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ZOOLOGY

Nutritive Value of Red-Osier Dogwood and Mountain Maple as Deer Browse¹

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Introduction: The casual observer traveling through northern Minnesota sees the woods and swamps covered with brush. He might think browsing animals such as the white-tailed deer would never lack for food. Unfortunately this is not so: browse plants vary greatly in palatability and nutritive value for deer and even in the best of brushy areas there is often a limited supply of the tender twigs suitable for deer food.

In Minnesota the more palatable deer foods include the white cedar, red maple, black ash, red-osier dogwood, mountain maple and staghorn sumac. White pine, jack pine, basswood, aspen, chokecherry and hazel are among those foods of intermediate preference, and red pine, tamarack, black spruce and alder represent food plants of low preference by deer. The more palatable foods will of course be eaten first and those of intermediate and poor palatability will be eaten when the better foods become scarce. These foods may constitute a portion of the deer's diet but are inadequate to maintain the health and vigor of the animal. They usually serve as stuffing. During severe winters deer are often found starved with full stomachs of poor quality browse.

In summer food for deer is readily obtainable and the animal's movements are unrestricted as it ranges for food. In the winter, however, the deer must depend almost entirely on the twigs and sprouts of trees and shrubs. Deep snow frequently causes the deer to move into winter yarding areas where movement is restricted and severe overbrowsing may occur.

Deer prefer the growth of the preceding summer as food. The tender portions of the twigs are pulled and twisted off with the aid of stout molar teeth rather than being cleanly clipped off as they are by the incisors of the snowshoe hare.

¹ This study was conducted with Federal Aid to Wildlife Restoration Funds; Pittman-Robertson Project W-11-R.

Deer require a considerable amount of browse each day. Feeding studies in Wisconsin indicate a consumption of 3.5 to 5.5 pounds of natural browse a day per hundredweight of deer. When good grade alfalfa hay is substituted, the consumption is reduced to about 2.5 pounds per hundredweight (Dahlberg and Guettinger, 1956).

It is well known that heavy browsing by deer is injurious to forest reproduction. The resulting deterioration of the range causes a reduction in deer numbers. It is essential therefore that deer populations be kept in balance with the food supply, especially that in wintering areas. This has been accomplished in Minnesota by having an "any deer" season each year. In recent years about 100,000 deer a year have been taken by hunters. This is estimated to be approximately one-fifth of the fall herd and maintains the population over most of the range at about twelve deer per square mile.

For some time studies have been conducted in Minnesota and elsewhere concerning the quantity of deer browse as a means of evaluating range conditions. Little had been done with regard to quality. The importance of quality had long been recognized but the difficulties involved in quality analysis were also apparent.

In 1957 a study was initiated in Minnesota directed toward this goal of quality analysis. Many of the results obtained were rather inconclusive but a start had been made. Additional studies concerning browse quality were to follow and some aspects of these studies are currently being investigated. This report concerns the pilot study, portions of which have been prepared as Pittman-Robertson Game Research Job Completion Reports which normally receive limited circulation.

Methods: Since red-osier dogwood (*Cornus stolonifera*) and mountain maple (*Acer spicatum*) are eaten extensively by deer and are quite common, they were selected

for this pilot study concerning the nutritive values of deer browse. Red osier is found throughout the state in low wet places, especially along the open edges of swampland. Mountain maple is abundant in the northern and particularly the northeastern portion of Minnesota. It thrives best in moist wooded uplands.

Browse samples were collected each month during the period September 1957 to June 1958 from four locations in northern Minnesota—Grand Marais, Grand Rapids, Lake Agassiz National Wildlife Refuge, and the Camp Ripley State Game Refuge. In collecting the browse each individual site was covered in a random manner with personnel clipping a few twigs from a plant here and there to simulate the natural browsing habits of deer. Except as otherwise noted only the upper one-third of the previous year's growth of each twig was taken and no twigs were gathered at a height in excess of seven feet. Leaves were removed from twigs taken during the growing season.

In preparation for standard proximate food analysis browse samples of approximately 125 grams were cut into convenient one-inch lengths, placed in special airtight envelopes, weighed and sent to a commercial laboratory in Minneapolis. Here analysis was made for moisture, protein, fat (ether soluble extract), crude fiber, nitrogen-free extract, ash (with particular attention to calcium and phosphorus), and carotene.

