

A STUDY OF THE APPARENT DIGESTIBILITY OF
IDENTICAL DIETS BY DIFFERENT SPECIES

by

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ABSTRACT

A digestibility study was conducted in which an identical diet was fed to five species, namely, rats, pigs, sheep, guinea pigs and humans. The diet consisted mainly of whole wheat. As fed, it was found to be unsuitable for digestibility studies with guinea pigs. With sheep, a basal hay diet was fed and digestion coefficients determined indirectly. Variability between individuals was relatively low, for all species, for food fractions other than crude fiber and ether extract. Humans digested crude fiber to the same extent as pigs and rats. The range of the digestion coefficients for crude protein, nitrogen-free extract and digestible energy was remarkably small, considering that the species used in this study had anatomically different digestive systems. All species showed significant differences in the total digestible nutrients and digestible energy of the diet. Further research is needed in comparative species digestibility studies with humans.

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Introduction

The apparent digestibility of a feed is a measure of the extent to which it is absorbed. Although studies have been made of the digestibility of all types of feeds and feed combinations, these have been limited, mostly, to animals with anatomically similar digestive systems. Rats or other small laboratory animals are constantly used as pilot animals in human nutrition studies. However, there is little evidence to justify the assumption that digestion coefficients obtained with rats, can be used to indicate the digestibility of the same food by humans. More data are needed on the relative ability of the different species to digest the same food fractions before reliable constants can be established.

Therefore, the specific object of this research was to devise a suitable diet which could be fed to five different species, namely, humans, rats, pigs, guinea pigs and sheep, and to observe the differences in digestibility between the species.

Review of Literature

There are no digestibility studies reported in the literature in which humans are compared to sheep, pigs or guinea pigs. Comparisons have been made between sheep and pigs and digestibility studies have been conducted with herbivora, ruminant and non-ruminant.

Comparative Digestibility Studies

In digestibility studies with ruminants, the emphasis has been on the digestibility of the crude fiber fraction of the diet. Axelsson (1943) using 212 cattle, 547 sheep and 43 goats, showed that the crude fiber fraction of the diet has a greater effect upon digestibility of the diet as a whole than any other fraction. There was no significant difference between the cattle, sheep and goats in the effect of crude fiber in the diet.

An early investigator, Emery (1892) in North Carolina, compared the ability of sheep, cows and goats to digest cotton seed hulls and concluded that the coefficients of digestion obtained with the goat could be used with confidence in calculating rations for other domestic ruminants, the cow and sheep.

Wolberg, Hodgson, Knott and Ashworth (1943), measured the digestibility of corn silage and mixed hay using cattle and sheep, as experimental animals. They found that the total digestible nutrients of the two feeds with cows, heifers and sheep showed little difference, and that the digestibility coefficients obtained with sheep may be applied to cattle.

The need for a suitable pilot animal for digestibility studies with cattle led to comparative digestibility trials with rabbits. The rabbit is a non-ruminant herbivore and its willingness to consume roughage feeds, its low feed requirements and the ease with which it can be managed in the laboratory, suggested its use as a pilot animal. However, Watson and Horton (1936) showed that the rabbit does not digest fiber as efficiently as does the sheep and values obtained with the former cannot be applied to the latter.

Jarl (1945) carried out digestibility trials with rabbits, bullocks and pigs and found that when crude fiber was approximately nine per cent of the diet, rabbits showed greater ability to digest this fraction than did cattle; over nine per cent, cattle exceeded rabbits in the digestion of the crude fiber. The difference increased with the crude fiber content of the feed. The results

obtained for the digestion of crude fiber with rabbits and pigs showed that both species digested this fraction to an equal extent.

The horse, also a non-ruminant herbivore, is cited by Mitchell and Hamilton (1933) as being better able to digest crude fiber than swine, but less able to digest this food fraction than sheep.

The guinea pig was found to be unsuited as a species for comparative growth and digestibility studies with sheep, on rations of hay and mature grass alone (King, 1940). No other information is available regarding comparative digestibility studies with guinea pigs.

