepis fraterna_, however, lives as a tissue dweller in the mucosa for the first four or five days, thus resembling _Ascaridia lineata_ in this regard. To experimental rats one month old, Shorb gave only white bread as a deficient diet; to other rats of the same age he fed a standard diet consisting of whole wheat, corn, casein, flaxseed, powdered milk, alfalfa meal, ferric citrate and calcium carbonate. After 15 days the average weight gains for the two groups were 3 grams and 50 grams, respectively. Each rat was given 1213 eggs of the mouse strain of _Hymenolepis fraterna_. At autopsy after 15 days, significantly greater numbers of worms were found in the experimental rats than in the controls. Weight gains in the last 15 days were 6 and 35 grams for the averages of the two groups. In a second similar experiment carried on over a longer period there were again more worms in the deficient rats, but these were shorter than those found in the controls. The resistance of old rats to the mouse strain was broken slightly by a long continued deficient diet before infection. In mice, however, dietary deficiency before infection apparently rendered the mice refractory to _Hymenolepis fraterna_. To determine whether this effect was the direct result of the diet on the worm or was produced indirectly through an effect on the host, mice were infected and then placed on the deficient diet for varying lengths of time before autopsy. The controls, fed the
same number of eggs, were maintained on the regular diet. All 10 of the mice in the control group were positive, having 1 to 145 worms apiece. The worms from the deficient group were smaller than those of the same age from normal hosts (one-half as long as 9 days; one-fourth, at 11 days). On a deficient diet for varying lengths of time, none of the hosts retained parasites for more than two weeks; worms were lost rapidly. Since the diet was not so deficient as to have a very profound effect on the mouse in so short a time, the effect was considered to be exerted directly on the worms, which did not develop to maturity in mice on this diet.

Becker (16) reported that 15 rats, all passing eggs of *Hymenolepis nana* were given only whole milk (plus copper sulfate and iron chloride for seven of the hosts). The rats were kept on screen to prevent coprophagy. After five and one-half days, no eggs could be found by smear or flotation, nor were eggs passed subsequently during the 30 days that the rats were on a milk diet. After this time the rats were again given a grain diet, and eggs reappeared in the feces of 11. No tape-worms were found in the others. Milk apparently produced a cessation of egg production but not death.

Levine (77) observed that the poultry cestode *Davainea proglottina* produced about one ripe segment each day. The numbers of segments discharged by a host tended to remain at about the same level so long as diet and other environmental
conditions were constant. When the host was starved for 24 hours the number of segments discharged was decreased for a period of a week. When the hosts were fed on rations with little or no food value, such as sawdust or bran and ground cellophane, segment production declined or ceased. Autopsies revealed that not all the worms reached the same degree of development, though all were the same age.

In connection with the subject of dietary modifications and intestinal helminths, it might be of interest to note Bahrs' observations on free-living flat worms (13). She reported that the growth promoting power for planarians of the digestive mucosa of rabbits was diminished when the rabbits were fed an inadequate diet of bread and old raw carrots or a limited diet of rolled barley or when they had fasted before death.
THE INVESTIGATION

Materials

The albino rats (Mus norvegicus albinus) used in this investigation were of the Wistar A inbred strain, born in the Foods and Nutrition Laboratory of the Home Economics Division of the Iowa State College and obtained from there shortly after weaning.

A culture of Tribolium confusum was received from Mr. Harold Gunderson, formerly of the Extension Service of the Iowa State College.

A specimen of Hymenolepis diminuta was taken at autopsy from a rat received from the Physiological Chemistry Laboratory, Chemistry Department, Iowa State College. The gravid proglottids of this tapeworm were used to start the infestation in the experimental hosts.

A local feed store made up the Steenbock's growing ration and also furnished the soy bean oil meal, which had been produced by the expeller process, and the wheat middlings.

For use in some of the diets, Fleischmann's yeast was autoclaved for two hours at 120°C, and subsequently dried. Other diets contained the same type of yeast unautoclaved.

The Harris Laboratories of Tuckahoe, New York, supplied a complete inorganic salt mixture and the Casein Company of
America, New York, the vitamin-free casein. Tiki tiki, a vitamin B₁ extract, was obtained from the Bureau of Science, Manila, Philippine Islands.

Procedure

Rats to be used in these investigations were placed in separate cages of hardware cloth and supplied freely with water and a growing ration (yellow corn meal, 71 per cent; linseed oil meal, 16 per cent; ground alfalfa, 2 per cent; sodium chloride, 0.5 per cent; calcium carbonate, 0.5 per cent; and dried skim milk, 10 per cent.)

After a preliminary examination of the pellets for tapeworm eggs, the uninfected animals were fed varying numbers of cysticercoids of *Hymenolepis diminuta* through the use of the flour beetle *Tribolium confusum* as a vector. A culture of these beetles in wheat middlings was kept during the entire period of the investigation. As needed, beetles were removed and fed upon gravid proglottids from the posterior portions of rat tapeworms or feces of rats passing large numbers of eggs, mashed with a small amount of growing ration or wheat middlings. After a period of three weeks, the heads were removed from the beetles exposed to infection and both bodies and heads of six to twelve beetles added to the food of each rat to be infected. In order to insure prompt ingestion of the vectors, the
rats were deprived of food for a half day, then given only a small amount of food containing the dead beetles.

Fifteen days after the feeding of the intermediate hosts, enameled pans were placed under the cages. The half inch mesh of the hardware cloth used for floors of cages permitted the pellets to drop through and be caught in the pans. This arrangement prevented coprophagy. Each pan contained water to the depth of approximately one-half inch in which was dissolved a small amount of trisodium phosphate that served to soften the pellets somewhat and to retard bacterial growth. Every two days the pans were removed and replaced by clean ones, and the contents, which included the entire number of pellets passed for the two preceding days, were examined for eggs. Rats which did not show eggs in the droppings by the thirtieth day after ingestion of the vectors, were considered to be uninfected and were not used.