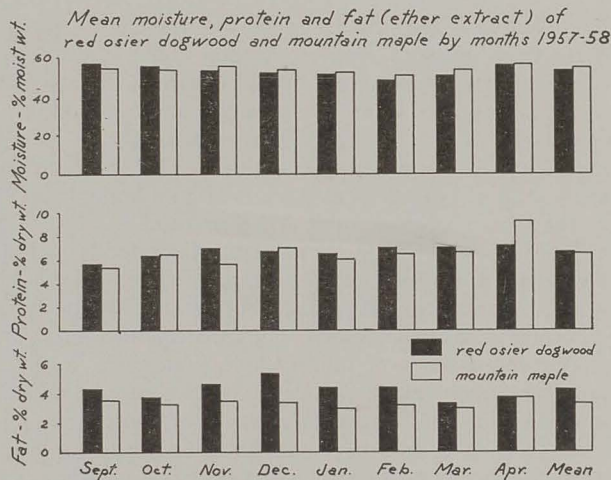
Discussion: The data presented in the accompanying tables and figures represent the major findings in this study.

In all the study areas the moisture content of both species combined exhibits a similar trend, declining in a fairly regular manner from approximately 54 percent moisture in September to 45 percent in March and then rising to 54 percent in April (Figure 1). Undoubtedly moisture changes correspond closely to plant sap conditions, with the minimum moisture content reached during the dormant period. Other studies also indicate a decline in the moisture content of browse species during dormancy. Experiments in animal feeding indicate that the more moisture a twig contains the more palatable it is (Alkon, 1961). Swank (1956) notes that in the arid southwest non-preferred browse species contain less water than preferred species. Palatability of feeds is recognized as an important factor in the efficient feeding of stock (Morrison, 1956). Preferred feeds are digested better than those which are equally nutritious but less palatable.

Protein analyses occurred mostly within the 5 to 7 percent (dry weight) range, displaying an average increase for both species combined from 5.6 percent in September to 6.7 percent in December to 6.9 percent in March and 7.9 percent in April (Figure 1). Einarsen (1946) showed that the time of year in which browse plants in Oregon reached their highest protein content varies with the species. According to Swank (1956) a minimum protein content for deer is 5 to 7 percent. Thirteen to 16 percent is proposed as the optimum protein concentration. By these standards our analyses indi-

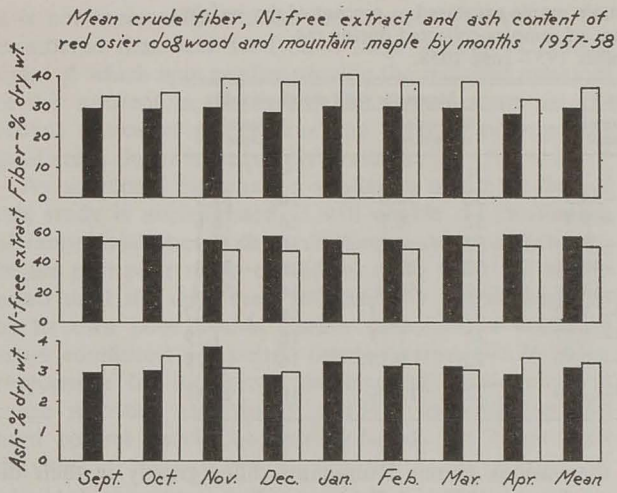
cate red-osier and mountain maple to be near the minimum. McEwen (1957) in experimental feeding of deer in Pennsylvania found, however, that deer wintered well on a diet of 7 percent protein, even though food consumption dropped to 3 percent (dry weight) a day. Greatest skeletal and antler growth was achieved with a 17 percent protein diet. Deer on a 4 to 5 percent protein level barely survived. By comparison high quality alfalfa hay, which will readily sustain deer for several months, contains 16 to 18 percent protein; and timothy hay, which has been found unsatisfactory for deer, has 5 to 10 percent protein (Morrison, 1956).

Crude fat obtained by ether extraction from the Minnesota samples range from 2.6 to 5.6 percent (dry weight) for the two species, with red-osier having a slightly greater amount (Figure 1). There is no obvious trend in the fat content of either species throughout the sampling period. Crude fat content of this same magnitude is given by Hellmers (1940) for Pennsylvania browse. Since ether extraction methods of fat determination result in the inclusion of waxes and oils which may or may not be digestible and nutritious, the interpretation of such analyses is uncertain.