Because of the economic factor, the digestibility of feeds by pigs has been widely studied. Fraps (1921, 1932) showed that pigs are less able to digest the crude fiber of cracked wheat than are sheep and that, as a rule, pigs have lower digestive powers than ruminants but higher than poultry. Ellis, Kauffman and Miller (1939) found that the total digestible nutrient values for many feeds were different when determined on swine as compared to cattle and sheep. Crampton (1943) calculated that the total digestible nutrients for basal diets of barley, wheat screenings and feed oats may be at least twenty per cent too high for swine, if estimated by using digestibility coefficients applicable to cattle.

Working with eight pigs, Watson et al (1943) concluded that differences in age and weight did not affect the ability of the pigs to digest rations of grains and concentrates.

In studies with humans, Mangold (1934) found that the range of variation was very great, particularly with the crude fiber fractions. This is attributable in part, to the great divergence between the experimental diets used and the diets to which the individual subjects have been habituated, and consequent differences in intestinal flora.

Direct Versus Indirect Digestibility Coefficients

In digestibility trials which include humans and ruminants, experimental diets often cannot be fed alone, hence two separate feeding trials are necessary. In the first, a basal diet is fed for a suitable period and the digestibility is calculated. The test diet is then added to the basal diet and fed for the second period. Digestibility coefficients can then be computed by difference. In calculating the digestibility of the test diet in this manner, a wide range of uncertainty may be introduced, since experimental errors of both diets would be reflected in the digestibility of the test diet.

The recent summary by Schneider (1947) of the results of many digestibility trials indicates that there is a marked difference between digestion coefficients obtained by direct and indirect methods. These differences are probably due to the associative effect of one feed on another, which was defined by Ewing and Wells (1915) as a change in the digestibility of a feed due to its incorporation into a ration with one or more feeds.

Mitchell, Hamilton and Haines (1940) and Watson et al. (1947) have made a study of the associative effect of one feed on the digestibility of another, with feeds for farm animals, and have shown that this effect can be quite marked in some instances. This fact must be considered when comparing digestibility coefficients obtained by indirect methods.

EXPERIMENTAL PROCEDURE

A comparative digestibility study was planned to determine the digestibility of a diet with five different species, namely, sheep, guinea pigs, swine, rats and humans. The diet consisted mainly of wheat, ground and baked into loaves for feeding; the major consideration being that species with anatomically different digestive systems should receive the same diet.

General Procedure

The same proportions and methods were used in preparing the bread for consumption by all species. Individual loaves were baked daily for the human subjects, and were made up, per loaf, as follows:

300 grams ground wheat
9 grams sucrose
3 grams salt
9 grams compressed yeast

To obtain a satisfactory loaf from ground wheat it was found necessary to knead the dough approximately twice as much as for bread made from whole wheat flour, which usually contains 50 per cent or more white flour.

This is due to the fact that the ground wheat has not been "agene-ized" or otherwise treated to improve the baking qualities.

With all species other than the humans, the diet consisted of the bread which was crumbled or ground, then air-dried for feeding. Additional fat in the form of corn oil was added to the ground bread at the time of feeding and at the rate of eight grams per 100 grams of air-dry bread. This compensated for the fat which was included in the human diet as butter and cream.

All the feces voided by the humans, rats and guinea pigs, and aliquots of the sheep and pig feces, were retained for analysis. The feces were oven dried at 105° C., weighed and ground.

Procedure with Humans

The human subjects were five healthy adult women. All were graduate assistants in the Nutrition Department at Macdonald College.

In addition to one loaf of bread (approximately 1100 calories), the human subjects consumed the following per day:

24 grams butter

75 grams strained honey

40 grams 15% cream

One loaf of bread, plus supplements, furnished approximately 1800 calories per day. Additional bread was provided if requested. A hot drink, either tea or coffee, with saccharin, was provided three times per day at regular meal hours.

The diet was fed for a two day collection period. Charcoal markers were used to separate the feces. Four tablets totalling approximately 3 grams, were taken before the first meal of the test period and with the first meal following the last day of the test period.

To facilitate the collection of feces when using ordinary bathroom fixtures, a large sheet of washable plastic cloth was placed under the wooden seat of a flush toilet and a sheet of heavy waxed paper, which had been previously cut to the right size, was placed on the plastic sheet. The feces were collected on the wax paper, transferred to tared enamel pans and dried at 105° C. The entire sample was retained for analysis.

Procedure with Small Animals

Twelve male white rats of about 90 days of age and twelve adult, female, non-pregnant guinea pigs were used as experimental animals.