The pellets were broken and the material collected from each pan was thoroughly mixed with an electric beater and diluted with water to one liter. This material then was poured from one container to another a number of times to insure, so far as possible, a homogeneous mixture. A sample of approximately 150 cubic centimeters was immediately poured off into a glass jar fitted with a tight screw top, and set aside until a convenient time for counting, usually within a short time after collection.
Each such sample was thoroughly mixed by repeated pouring from one container to another and immediately a small amount of the fluid was drawn into a pipette fitted with a rubber bulb, and dropped into a mold counting chamber having a volume of 28.35 c.c. The entire area of the counting chamber was examined microscopically and the eggs present in the sample determined. Two such determinations were made for each collection of pellets from the pans. By multiplying the average of these two counts by 35,273.3, the approximate number of eggs in the entire liter of material could be determined. Half of this number represented the average number of eggs eliminated per day for the previous two-day period.

Collections of material and counts of tapeworm eggs were made every other day for each rat during the entire course of the experiment.

If the diet intended as the control ration was not the same as the growing ration, the rats were placed on the control diet between the time of infection and the time when eggs first appeared. For at least a month after the first appearance of eggs in the feces, all of the rats in each group were given the same diet, the control ration. After that period, part of the hosts were given the experimental diet. The details of dietary procedure with the various groups of rats will be described in connection with each experiment. Rats were weighed each week.
At the termination of the investigation upon each group of rats, the hosts were killed with illuminating gas, the intestines opened and the tapeworms present removed and counted. The parasites were allowed to relax for one hour in cold water and then were measured.

Some of the worms from each rat were arranged on slides, upon which other slides were laid and held with rubber bands while the parasites were placed in a cestode fixative (Becker and Roudabush, 27). After fixation the rubber bands and covering slides were removed and the worms washed, dehydrated and stained in hematoxylin. After being cleared in beechwood creosote, the worms were mounted in balsam and examined.

Others of the worms were not mounted but were used to infect more flour beetles.

Results

1. Effects of an Exclusive Milk Diet.

As a preliminary study, two rats passing *Hymenolepis diminuta* eggs were given only whole milk as an experimental diet instead of the growing ration previously fed. Egg counts had been made in the manner described for the ten preceding days, and were continued during the period of the milk diet and subsequently.
The results obtained are shown graphically in Figure 1. It may be seen that, whereas rat R had been eliminating numbers of eggs in the neighborhood of three million daily, the counts began at once to decline and on the twenty-first day, the eleventh of the milk diet, no eggs could be found. On the twenty-fourth day this rat was again given Steenbock's growing ration ad libitum, but eggs did not reappear in the pellets until the thirty-third day. The trend of the counts after this time was upward, although the numbers of eggs passed were not as great as those before the milk diet was used.

Rat L at first passed about four million eggs per day. The counts dropped sharply upon an exclusive milk diet, but eggs were never absent entirely. After being restored to the Steenbock ration, this rat within two weeks was eliminating numbers of eggs comparable to those found before the period of the milk diet.

These two rats were not autopsied but were kept to serve as a source of infection.

Since it appeared that the numbers of eggs produced by the rat tapeworm could be influenced by the diet of the host, this preliminary investigation was followed by a rather similar study in which more rats were used. Six young rats maintained on Steenbock's growing ration were fed infected flour beetles in the manner described. All rats began to pass eggs of *Hymenolepis diminuta* in from 19 to 25 days. As soon as eggs
Figure 1. Numbers of tapeworm eggs eliminated daily from rats R and L on an exclusive milk diet and on Steenbock's growing ration.
EGGS PER DAY IN TENS OF THOUSANDS
& WEIGHT IN GRAMS

FIGURE 1.

DAY OF INFECTION

25 33 41 49 57 65

L-EGG Count
R-EGG Count

L-Weight
R-Weight

Milk
were observed, the numbers being eliminated were determined every two days. On the thirtieth day after the first appearance of eggs, three of the rats, G9, C10 and C11, were taken off the growing ration and given only whole raw milk. The other three rats were maintained on the growing ration as before. Egg counts were made regularly over a period of five months. On the one hundred thirty-fifth day of the infection, one rat, C10, was restored to the growing ration, but rats G9 and C11 were continued on milk. The egg counts for C10, typical of the results for the experimental rats, and for C12, representative of the controls, are shown graphically in Figure 2. The weight variations of the two rats are indicated in the same figure.

Figure 3 shows a graphic comparison of total numbers of eggs eliminated each day by the three experimental rats, G9, C10 and C11, with those passed by the three controls, C12, C13 and C14, from the first to the one hundred thirty-fifth day. The three experimental rats can not be grouped subsequent to that day, as they no longer all received the same diet.

At autopsy the worm burden of the hosts and the average lengths of the parasites in each host were found to be as follows: G9, seven, 41 cm.; C10, two, 74 cm.; C11, three, 64 cm.; C12, nine, 38 cm.; C13, five, 57 cm.; C14, three, 59 cm.

It is difficult to find a satisfactory basis for comparing the lengths of worms in the control and experimental animals.
Figure 2. Variations in body weight and numbers of tape-worm eggs eliminated daily for rat C12, on Steenbock's growing ration, and rat C10 alternately on Steenbock's ration and milk.
Figure 3. Comparison of the total numbers of tapeworm eggs eliminated daily by rats C12, C13 and C14 on Steenbock's growing ration and by rats C9, C10 and C11, alternately on Steenbock's ration and milk.
Figure 3.
since the factor of worm burden is also involved. In Table I the numbers of worms harbored in each host and the average lengths of the worms are recorded.

Table I. Numbers and Average Lengths of Tapeworms Harbored by Rats C9, C10, C11, C12, C13 and C14.