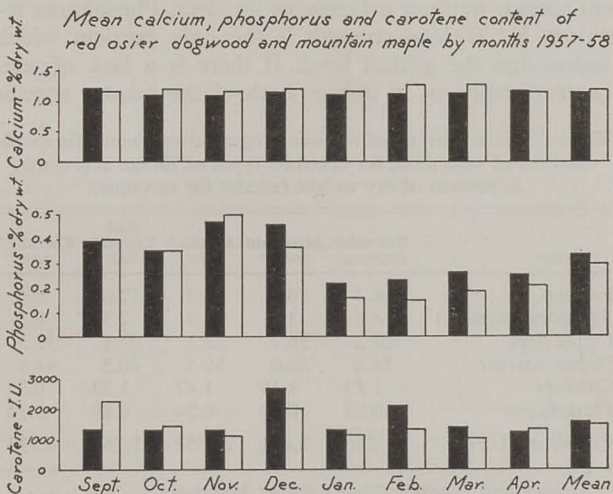
Crude fiber representing the non-digestible carbohydrates, including cellulose and the related substance lignin, in the browse samples ranged from 24.3 to 41.1 percent of the dry weight (Figure 2). Mountain maple averaged 7.8 percent more crude fiber for the two sites where both species were sampled and exhibited a gradual increase as mid-winter approached followed by a gradual decrease as spring arrived. Statistical treatment reveals that the difference between the two species in crude fiber content is highly significant. The analyses of Hellmers (1940) for other species of browse in Pennsylvania are very similar—red maple being 37.0 percent, hazel 34.2 percent and panicked dogwood 31.5 percent crude fiber.

Nitrogen-free extract, which represents the more readily digestible carbohydrates such as the sugars and starch ranged from 53.3 to 61.0 percent for red-osier and 44.7 to 54.4 percent for mountain maple, the latter species exhibiting a decided decline in these carbo-



hydrates in mid-winter (Figure 2). Statistical analysis shows that the greater content of digestible carbohydrates in red-osier is highly significant. Again similar figures are given by Hellmers for Pennsylvania browse. For comparison carrots and beets contain about 9 percent carbohydrates and seeds of cereal grains about 75 percent (Heinz, 1956). In terms of wet weight the two browse species are roughly one-fourth carbohydrate.

The ash content in the browse analyzed ranged from 2.46 to 5.00 percent (dry weight), with the two species having similar concentrations (Figure 2). Ash was analyzed further for calcium and phosphorus. Calcium ranged from 0.95 to 1.75 percent, with no appreciable difference between the two species and no apparent trends during the sampling period (Figure 3). McEwen (1957) found in Pennsylvania that calcium as low as 0.3 p.p.m. was tolerated by deer in winter with no signs of stress. Greatest skeletal and antler growth was achieved with 0.64 percent calcium, other foods being adequate. He concludes calcium becomes deficient in the diet of deer at about 0.08 percent, which is far below any of our analyses. Few of the common forage types exceed the amount of calcium found in our samples



by any appreciable amount. Alfalfa hay contains 1.0 to 1.7 percent calcium and timothy hay 0.25 to 0.35 percent (Sullivan and Wilkins, 1948).

Phosphorus in the two browse species ranged from 0.20 to 0.80 percent for red-osier and 0.13 to 0.60 percent for mountain maple (Figure 3). There appears to be some decline throughout the winter and little recovery in April. McEwen (1957) noted that 0.30 percent phosphorus was satisfactory for winter diet of deer. The deficiency level was approached at about 0.27 percent. Nearly all the Minnesota analyses were below this deficiency level during the months of January, February, March and April. Lower satisfactory levels are given for cattle. Studies indicate that deficiency levels in cattle occur at 0.16 to 0.18 percent concentration (Morrison, 1956). Phosphorus deficiency is fairly common in cattle and is remedied by feeding phosphorus-rich foods or applying phosphate fertilizers to soils.