The rats and guinea pigs were allotted to individual wire-bottomed cages. A removable tray, lined with a paper towel, was fitted under each cage and permitted the quantitative collection of feces. They had free access to their individual feed containers and water. In addition to the diet, each guinea pig was given two milligrams of ascorbic acid per day, administered orally.

A weighed amount of the air-dry ground bread was stored in a separate container for each animal from which the individual feeders were filled as needed. If spilled feed had to be discarded because of contamination by urine, the amount discarded was subtracted from the total in the storage container. At the end of the test the total consumption was computed by difference.

For both rats and guinea pigs the diet was fed for a three day preliminary period followed by a seven day collection period.

The feces were collected separately for each animal, and all feces were retained and composited for analysis.

Procedure with Swine

Four male Yorkshire pigs averaging approximately 150 pounds each, were used as experimental animals.

The pigs were placed in individual digestion crates and feed was supplied to the animals twice daily. The bread was moistened with three times its weight of water and fed as a slop.

The diet was fed for a three day preliminary period followed by a four day collection period.

A four day time collection was made for each pig. Feces were collected twice daily, pooled and weighed once daily. After thorough mixing, a 100 gram daily sample was retained and composited for analysis.

Procedure with Sheep

Two male Cheviot sheep were used as experimental animals.

The sheep were penned in individual digestion crates and feed was given twice daily. It was hoped that the bread diet could be fed alone to the sheep without additional roughage. This was attempted and the diet was at first readily consumed by the sheep, but after two days appetite failed. A basal hay ration was

was then fed for a five day preliminary period, followed by a ten day collection period. The test diet, consisting of two-thirds hay and one-third bread, was fed for a five day preliminary period and a ten day collection period. Water was allowed ad libitum.

Feces bags were fitted several days before actual collection started in order to accustom the animals to them. Bags were emptied twice daily, feces pooled and weighed once daily. After thorough mixing, a 100 gram daily sample was retained and composited for analysis.

Chemical Analysis

The dried bread and feces samples were ground in a hammer mill and proximate principle analyses were carried out using A.O.A.C. Methods, except for the crude fiber determination where a slight modification was introduced. The boiling alkali suspension was filtered through a double thickness of fine bolting silk (72 threads per inch), in a Buchner funnel, using suction. The residue was then washed with boiling water followed successively by hot alkali, hot benzene and ether. The material was allowed to dry and transferred from the silk to a crucible, using a spatula. The crucible and contents were then dried, weighed and fired in the usual manner.

Energy Value Determinations

The gross energy value of the diet and of the feces were determined by use of a Parr bomb calorimeter.

Statistical Analysis

The digestibility data were statistically analysed by the method of variance. Bartlett's Test for Homogeneity, Snedecor (1937), showed that the variances were not homogeneous. Therefore, the standard deviations of the digestion coefficients for each food fraction were calculated separately, for the various species, and Fisher's (1934) "t" Values were used to test the significance of differences between the means of the groups.

OBSERVATIONS

One of the principal objects in this research was to devise a diet which the animals of all species would eat, and which would be sufficiently palatable for consumption by the human subjects. Therefore, observations were made of the reaction of the different species to the diet.

(a) Humans

The diet consisted mainly of the bread which was fairly palatable if eaten fresh, but dried out quickly and became hard. This is characteristic of bread made without fat and for this reason baking was done daily. The allowance of butter and honey was only sufficient for a thin spread, and was not enough to entirely disguise the slightly bitter flavour of the ground wheat. This distinctive flavour was noticed by Woods and Merrill (1904), who described bread made from ground whole wheat as being coarse in texture, dark in colour, and rather strong in flavour. The same authors also state that these objectionable features are more pronounced in a hard spring wheat such as was used for this study, than in a soft winter wheat.

During the diet period all subjects complained of discomfort. There was some flatulence and a slight sensation of bloating. With some subjects there was a lag in appetite. This palling of appetite for whole wheat bread was noted also by Rostorfer, Kochakian and Murlin (1943). In referring to dietary studies with human subjects, Murlin and Matill (1938) make the following statement. "In dealing with human subjects whether sick or well, it is unscientific to disregard the physiological effects of food. Colonic pains, except in perhaps author-subjects can quickly ruin a built-up morale".