<table>
<thead>
<tr>
<th>Numbers of tapeworms present</th>
<th>Rat</th>
<th>Average length of worms</th>
<th>Diet previous to autopsy</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>C10</td>
<td>74 cm.</td>
<td>Control</td>
</tr>
<tr>
<td>3</td>
<td>C11</td>
<td>64 cm.</td>
<td>Experimental</td>
</tr>
<tr>
<td>3</td>
<td>C14</td>
<td>59 cm.</td>
<td>Control</td>
</tr>
<tr>
<td>5</td>
<td>C13</td>
<td>57 cm.</td>
<td>Control</td>
</tr>
<tr>
<td>7</td>
<td>C9</td>
<td>41 cm.</td>
<td>Experimental</td>
</tr>
<tr>
<td>9</td>
<td>C12</td>
<td>38 cm.</td>
<td>Control</td>
</tr>
</tbody>
</table>

2. Effects of a Diet Deficient in Vitamins $B_1$ and $G$.

Four young rats (A1, A2, A3 and A4) which had been given flour beetles fed with eggs of *Hymenolepis diminuta* were maintained on a diet made up as follows: beet sugar, 63 per cent; casein, 15 per cent; cellulose, 3 per cent; complete salt mixture, 4 per cent; cod liver oil, 2 per cent; lard, 3 per cent; Fleischmann's yeast, 10 per cent.

Eggs appeared in the material collected from pans under each of these rats within 17 to 23 days after ingestion of the
beetles. After egg counts had been made for a control period, two of the rats, A2 and A3, were given a ration similar to that described above, but without any yeast and with ten percent more sugar. This diet is comparable to those frequently used for vitamins B1 and G deficiency. On this diet the rats declined rapidly, both in weight and in general appearance of health, and the numbers of worm eggs also declined, disappearing completely from the droppings of one of the hosts. After being restored to the control diet the rats improved in weight and appearance and the numbers of eggs eliminated mounted. Forty days later, rats A1 and A2 were given the experimental diet; eggs disappeared from the droppings of both and no tape-worms could be found in the intestines at autopsy. Rats A3 and A4 were found to have harbored three tapeworms and one tapeworm, respectively.

The results obtained for the rat designated as A2 may be taken as an example and are represented in Figure 4. This host was first maintained on the control diet, then on the experimental ration, restored to the adequate diet for a time and then again given the ration lacking in yeast. The variations in the egg counts and in the body weight of the host are indicated in the figure.
Figure 4. Variations in the numbers of tapeworm eggs eliminated daily by rat A2 alternately on a control diet and one lacking in vitamins B₁ and G.
Figure 4:
3. Effects of a Diet Deficient in Vitamin B₁.

Four young rats harboring rat tapeworms were maintained on the control diet described in the foregoing account for a preliminary period during which egg counts were made every two days. Three of the four were then given a ration similar in all respects to the control diet except that the yeast used had been autoclaved for two hours at 120°C. This diet is not adequate for vitamin B₁. Because the numbers of eggs passed were maintained at the previous level for two of these experimental rats, but declined somewhat in one case, it was considered desirable to try the effect of this diet a second time.

Seven young rats were fed flour beetles exposed to infection with Hymenolepis diminuta in the manner described. In the droppings of all but one, eggs were found in from 19 to 23 days. The six young infected rats were fed the control diet containing unautoclaved yeast and determinations of the numbers of eggs eliminated were made for a control period of 45 days. At that time the three rats, D20, D21 and D22 were given the diet in which the autoclaved yeast was substituted, whereas the other three, D16, D17 and D18, were continued on the control diet.

The animals on the experimental diet ceased making normal gains and after several weeks fell off sharply in body weight. There was, however, no marked decrease in the numbers of eggs.
eliminated during this time as compared to those passed during the 45-day control period.

On the eighty-fourth day, one of the experimental animals, D20, was restored to the control diet. This animal made gains in weight, but did not show a notable increase in the numbers of worm eggs passed.

The variations in the weights and numbers of eliminated eggs for the two rats D16 and D20 are shown in Figure 5. Rat D16 was maintained continuously on the control diet; rat D20 was shifted to the experimental diet and then again to the control ration.

The total numbers of eggs eliminated by rats D16, D17 and D18 are compared graphically with those passed by rats D20, D21 and D22 in Figure 6. Until the forty-fifth day, rats in both groups were given the same diet, the control ration containing unautoclaved yeast. At that time, autoclaved yeast replaced the unautoclaved for the one group. This graphic representation is continued only until the eighty-third day, although egg counts were made for an additional two weeks, because after that day the three rats D20, D21 and D22 could not be grouped together, as D20 was again given the control diet.

The numbers of worms found in each host at autopsy and the average lengths of the worms are indicated in Table II.
Figure 5. Variations in body weight and numbers of tape-worm eggs eliminated daily by rat D16 on a control diet and by rat D20, alternately on a control and a vitamin B₁ deficient diet.
Figure 6. Comparison of the total numbers of tapeworm eggs eliminated by rats D16, D17 and D18 maintained on a control diet and by rats D20, D21 and D22 maintained alternately on a control and a vitamin B₁ deficient diet.
Figure 6.

Vitamin B deficient diet

$D_{20}, D_{21}, \& D_{22}$

$D_{16}, D_{17}, \& D_{18}$
4. Effects of a Diet Deficient in Vitamin G.

Eight young male rats were fed flour beetles which had been given gravid proglottids of Hymenolepis diminuta and all eight became infected. They were maintained on the same control diet, containing unautoclaved yeast, described above. After a month during which the numbers of eggs being passed by each rat were determined every two days, four of the rats, C1, C2, C3 and C4, were given a diet made up as follows: beet sugar, 73 per cent; casein, 15 per cent; cellulour, 3 per cent; salt mixture, 4 per cent; cod liver oil, 2 per cent; lard, 3 per cent. This diet would be deficient in both vitamins B1 and G. Vitamin B1 was added by the administration of
four drops of tiki tiki daily to each experimental rat. This was readily taken from a pipette by those animals whose diet lacked yeast.

The rats on the experimental diet lost weight although they continued to eat fairly well. The skin became coarse; the hair, matted and unkempt.

On the one hundred thirty-ninth day of the infection, two of the experimental rats were again given the control diet. These animals regained weight and a general appearance of health and tidiness.

The numbers of eggs passed by rats maintained on the experimental diet were greatly decreased. Typical results are presented graphically in Figure 7. Rat C1 was fed the control ration for the first month of the infection, transferred to the experimental diet for three and a half months and again placed on the control ration for a month. Rat C4 was transferred to the experimental ration for the duration of the experiment after being given the control ration for the first month of infection. Rat C7 was maintained for the entire period on the control diet. Both the egg counts and the body weights of the hosts are represented in the figure.