The browse samples were also analyzed for carotene, which is a precursor of Vitamin A. The carotene content for the two species is about the same, ranging from 400 to 5,800 I.U. (International Units) per pound, with no pattern indicated for the sampling period (Figure 3). These analyses are quite high, approximating the range of asparagus and whole corn. Carotene analysis is rather complicated and subject to analytical errors since the analysis is influenced by extracted photosynthetic pigments such as chlorophyll. It is believed that an appreciable source of error occurs in the carotene analyses presented here. Dietz *et al.* (1962) were compelled to discard the carotene data secured in a very detailed study of deer browse in Colorado. They listed enzymatic action and oxidative destruction of carotene in fresh plant material as detrimental to accurate analysis.

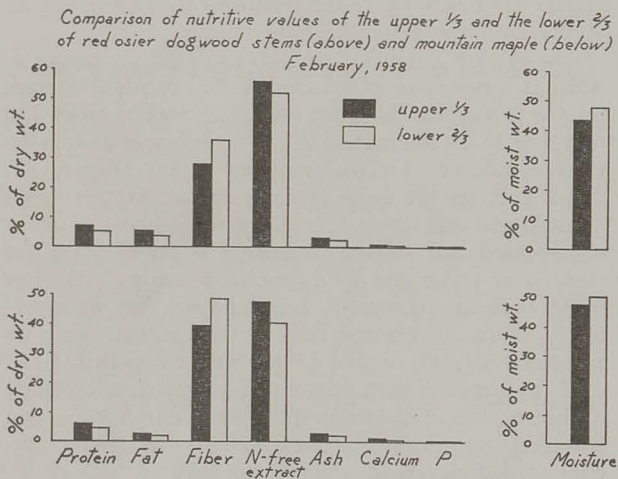
The deer's urgent need for an adequate supply of Vitamin A to prevent night blindness is apparent as it generally feeds and is active during periods of low light intensity. Vitamin A is also essential for the healthy condition of the mucous membranes. Deficiency of this vitamin reduces the animal's ability to resist infection. This resistance to infection is particularly important to deer since their diet consists largely of coarse twigs during much of the year, thereby subjecting the oral membranes to injury.

To determine whether the terminal portion of new twig growth is more nutritious than the lower portions, samples of browse were collected accordingly at the Grand Rapids site in February, 1958. The results of the analysis are shown in Table 2 and Figure 4. Both red-osier and mountain maple displayed the same nutritional characteristics in this regard. The protein, fat, nitrogen-free extract and mineral content of the upper one-third of the twigs were greater than that of the lower two-thirds. The reverse was true with regard to moisture and crude fiber. Since crude fiber consists largely of relatively undigestible cellulose, it is desirable that the quantity of this substance is less in the tender upper portions of the twigs which are normally selected by the deer.

These analyses point out the unfavorable conditions

TABLE 1. Analyses of red-osier dogwood and mountain maple expressed as percent of dry weight (except for carotene). Ranges and means of samples collected during the eight month period September 1957-June 1958.

Nutrient	Range of monthly means		Means for eight month period			
	Red-osier dogwood	Mountain maple	Red-osier dogwood		Mountain maple	
			N	\bar{X}	N	\bar{X}
Moisture	43.8 - 55.4	47.3 - 54.3	32	50.0	16	51.5
Protein	5.7 - 7.2	5.4 - 9.3	32	6.7	16	6.6
Fat (ether extract)	3.3 - 5.3	3.0 - 3.7	32	4.2	16	3.3
Crude fiber	27.4 - 30.2	32.6 - 40.9	32	29.2	16	36.8
N-free extract	54.7 - 58.9	46.4 - 53.9	32	56.8	16	50.0
Ash	2.86 - 3.79	3.00 - 3.57	32	3.15	16	3.27
Calcium	1.09 - 1.21	1.15 - 1.27	32	1.13	16	1.19
Phosphorus	0.22 - 0.47	0.15 - 0.50	32	0.33	16	0.29
Carotene I. U./lb.	1,175-2,875	1,000-2,250	32	1,586	16	1,441



which arise when the deer, living under conditions of winter stress, are forced to utilize the lower, less nutritious portions of an over-browsed food supply. It is an established concept in game management that quantity will not substitute for quality.

TABLE 2. Comparison of analyses of upper and lower portions of stems of red-osier dogwood and mountain maple expressed as percent of dry weight (except for carotene). Single sample collected in February, 1958.