There was no diarrhea but with some subjects soft stools interfered with the quantitative separation of the marked feces.

(b) Small Laboratory Animals

The diet was readily accepted by the rats and all showed gains in weight by the end of the feeding period.

Of the twelve original guinea pigs, all but two refused the diet, two died and the remaining eight had to be replaced as they were near death. Of the eight replacements, three refused the diet in spite of

precautions taken to accustom the animals to their environment and to introduce the change very gradually.

Post-mortem examinations were performed on all guinea pigs which died during the test, and the findings of these examinations, together with the fact that food consumption was less than half the average for guinea pigs in the stock colony, led to the conclusion that death was probably due to starvation. Although Forbes, Bratzler, Black and Braman (1937) showed with sheep and cattle that digestibility is at a maximum at the maintenance plane of nutrition and only slightly lower at the half maintenance level, nevertheless, the behaviour of the guinea pigs on this diet could not be considered as normal. All animals lost abnormally large quantities of hair and there was an immediate loss in body weight after one day on the diet. A few animals had slight diarrhea and all had abnormally soft feces, which interfered with quantitative collections.

(d) Sheep

Both the basal hay diet and the test diet, consisting of one-third bread and two-thirds hay, were readily consumed by the sheep.

RESULTS AND DISCUSSIONS

This research was undertaken as a preliminary study for a long-term project on the comparative digestibility of an identical diet with several species, including humans. Emphasis has been placed on devising a diet which all species would eat, and on the development of technique in conducting digestibility studies with humans.

Observations were made on the diet as fed, and digestibility coefficients were calculated. Comparisons were made on the ability of the different species to digest the several food fractions of the diet.

A summary of the digestibility data is shown in Table I.

The coefficients of variation shown in Table I indicate that with the exception of the crude fiber fraction and the ether extract fraction, the variability between individuals, within species, was relatively low on this diet.

The range of the digestion coefficients for the crude protein of the diet is remarkably small, considering that ruminant and non-ruminant herbivora, as well as omnivora, were used in this study.

The crude fiber fraction of the diet was poorly digested by humans, pigs, rats and guinea pigs. It is surprising that the guinea pig, a non-ruminant herbivore, showed a low digestibility for this fraction of the diet.

The ether extract fraction of the diet, for species other than the humans, was made up of the ether extract of corn oil as well as the ether extract of the bread. The ether extract of the bread alone was very low, (0.1 per cent). Swift et al (1947) consider that corn oil itself is highly digestible and showed, with sheep, that the percentage fed did not affect the digestibility of the ether extract of the diet.

With pigs, the digestion coefficients for the ether extract of the diet ranged from -4 to 19. These

coefficients are exceptionally low and show greater variability than would be expected with pigs. However, other investigators have obtained negative digestion coefficients for the ether extract of many different feeds with pigs, and Schneider (1947) cites several digestibility trials with swine where large negative digestibility coefficients were obtained for the ether extract of the feeds.

Sheep also show a comparatively low ether extract digestibility. This is unusual in view of the high digestibility attributed to corn oil by Swift et al. (1947). The low ether extract digestibility shown with sheep on this diet may be due to the associative effect of the bread on the digestibility of the corn oil.

The nitrogen-free extract of the diet was well digested by all species, and the digestible energy of the diet shows that all species, except the sheep, utilized the energy of the diet to good advantage.

Table II shows the total digestible nutrients of the diet.

Table II Total Digestible Nutrients of the Diet, Their Standard Errors and Coefficients of Variation

Species	Average total digestible nutrients	Standard error of mean (S.E. _m)	Coefficient of variation $\left(\frac{\text{S.D.} \times 100}{\text{mean}} \right)$
Humans	101	1.4	3.2
Pigs	91	0.8	1.8
Rats	106	0.1	0.6
Guinea pigs	105	1.2	3.1
Sheep	95	0.7	1.0

The total digestible nutrients of the diet shown in Table II are not percentages, but represent the total digestible nutrients in 100 grams of the diet, on the basis of four calories per gram. The practice of multiplying digestible fat by the factor 2.25 accounts for the totals which exceed 100. Since fat coefficients are subject to error which is attributable to the ether extract method, the digestible energy is probably a more accurate measure of the digestibility of the diet. For instance, the low ether extract coefficient obtained with pigs has lowered the total digestible nutrients measure of the diet, whereas the digestible energy measure of the diet is relatively the same for pigs as for rats.