Figure 8 compares graphically the total numbers of eggs passed by rats C1, C2, C3 and C4 which were transferred to the experimental diet, and those eliminated by rats C5, C6, C7 and C8 which continued to subsist on the control diet. The
Figure 7. Variations in body weight and numbers of tapeworm eggs eliminated daily for rats C1, C4 and C7 on vitamin G deficient and control diets.
Figure 7.
Figure 8. Comparison of the total numbers of tapeworm eggs eliminated by rats C5, C6, C7 and C8 maintained on the control diet and by rats C1, C2, C3 and C4 given alternately a control and a vitamin G deficient diet.
figure indicates the course of the infection from the first to the one hundred thirty-ninth day.

If the rats in this experiment are arranged in a series according to the number of tapeworms found at autopsy, the average lengths of the worms in each host will fall as shown in Table III.

Table III. Numbers and Average Lengths of Tapeworms found at Autopsy in Rats C1, C2, C3, C4, C5, C6, C7 and C8.

<table>
<thead>
<tr>
<th>Number of tapeworms</th>
<th>Rat of worms</th>
<th>Average length</th>
<th>Diet previous to autopsy</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>C5</td>
<td>89 cm</td>
<td>Control</td>
</tr>
<tr>
<td>1</td>
<td>C7</td>
<td>78 cm</td>
<td>Control</td>
</tr>
<tr>
<td>4</td>
<td>C8</td>
<td>51.5 cm</td>
<td>Control</td>
</tr>
<tr>
<td>6</td>
<td>C1</td>
<td>43 cm</td>
<td>Control</td>
</tr>
<tr>
<td>10</td>
<td>C3</td>
<td>37.5 cm</td>
<td>Experimental</td>
</tr>
<tr>
<td>11</td>
<td>C4</td>
<td>39 cm</td>
<td>Experimental</td>
</tr>
<tr>
<td>14</td>
<td>C2</td>
<td>38 cm</td>
<td>Control</td>
</tr>
<tr>
<td>42</td>
<td>C6</td>
<td>32 cm</td>
<td>Control</td>
</tr>
</tbody>
</table>

It was noted that 3 of the 14 tapeworms found in rat C2 and 16 of the 42 found in rat C6 were much shorter and somewhat narrower than the others. Microscopic examination revealed
that these smaller worms possessed scolices, necks and young proglottids similar to those of normal specimens of *Hymenolepis diminuta*, but that no gravid proglottids were present. The average length of these shorter worms was 10 cm. in rat C2; 9.9 cm. in rat C6. The average length of the more nearly normal tapeworms was 45.6 cm. in rat C2; 46.5 cm. in rat C6.

5. Effects of Limiting the Amount of Food.

Fifteen young rats were exposed to infection with *Hymenolepis diminuta* using the flour beetle as a vector. Of these, 12 began to eliminate eggs within 17 to 24 days. For 29 days the young rats had free access to the control diet described above while determinations of the numbers of eggs being passed were made every two days. For the last week of this period the weight of the food eaten each day by each rat was determined. One-half this average daily intake was given to six of the rats, D2, D3, D4, D8, D10 and D12, each day for the next two weeks, while the other six rats, D5, D6, D7, D13, D14 and D15, were given the same ration but in any desired amount. The amount of the ration eaten by these control animals was determined each day. From the sixth to the ninth week, each experimental animal was given only one-third the average amount of the feed eaten by the controls for the preceding week. At the beginning of the ninth week, the groups were reversed in
treatment, rats D2, D3, D4, D8, D10 and D12 being given the control diet *ad libitum* and the other six allowed only one-third the average amount eaten by the control group.

When the diet was limited as to amount in this fashion, the rats lost weight but maintained a general appearance of health. The egg counts during the periods of partial starvation did not decline appreciably.

Figure 9 illustrates typical weight and egg count variations for two rats, D12 and D15, one in each of the two groups described above. The variations in the total numbers of eggs eliminated by rats of the two groups are graphically represented in Figure 10.

These rats were not autopsied at this time but were kept for use in the succeeding experiment.

6. Comparison of the Effects of Soy Bean Oil Meal and Wheat Middlings in the Diet.

The rats used in the preceding experiment, after a recovery period when the control ration was given *ad libitum*, were again divided into groups of six rats each. The rats in one group were given a modification of the control diet in which 10 per cent soy bean oil meal was substituted for the 10 per cent yeast; the other, a diet in which 30 per cent wheat middlings was substituted for the 10 per cent yeast and 20 per cent of
Figure 9. Variations in body weight and numbers of eggs eliminated for rats D12 and D15 with free and limited food intake.
Figure 9.
Figure 10. Comparison of the total numbers of tape-worm eggs eliminated daily by the group of rats D2, D3, D4, D8, D10 and D12, and the group D5, D6, D7, D13, D14 and D15 with free and limited food intake.
Figur-E 10.
the sugar.

After 46 days on these rations, three of the rats in each group were shifted to the alternate diet; the other three were allowed to continue as before.

The rats continued to gain on both rations at approximately the same rate. The numbers of eggs eliminated, however, were appreciably higher when the modified diet included wheat middlings than when soy bean oil meal was substituted, as may be seen in Figure 11. This figure represents graphically the total numbers of eggs eliminated by rats D2, D3 and D4 which were maintained on the soy bean oil meal diet for the course of the experiment, the numbers passed by rats D5, D6 and D7 which were first maintained on the soy bean oil meal ration and then shifted to that containing wheat middlings, the total egg counts for D8, D10 and D12 on the wheat middlings diet and for D13, D14 and D15 first on wheat middlings and then on soy bean oil meal. In this way comparisons may be made between the results obtained for those rats on each of the diets for the entire period of observation, and for those transferred from one diet to the other.

If the rats used in this experiment are arranged in an ascending series according to the number of tapeworms present at autopsy, the average lengths of the worms in each host fall, with a few minor exceptions, in a descending series regardless of diet, as shown in Table IV.
Figure 11. Total numbers of tapeworm eggs eliminated daily by the group of rats D2, D3 and D4; the group D5, D6 and D7; the group D8, D10 and D12 and the group D13, D14 and D15 maintained on diets containing soy bean oil meal or wheat middlings.
Figure 1.