Nutrient	Red-osier dogwood		Mountain maple	
	Upper 1/3	Lower 2/3	Upper 1/3	Lower 2/3
Moisture	43.7	47.8	47.2	49.9
Protein	7.1	5.3	6.4	5.1
Fat (ether extract)	5.6	3.9	3.0	2.3
Crude fiber	28.0	36.5	39.6	48.7
N-free extract	56.2	52.1	47.7	41.3
Ash	3.12	2.22	3.32	2.62
Calcium	1.20	0.76	1.20	0.80
Phosphorus	0.25	0.21	0.17	0.12
Carotene I.U./lb.	2,100	1,400	900	1,200

Hundley (1959) points out the difficulty of interpreting proximate analyses of browse such as those discussed. The analyses show "available nutrients" and can only indicate what an animal *might* derive from them. Little is known about the ability of deer to digest

the various plants. Ruminants differ greatly in their digestive capabilities. For example, moose can thrive on balsam fir but cannot be sustained on white cedar; the reverse is true for deer. Also since only a portion of the nutrients ingested are utilized by the animal this factor must be taken into consideration in determining the feed requirements.

Experiments concerning digestion coefficients and total digestible nutrients (TDN) will indicate the actual utilization by the deer of the various nutrients and reveal the energy value of the browse. Bear and Bender (1948) point out in a study of domestic cattle that 70 percent of the ingested nitrogen was lost in excretion, together with 63 percent of the phosphorus, 86 percent of the potassium and 65 percent of the calcium. These losses occurred in both the feces and the urine. Bissell *et al.* (1955) conducted this type of study with deer in California involving some common forage and native deer browse species. Coefficients of digestion of protein for alfalfa hay was found to be 71.4 percent (dry weight) and as much as 56.8 percent for a native plant, bitterbrush. TDN is given as 65.5 percent for alfalfa hay and as much as 58.8 percent for another native plant, chamise.

These analyses of two Minnesota browse species—red-osier dogwood and mountain maple—indicate no apparent serious nutrient deficiencies for deer. Phosphorus required for skeletal strength is the only nutrient which approaches the critical level. If there is a lack of adequate phosphorus in one or both of the browse species

TABLE 3. Mean analyses of red-osier dogwood and mountain maple compared with those for common types of forage expressed as percent of dry weight (except for carotene).

Nutrient	Red-osier dogwood	Mountain maple	Alfalfa ¹ hay	Red Clover ¹ hay	Timothy ¹ hay
Protein	6.7	6.6	15.3	12.0	6.6
Fat (ether extract)	4.2	3.3	1.9	2.5	2.3
Crude fiber	29.2	36.7	22.7	27.1	30.3
N-free extract	56.8	50.0	39.5	40.3	44.8
Calcium	1.13	1.19	1.47	1.28	0.35
Phosphorus	0.33	0.29	0.24	0.20	0.14
Carotene I.U./lb.	1,586	1,441	13,667	12,167	7,333

¹ Feeds and Feeding, 22nd Edition, Morrison.

it is not necessarily a cause for concern. It must be remembered that deer feed on a large variety of plants, some of which may readily provide the required amounts of this nutrient in the deer's diet. Legumes are an excellent source of phosphorus and even in non-agricultural areas clover is frequently available.

As additional information similar in nature to that of this study is accumulated, it will enable the evaluation of range conditions both qualitatively and quantitatively. In the past poor range conditions often were not recognized until the deer herd reflected the range condition by its own poor health. Earlier detection of declining range conditions will permit timely intervention by those responsible for our game management. A deteriorated range recovers very slowly. Habitat manipulation and herd control should be applied before the range "hits the skids".

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Temperature Effects Upon Egg Development in *Drosophila Melanogaster*

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Introduction: Temperature effects upon the acceleration of physical and chemical processes have attracted the attention of workers both in the physical and the biological disciplines. One of the earliest attempts to explain the occurring phenomena was made by Van't Hoff by means of the so called Q_{10} relationship which may be written:

$$Q_{10} = \left[\frac{y_1}{y_2} \right]^{10/(x_1-x_2)} \quad (1)$$

where y represents reaction velocity for development at the given temperature x in degrees centigrade. However this relationship has been criticized on various grounds, among the more important perhaps being the one forwarded by Belehrádek (1930). In this work he suggests that this function will vary according to the intervals of x_1 and x_2 that are selected. Thus at points near the threshold of development and near the lethal point this equation does not give as good a fit for the observed results.