The total digestible nutrients and the digestible energy measure the ability of the species to utilize the energy yielding components of the diet. The lower digestibility of some fractions of the diet have been compensated for by higher digestibility in other fractions, and with the exception of the sheep, the digestible energy coefficients and the total digestible nutrients show that the energy of the diet was well utilized by all species.

Table III shows the difference between the mean of the digestion coefficients for any two species and indicates which species differ significantly in their ability to digest the various food fractions.

Comparison Between Species, Indicating
Significant Differences Between Digestibility Co-
efficients and Total Digestible Nutrients.

Food fraction	Species	Pigs	Rats	Sheep
Crude protein	Humans (76)** Pigs(92) Rats (87) Sheep (78)	+16***	+11 - 5	+ 2* -14 - 9
Crude fiber	Humans (11) Pigs (13) Rats (3) Sheep (52)	+ 2*	- 8* -10	+41 +39 +49
Ether extract	Humans (78) Pigs (9) Rats (94) Sheep (68)	-69	+16 +85	-10 +59 -26
N-free extract	Humans (92) Pigs (94) Rats (94) Sheep (88)	+ 2	+ 2 0*	- 4 - 6 - 6*
Digestible energy	Humans (81) Pigs (89) Rats (90) Sheep (67)	+ 8	+ 9 + 1	-14 -22 -23
Total digestible nutrients	Humans (101) Pigs (91) Rats (106) Sheep (95)	-10	+ 5 +15	- 6 + 4 -11

* The difference between the two species indicated is not significant statistically.

** Figures in brackets are mean per cent digestibility and mean total digestible nutrients

*** i.e. Pigs digested crude protein 16, rats 11, and sheep 2, percentage units, more completely than did humans on this same diet.

(a) Humans, Pigs and Rats

In comparing the digestibility of the diet by humans, pigs and rats, it is evident from Table III that these species differed significantly in the digestibility of all fractions of the diet other than the crude fiber and nitrogen-free extract.

Rats and pigs digested the nitrogen-free extract of the diet to the same extent.

There was no significant difference between humans and rats, and humans and pigs, in the digestibility of the crude fiber of the diet.

The humans, pigs and rats showed high variability in the digestion of the crude fiber of the diet. With ruminants, the importance of the microflora of the intestinal tract in the digestion of forage feeds has been known for a long time. With non-ruminants, less thought has been given to the part played by these micro-organisms. Mangold (1934) stated that in almost all species, including the human, the digestion of crude fiber is due to enzymes of the symbiotic micro-organisms, and that variations are due to individual differences in intestinal flora and environmental conditions of the bacteria in the intestines. He also reports a range of

59 per cent to 85 per cent in the digestibility of the crude fiber of rye by three human subjects, on a two day collection period, and states that a wide range of variability in the digestion of crude fiber with pigs is probably due to individual differences in intestinal bacteria.

(b) Sheep and Guinea Pigs

Since guinea pigs and sheep can both be classed as herbivora, non-ruminant and ruminant, it would be expected that these species would show some similarity in the digestion of the crude fiber of the diet. However, the reaction of the guinea pigs to the diet could not be considered normal and comparisons between the digestibility of the diet by the guinea pigs and other species are not justified under the conditions existing in this experiment.

Also, the sheep digestibility data were obtained by indirect methods, and this must be considered when comparing sheep with other species. Under these conditions, the digestibility of the crude fiber of the diet was markedly higher for the sheep which is a ruminant herbivore, than for any other species.

The sheep and humans were apparently able to digest the crude protein of the diet to the same extent.

However, Johnson et al (1944) showed that the protein in the feces of sheep is of bacterial origin.

Sheep and rats showed no significant difference in the digestibility of the nitrogen-free extract of the diet.

Finally, it is evident from Table III that all species showed significant differences in the total digestible nutrients of the diet. Since some of the uncertainties inherent in the total digestible nutrients measure of the diet are eliminated by determining the digestible energy, then, the latter constitutes a check as to the accuracy of the former. Therefore, since all species also showed significant differences in digestible energy, it may be concluded that all species differed in the ability to utilize the energy of the diet as a whole.