- Soybean oil meal diet
- Wheat middlings diet
- Soybean oil meal diet
- Wheat middlings diet
- Soybean oil meal diet
- Wheat middlings diet

EGGS PER DAY IN TENS OF THOUSANDS

DAY OF INFECTION

DAY OF INFECTION
Table IV. Numbers and Average Lengths of Tapeworms in Rats D2, D3, D4, D5, D6, D7, D8, D10, D12, D13, D14 and D15.

<table>
<thead>
<tr>
<th>Number of worms harbored</th>
<th>Average length of worms</th>
<th>Diet previous to autopsy</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>D2</td>
<td>91 cm.</td>
</tr>
<tr>
<td>1</td>
<td>D8</td>
<td>88 cm.</td>
</tr>
<tr>
<td>1</td>
<td>D12</td>
<td>76 cm.</td>
</tr>
<tr>
<td>1</td>
<td>D3</td>
<td>71 cm.</td>
</tr>
<tr>
<td>2</td>
<td>D15</td>
<td>71.5 cm.</td>
</tr>
<tr>
<td>2</td>
<td>D13</td>
<td>69.5 cm.</td>
</tr>
<tr>
<td>2</td>
<td>D4</td>
<td>58 cm.</td>
</tr>
<tr>
<td>2</td>
<td>D5</td>
<td>53 cm.</td>
</tr>
<tr>
<td>4</td>
<td>D6</td>
<td>54.5 cm.</td>
</tr>
<tr>
<td>7</td>
<td>D10</td>
<td>47 cm.</td>
</tr>
<tr>
<td>7</td>
<td>D7</td>
<td>44 cm.</td>
</tr>
<tr>
<td>8</td>
<td>D14</td>
<td>36 cm.</td>
</tr>
</tbody>
</table>

7. Relation of the Worm Burden to the Numbers of Eggs Eliminated.

For those rats in the various experiments which were maintained on the ration designated in this paper as the control diet, for the first month of infection, it was possible at autopsy to obtain data on the relationship of the egg counts to the numbers of tapeworms harbored. There was revealed no
direct correlation between the numbers of eggs found in the droppings and the worm burden, but rather it appeared that the number of eggs produced by a worm was influenced to some extent by the number of parasites present, so that a rat harboring a considerable number of worms might pass no more eggs than one harboring only a few or even a single parasite, as shown in Table V. In this table, those rats found to have harbored the same number of parasites are grouped, and the average number of eggs eliminated per day by each rat during the first month of infection noted, together with the range and the mean for each group. The average number of eggs produced per day for each worm was calculated and also appears in the table. During the period involved, all of these rats had similar diets.

These results are represented graphically in Figure 12 which shows the average numbers of eggs passed per day per rat for each group harboring different numbers of parasites, and in Figure 13, which represents the average number of eggs produced per day per worm for the same groups.
Table V. Mean numbers of tapeworm eggs eliminated per day per rat and per day per worm for rats on the same diet but harboring different numbers of parasites.

<table>
<thead>
<tr>
<th>Number</th>
<th>Average number of eggs ((10^3)) eliminated per day for first month of infection, Control diet</th>
<th>Average number of worms ((10^3)) per day per worm</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>D8 : 1777</td>
<td>1777</td>
</tr>
<tr>
<td></td>
<td>C7 : 1439</td>
<td>1439</td>
</tr>
<tr>
<td></td>
<td>D19 : 1246</td>
<td>1246</td>
</tr>
<tr>
<td></td>
<td>D12 : 1233</td>
<td>1233</td>
</tr>
<tr>
<td></td>
<td>D2 : 978</td>
<td>978</td>
</tr>
<tr>
<td></td>
<td>D12 : 940</td>
<td>940</td>
</tr>
<tr>
<td></td>
<td>C5 : 430</td>
<td>430</td>
</tr>
<tr>
<td></td>
<td>((\text{Range: } 430-1777; \text{ Mean: } 1149)) ((\text{Range: } 430-1777; \text{ Mean: } 1149))</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>D4 : 1478</td>
<td>739</td>
</tr>
<tr>
<td></td>
<td>D5 : 1460</td>
<td>730</td>
</tr>
<tr>
<td></td>
<td>D15 : 1378</td>
<td>689</td>
</tr>
<tr>
<td></td>
<td>D16 : 1284</td>
<td>642</td>
</tr>
<tr>
<td></td>
<td>D13 : 994</td>
<td>497</td>
</tr>
<tr>
<td></td>
<td>((\text{Range: } 994-1478; \text{ Mean: } 1319)) ((\text{Range: } 497-739; \text{ Mean: } 659))</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>D22 : 1359</td>
<td>453</td>
</tr>
<tr>
<td></td>
<td>D17 : 782</td>
<td>294</td>
</tr>
<tr>
<td></td>
<td>((\text{Range: } 782-1359; \text{ Mean: } 1070)) ((\text{Range: } 294-453; \text{ Mean: } 373))</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>D6 : 1684</td>
<td>421</td>
</tr>
<tr>
<td></td>
<td>D8 : 1520</td>
<td>380</td>
</tr>
<tr>
<td></td>
<td>((\text{Range: } 1520-1684; \text{ Mean: } 1602)) ((\text{Range: } 380-421; \text{ Mean: } 400))</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>D21 : 1735</td>
<td>347</td>
</tr>
<tr>
<td>6</td>
<td>C1 : 1848</td>
<td>308</td>
</tr>
<tr>
<td>7</td>
<td>D10 : 1950</td>
<td>280</td>
</tr>
<tr>
<td></td>
<td>D7 : 1715</td>
<td>245</td>
</tr>
<tr>
<td></td>
<td>((\text{Range: } 1715-1950; \text{ Mean: } 1832)) ((\text{Range: } 245-280; \text{ Mean: } 262))</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>D14 : 1803</td>
<td>226</td>
</tr>
<tr>
<td>9</td>
<td>D9 : 1803</td>
<td>226</td>
</tr>
<tr>
<td>10</td>
<td>C3 : 1790</td>
<td>179</td>
</tr>
<tr>
<td>11</td>
<td>C4 : 1595</td>
<td>145</td>
</tr>
<tr>
<td>12</td>
<td>D18 : 1404</td>
<td>117</td>
</tr>
<tr>
<td>14</td>
<td>C2 : 1694</td>
<td>121</td>
</tr>
<tr>
<td>42</td>
<td>C6 : 672</td>
<td>16</td>
</tr>
</tbody>
</table>
Figure 12. Mean numbers of tapeworm eggs eliminated per day by rats harboring various numbers of worms.

Figure 13. Mean numbers of eggs produced per worm per day by worms grouped according to the numbers of worms present.
8. Relation of the Worm Burden to the Lengths of Worms Harbored.

The information given in Tables I, II, III and IV is brought together in Table VI. The hosts are arranged in groups in an ascending series according to the numbers of tapeworms harbored, and the average length of the parasites in each host is recorded, together with the diet which that host had been receiving prior to its death. The diet indicated as "Steenbock's" is Steenbock's growing ration; "milk" refers to an exclusive whole milk diet; "soy bean oil meal" and "wheat middlings", to the diets described above including these supplements. The "control" diet is the one previously described and designated as such throughout this paper.
Table VI. Mean Lengths of Tapeworms Found in Rats Harboring Different Numbers of Worms.

<table>
<thead>
<tr>
<th>Number of worms present:</th>
<th>Average length of tapeworms (cm.)</th>
<th>Diet of host before death</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 : D20</td>
<td>92</td>
<td>Control</td>
</tr>
<tr>
<td>1 : D21</td>
<td>91</td>
<td>Soy bean oil meal</td>
</tr>
<tr>
<td>1 : C5</td>
<td>89</td>
<td>Control</td>
</tr>
<tr>
<td>1 : D8</td>
<td>88</td>
<td>Wheat middlings</td>
</tr>
<tr>
<td>1 : C7</td>
<td>78</td>
<td>Control</td>
</tr>
<tr>
<td>1 : D12</td>
<td>76</td>
<td>Wheat middlings</td>
</tr>
<tr>
<td>1 : D3</td>
<td>71</td>
<td>Soy bean oil meal</td>
</tr>
<tr>
<td></td>
<td>(Range: 71-92; Mean: 83.6)</td>
<td></td>
</tr>
<tr>
<td>2 : D16</td>
<td>86.5</td>
<td>Control</td>
</tr>
<tr>
<td>2 : C10</td>
<td>74</td>
<td>Steenbock's</td>
</tr>
<tr>
<td>2 : D15</td>
<td>71.5</td>
<td>Soy bean oil meal</td>
</tr>
<tr>
<td>2 : D13</td>
<td>69.5</td>
<td>Soy bean oil meal</td>
</tr>
<tr>
<td>2 : D4</td>
<td>58</td>
<td>Soy bean oil meal</td>
</tr>
<tr>
<td>2 : D5</td>
<td>53</td>
<td>Wheat middlings</td>
</tr>
<tr>
<td></td>
<td>(Range: 53-86.5; Mean: 68.8)</td>
<td></td>
</tr>
<tr>
<td>3 : D17</td>
<td>93</td>
<td>Control</td>
</tr>
<tr>
<td>3 : D22</td>
<td>82</td>
<td>Vitamin B deficient</td>
</tr>
<tr>
<td>3 : C11</td>
<td>64</td>
<td>Milk</td>
</tr>
<tr>
<td>3 : C14</td>
<td>59</td>
<td>Steenbock's</td>
</tr>
<tr>
<td></td>
<td>(Range: 59-93; Mean: 74.5)</td>
<td></td>
</tr>
<tr>
<td>4 : D6</td>
<td>54.5</td>
<td>Wheat middlings</td>
</tr>
<tr>
<td>4 : C8</td>
<td>51.5</td>
<td>Control</td>
</tr>
<tr>
<td></td>
<td>(Mean: 53)</td>
<td></td>
</tr>
<tr>
<td>5 : C13</td>
<td>57</td>
<td>Steenbock's</td>
</tr>
<tr>
<td>5 : D21</td>
<td>56</td>
<td>Vitamin B deficient</td>
</tr>
<tr>
<td></td>
<td>(Mean: 56.5)</td>
<td></td>
</tr>
<tr>
<td>6 : C1</td>
<td>43</td>
<td>Control</td>
</tr>
<tr>
<td>7 : D10</td>
<td>47</td>
<td>Wheat middlings</td>
</tr>
<tr>
<td>7 : D7</td>
<td>44</td>
<td>Wheat middlings</td>
</tr>
<tr>
<td>7 : C9</td>
<td>41</td>
<td>Milk</td>
</tr>
<tr>
<td></td>
<td>(Range: 41-47; Mean: 44)</td>
<td></td>
</tr>
<tr>
<td>8 : D14</td>
<td>36</td>
<td>Soy bean oil meal</td>
</tr>
<tr>
<td>9 : C12</td>
<td>38</td>
<td>Steenbock's</td>
</tr>
</tbody>
</table>
Table VI. (continued)

<table>
<thead>
<tr>
<th>Number</th>
<th>Worms present</th>
<th>Average length of tapeworms (cm.)</th>
<th>Diet of host before death</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>C3</td>
<td>37.5</td>
<td>Vitamin G deficient</td>
</tr>
<tr>
<td>11</td>
<td>C4</td>
<td>39</td>
<td>Vitamin G deficient</td>
</tr>
<tr>
<td>12</td>
<td>D18</td>
<td>31.3</td>
<td>Control</td>
</tr>
<tr>
<td>14</td>
<td>C2</td>
<td>38</td>
<td>Control</td>
</tr>
<tr>
<td>42</td>
<td>C6</td>
<td>32</td>
<td>Control</td>
</tr>
</tbody>
</table>
DISCUSSION

A rather thorough search of the literature has not revealed that the confused flour beetle Tribolium confusum has ever before been recorded as a natural or experimental intermediate host for the rat tapeworm Hymenolepis diminuta. It is not surprising, however, that the cysticercoid should be able to develop in this insect, since it is known to occur in a large number of arthropods and has been reported for the closely allied species Tribolium ferrugineum. In this investigation, only the adult beetles were used as vectors. Because of the grain-infesting habit of this insect it seems probable that it might serve as a natural as well as an experimental vector. The successful infecting of rats with confused flour beetles three weeks after the ingestion of eggs by the insects, suggests that the time required for development of the cysticercoid in this host is comparable to that found by Joyeux (70) to obtain in other hosts.