Although more evidence is required before any definite conclusions can be drawn, results obtained in the study question the practice of assuming that digestion coefficients obtained with rats can be used for predicting digestibility of similar foods by humans. Also, digestibility coefficients obtained with any one species on this diet could not be considered as constants for the diet.

SUMMARY AND CONCLUSIONS

Identical diets were prepared and fed to five species, namely, rats, pigs, sheep, guinea pigs and humans. The diet consisted of whole wheat supplemented, for species other than the humans, by corn oil in the amount of eight grams of corn oil per 100 grams of wheat. With humans, the diet was supplemented by 8 grams of butter, 13 grams of cream (15%) and 25 grams of strained honey per 100 grams of wheat.

The diet, as fed, was found to be unsuitable for digestibility studies with guinea pigs. With sheep, it was found necessary to feed a basal hay diet, and the digestibility of the experimental diet was determined indirectly.

The variability between individuals was low, for all species, for the digestibility of food fractions other than crude fiber and ether extract. Humans, pigs, rats and guinea pigs showed high variability in the digestion of the crude fiber, and pigs showed high variability in the digestion of the ether extract of the diet.

The range of the digestion coefficients for crude protein, nitrogen-free extract and digestible energy of the diet was remarkably small, considering that the species used in this study included herbivora, both ruminant and non-ruminant, as well as omnivora.

The crude fiber fraction of the diet was poorly digested by all species other than the sheep. There was no significant difference in the digestibility of the crude fiber fraction of the diet by humans, as compared to the digestibility of this fraction by rats and pigs.

All species showed significant differences in the total digestible nutrients and digestible energy of the diet.

The results obtained indicate that there is need for further study of the comparative digestibility of identical diets by different species. The diet needs to be improved so that it can be eaten by all species with a minimum of supplements. The diet could then be used as a basal diet in digestibility studies involving concentrates or test diets. The technique of conducting digestibility studies with humans also needs further revision and development.

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APPENDIX

Table 1 Summary of Digestion Coefficients and Total Digestible Nutrients

Species	Subjects	Digestion Coefficients					Total Digestible Nutrients
		Crude Protein	Crude Fiber	Ether Extract	N-free Extract	Digestible Energy	
Humans	1	68	4	70	89	78	96
	2	78	7	85	91	74	102
	3	76	3	72	91	81	99
	4	77	25	80	92	83	102
	5	82	15	85	93	86	104
Pigs	1	93	19	19	94	90	93
	2	92	17	-4	94	89	89
	3	91	10	9	94	89	91
	4	92	5	11	93	89	90
Rats	1	89	3	93	95	90	106
	2	88	3	96	95	90	107
	3	88	3	96	94	91	106
	4	88	4	94	95	91	106
	5	86	3	94	94	89	105
	6	86	4	95	94	90	105
	7	86	4	96	95	90	106
	8	84	3	96	94	89	105
	9	85	3	95	94	90	105
	10	85	3	91	94	89	105
	11	86	3	93	94	90	105
	12	89	4	93	95	91	106
Guinea pigs	1	93	5	96	97	96	109
	2	87	3	95	96	91	107
	3	89	5	96	96	93	108
	4	86	1	92	95	91	106
	5	75	2	84	94	86	102
	6	75	1	87	94	85	102
	7	64	0	83	95	85	101
Sheep	1	76	51	68	87	68	94
	2	80	53	68	88	67	96

Table 2 Summary of Variance Homogeneity Tests

Species	D/F	Source of Variation					
		Crude protein	Crude fiber	Ether extract	N-free extract	T.D.N.	Digestible energy
Humans	4	26.3325	87.7825	25.0000	1.8875	10.2775	21.4475
Pigs	3	0.3100	39.8100	85.0710	0.1633	2.6100	0.1500
Rats	11	2.6591	2.6000	2.6000	1.6636	0.3800	0.4864
Guinea pigs	6	105.4117	32.7500	32.7500	1.0700	10.9016	18.8167
Sheep	1	10.5800	2.0000	0.0200	52.8900	0.9800	0.2400
Observed Chi-square		70.90	44.95	25.09	19.03	20.21	32.82
Expected Chi-square (n = 4, P = 0.05)		9.49	9.49	9.49	9.49	9.49	9.49

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