For several reasons, it seems probable that all the worms harbored by any one rat were received at the same time. The infected beetles were kept in glass jars with tight screw caps to prevent their escape, and the immediate dropping of the rat pellets through the bottoms of the cages into the trisodium phosphate solution in the pans makes it unlikely that any other insects would have been accidentally infected. It might
be noted in this connection that from time to time uninfected rats were kept for considerable periods in the same laboratory and none of them were ever found to have become hosts for the rat tapeworm, although the droppings were examined periodically. Moreover, Palais (88) reports his inability to infect rats with additional rat tapeworms once an infection was established.

On the other hand, no evidence was ever seen in the pans of spontaneous loss of a worm. Series of proglottids were sometimes present in the droppings, but these were always gravid proglottids from the posterior portion of the worm.

It seems, therefore, that during the course of any investigation, there was no change in the number of worms present in any one host and that the variations in the egg counts represent actual variations in the numbers of eggs being developed rather than changes in the worm burden of the host.

It is evident from the graphic representations of results that there is a considerable day to day variation in the numbers of eggs present in the fecal material. This is not unexpected since varying numbers of segments are separated from the major part of the worm from time to time and the parenchyma partially digested. Also, some of the variation may be attributed to the fact that it was not always possible to collect the material from the pans at precisely the same time each day, although an effort was made to have the times not
widely different.

This day to day variation made it necessary that egg counts should be continued for each rat over a fairly long period of time and that the general trend of the counts should be considered rather than that an attempt should be made to account for each rise and fall.

It was considered necessary to have a control period for each rat so that during the experimental period its elimination of eggs could be compared to its previous record in that respect. The egg counts for one rat could not be directly compared with those for another since there was no assurance that they were harboring the same numbers of worms.

Furthermore, it was not possible to compare results on a per worm basis, since the numbers of eggs produced per worm are not the same for different severities of infection (see Figure 13). Only the general trend of one egg count curve may legitimately be compared with that of another.

Reference to Table I and to Figure 12 will show that there was little difference in the numbers of eggs eliminated by rats harboring one, two or three tapeworms, and rats harboring from four to fourteen worms eliminated very nearly the same numbers. Admittedly, the numbers of rats for some of these determinations are very small, but the results show clearly the impossibility of predicting on the basis of egg counts, the numbers of parasites which will be found at
autopsy. A single parasite harbored in an intestine would seem to have optimum conditions for reproduction and the numbers of eggs developed by any worm decrease fairly regularly as the worm burden increases (see Figure 13).

Table VI illustrates the tendency for the parasites to be smaller as the worm burden increases. When as many as 42 worms were harbored, some remained extremely small and did not contain any eggs whatever. Young and mature proglottids were present but no gravid segments, and the width of the worms was less than the width of corresponding portions of normal worms. The differences in size of parasites as well as differences in the numbers of eggs produced in infections of differing severity might conceivably be due to competition for food or to crowding. If the decreased amount of food available for each parasite were the determining factor, it would be expected that limiting the food intake of the host would have shown similar results. Yet reducing the amount of food ingested by the host to one-half or even to one-third the normal amount produced no apparent decrease in reproductive rate or power, whereas worms dwelling in an intestine with one other worm produced only 57 per cent as many eggs as those worms which were the sole residents.

If the results observed be ascribed to crowding, the effects might have been produced by the actual pressure and lack of room for growth. Indeed, when many worms are harbored the
intestine gives the impression of being so full of parasites as to be nearly obstructed. The decrease of surface for absorption when many worms are crowded together may be a factor as may also a detrimental effect of the greater amount of excretory products present from the many parasites.

A decrease in reproductive power associated with an increased parasite population has been noted by other investigators. Hill (63) reports a decrease in the number of eggs produced per hookworm as the number of worms harbored by the human host increased. In the case of the dog hookworm, Sarles (96) found a smaller egg production per worm in heavy infestations than in light ones, but the differences of size of worms in light and heavy infestations was slight as compared to the variation between those of similar severity of infection in different dogs. Andrews (9) reports that, as the population of the sheep nematode Cooperia curticei increased, the egg production per female worm was found to decrease. In Hymenolepis fraterna infections in rats and mice, Shorb (99) found that after the eighth day the larger worms were present in the hosts having fewer parasites and he suggests that, as the worms grow, crowding becomes a factor in retarding growth.

That it is possible to influence the life processes of the rat tapeworm by the diet of the host seems evidenced by the experiments in which an exclusive milk diet, a vitamin G deficient diet and a soybean oil meal or wheat middlings diet
were used. There appears to be some factor present in yeast which is required for maximum reproductivity of the rat tape-worm. The fact that production of eggs did not decrease when the yeast had been autoclaved (see Figure 6) suggests that this factor is not the labile vitamin, \( B_1 \). The decline of reproductive power of the parasite when the host was maintained on a vitamin G deficient diet, however, indicates that it may be associated with the vitamin B complex from some sources. Milk appears to furnish an insufficient amount of this factor to keep the worm at its maximum reproductive level; wheat middlings seem to furnish more than does soy bean oil meal, although this latter supplement does not lack it entirely. It cannot be stated that this factor is identical with vitamin G.

It has been suggested verbally to the author that the decrease in numbers of eggs eliminated on some of the diets, such as that lacking vitamin G or that consisting only of milk, might be merely a secondary result of the decreased amount of fecal material because of slight residue or lowered food intake on the part of the host. However, since the rats were continually kept over pans so that all of the pellets passed were collected, and since the determinations were made not on the basis of numbers of eggs per weight of feces, but on numbers of eggs eliminated over a two-day period, it would seem that all the eggs produced would have been accounted for, whether they occurred in a small number of hard pellets or in
Furthermore, this interpretation would not explain why egg counts declined on the vitamin C deficient diet which was associated with loss of body weight on the part of the hosts, but were not decreased on the vitamin B1 deficient diet, also associated with decreased food intake and loss of weight. Nor would it account for the continued collection of large numbers of eggs when the food intake was limited to one-third the usual amount.

The fact that no greater structural differences could be observed in worms from rats on the modified diets as compared to those from the controls, which were not also present in worms from the same animal suggests only a difference in the tempo of egg development as an explanation for the differences observed in egg production.

It may be noted by referring to any of the graphic representations of egg counts, that a large initial production of eggs is characteristic of Hymenolepis diminuta infections in the rat. There follows more or less of a leveling off at a slightly lower level. The author has been questioned as to whether this may be accounted for by the development of some immunity on the part of the host. The question of immunity cannot be ruled out, but it would seem not to apply to a great extent to such a parasite as Hymenolepis diminuta which lives in the lumen and is not a tissue dweller, nor is there
any evidence of a continuous development of immunity since the numbers of eggs eliminated by the rats on control diet do not continue to decline beyond the first week or two of the infection.

Because of the nature of this study, in which it was necessary to continue observations on the same hosts over rather long periods of time, it was not possible to investigate the effects of a great number of dietary modifications. Since it has been demonstrated that it is possible to influence the number of eggs produced by the rat tapeworm through the diet of the host, it would be of interest to test a number of dietary supplements for the presence of a factor necessary for optimum reproduction and to test the ability of various diets to prevent initial infection. The factors necessary for growth and reproduction of this tapeworm might well be compared with those required for other parasites which are lumen dwellers as well as for those which for a time derive their nourishment directly from host tissues.
CONCLUSIONS

1. The adult flour beetle Tribolium confusum may serve as a vector for the rat tapeworm Hymenolepis diminuta.

2. The cysticercoids developing in the flour beetle are infective to the rat after approximately three weeks in the intermediate host.

3. There is no direct relationship between the number of rat tapeworms harbored and the numbers of eggs eliminated by the host.

4. There is an inverse relationship between the number of worms harbored by a rat and the average number of eggs produced by each worm, a fact possibly attributable to crowding.

5. There is a tendency for tapeworms to be shorter when present in large numbers within a host than when occurring singly.

6. When large numbers of worms are harbored, some of the worms may fail to develop gravid proglottids and to produce eggs.

7. Spontaneous loss of the tapeworm Hymenolepis diminuta does not occur readily from the rat.

8. It is possible to influence the numbers of eggs produced by the rat tapeworm through modification of the host's diet.

9. A diet deficient in vitamins B₁ and G is associated
with a decrease in egg output.

10. This effect is apparently not due to the labile vitamin B₁, as a diet deficient in this vitamin is not associated with a lowered production of eggs.

11. A diet consisting exclusively of whole milk produces a decrease in the number of eggs developed.

12. Partial starvation of the host by restriction of the food intake to one-third the normal amount does not cause a decrease in the numbers of tapeworm eggs eliminated.

13. There appears to be a factor associated with the vitamin G complex which is necessary for normal egg production by the rat tapeworm. A diet lacking in vitamin G does not furnish this factor. It is not maintained that the factor involved is identical with vitamin G.

14. A diet containing wheat middlings is associated with a higher production of tapeworm eggs than is one containing soy bean oil meal. This may be attributable to a larger amount of the factor necessary for reproduction in the former.

15. No constant structural differences could be found between worms taken from rats on experimental diets and those from hosts on control diets. It may be that there is only a difference in tempo of egg development.

16. It is suggested that the effects of the various diets are probably produced directly upon the parasite rather than indirectly through effects on the hosts, since certain
diets detrimental to the hosts are not associated with lowered egg production, whereas other diets appear to be deleterious to both host and parasite.

17. A high initial egg production is characteristic of Hymenolepis diminuta infections in the rat, followed by a more constant rate of egg development at a somewhat lower level.
SUMMARY

1. This paper includes a review of literature which concerns the morphology, life history, vectors and definitive hosts of the rat tapeworm *Hymenolepis diminuta* and which deals with the effects of dietary modifications on various intestinal parasites including protozoa, nematodes and cestodes. A total of 110 citations is given.

2. Adult flour beetles of the species *Tribolium confusum* were infected by being fed gravid proglottids of the rat tapeworm. After three weeks to allow for the development of cysticercoids in the intermediate hosts, the beetles were fed to white rats of known ancestry. Eggs were observed in the fecal pellets of 42 of the 47 rats so treated, in from 17 to 25 days after the ingestion of the beetles.

3. The rats were kept in cages of half-inch mesh hardware cloth. Pans containing water and trisodium phosphate were placed under the cages to catch the pellets as they were passed. Every two days the material in the pans was removed, thoroughly mixed with an electric mixer and diluted to a known volume. Random samples were examined in a mold counting chamber and the number of eggs present determined. The number of eggs eliminated per day by each rat was calculated.

4. An exclusive milk diet was found to decrease the numbers of tapeworm eggs produced as compared with Steenbock's
growing ration.

5. A diet deficient in vitamins B₁ and G decreased egg production greatly but vitamin B₁ deficiency alone had no such marked effect.

6. A diet deficient in the vitamin G complex was concomitant with decreased egg production, a fact suggesting the association with this vitamin of a factor necessary for maximum reproductive power of the rat tapeworm.

7. Wheat middlings appear to furnish more of the factor or factors responsible for egg production than does soy bean oil meal.

8. Limiting the amount of a normal diet to one-third the usual amount did not produce any lessened development of eggs.

9. The numbers of eggs produced on any diet were usually greater at the outset of the infection than at any later time. The numbers of eggs produced did not continue to decline, however, after the first week or ten days.

10. No gross structural abnormalities were found in the worms showing decreased egg production that were not also observed in worms from control hosts. Sterile proglottids and anomalies of position and number of testes were found in nearly all worms.

11. There was observed an inverse relationship between the average number of eggs produced by each worm and the number of worms present. The presence of large numbers of tape-
worms is also associated with less length or even with incom-
plete development of some of them, although there is evidence
that all the parasites were acquired at the same time.
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