One of the first authors to propose a slightly different relationship was Peairs (1914) who offered the opinion that the curve representing the increase in the time for development vs. temperature was a hyperbola which may be written:

$$y(t - a) = K \quad (2)$$

where y represents time, t the temperature in degrees centigrade, a a constant indicating the minimum temperature for development (threshold of development), and k a constant which has been designated as the "thermal constant". While outwardly this may seem like a plausible relationship, it breaks down when one attempts to apply this to the reciprocal of y , or the so-called velocity of development. If one were to take the reciprocal of equation (2) one finds that the curve obtained will be a straight line. That this is a representation of the experimental findings has been shown to be false by many, including Davidson (1944) and Powsner (1935).

More recently two other relationships have been proposed: a logistic curve by Davidson (1944) and a catenary curve by Janisch (1932) and Huffaker (1944).

The logistic curve

$$\frac{1}{y} = \frac{K}{1 + be^{-(a)(x-x_0)}} \quad (3)$$

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where y represents time for development,
 a & b are constants,

K is the upper asymptotic value of $1/y$,
 x is temperature and x_0 is the temperature
at the point chosen as the origin.

The catenary curve

$$\frac{1}{y} = \frac{2}{m} \frac{1}{a^{(T-x)} + a^{-(T-x)}} \quad (4)$$

where y represents time for development,
 m is the developmental time at optimum
temperature,

a is a constant representing the slope of the curve,
 x is temperature, and
 T is the optimum temperature.

It will be noted that both of these equations represent functions for the velocity or rate of development, and if each of their respective reciprocals are taken, one obtains curves where time is directly plotted against temperature. Both Davidson (1944) and Janisch (1932) assert that their proposed equation describes the actual happenings. However the mathematical basis for each is quite different so it hardly seems reasonable that the same phenomenon can be adequately described by both relationships. The present study has been an attempt to determine which description is applicable in the development of eggs in *Drosophila melanogaster*. In order to reduce the computation involved with the catenary equation, the following equivalent equation was used:

$$\frac{1}{y} = \frac{1}{m} \frac{1}{\cosh[(T-x) \ln a]} \quad (5)$$

where the letters represent the same as in
(4), and where \cosh and \ln represent respectively the hyperbolic cosine and the natural log.

Methods and Procedures: Eggs for study were collected from laboratory stock *D. melanogaster* by the insertion into the culture bottles of narrow strips of blotter paper which had been moistened and on which had been placed small amounts of a yeast-honey mixture as an inducement for ovipositing. These strips of paper were left in this position for 1½ hours while the temperature of the culture bottles was about 23°C. The effect of this "ovipositing temperature" will be discussed later. Following this period of 1½ hours lots of 15 eggs were removed and placed on a clean piece of blotter paper which in turn was inserted into a small test tube. This tube,

which was then closed, contained about one inch of water in order to maintain the blotter paper in a moistened condition.

These test tubes were then placed in a Jamesway incubator whose temperature control had been slightly modified. With this apparatus constant temperature ($\pm 0.2^\circ\text{C}$) was maintained between a range of 20.0°C to 34.0°C . Temperatures lower than this could not be kept constant and at temperatures higher than this the eggs were killed.

Temperature checks were made by two different fashions: (1) An overall indication of the constancy of the temperature was indicated by means of a thermograph which was located directly in the incubator, and (2) more precise measurement was made with a potentiometer equipped with a copper-constantan thermocouple which was positioned upon the blotter paper in the test tube.

Checks upon the development were usually made at one hour intervals (a point to be discussed later) by examining the blotter paper under a dissecting scope. This examination took approximately 30 seconds.

Results: The findings of this study may be summarized as follows:

- 1) The temperature at which the developmental time was shortest (16.15 hours) could be considered to lie within the interval of 29.0 — 29.5°C .
- 2) The curve relating time needed for development vs. temperature is best indicated by the reciprocal of the logistic equation (equation 3).
- 3) The curve relating velocity (rate) of development is best described by the logistic curve represented in equation (3). The maximum per cent error between observed results and calculated results from the logistic curve was 4.8% compared with a maximum error of 17.9% in the case of calculated values using the catenary equation (5).

TABLE 1. Comparison of Observed Data with Calculated for Logistic and Catenary Curves.

Temp. °C	Hours(y)	Observed (100/y)	Calculated (100/y) Logistic	Calculated (100/y) Catenary
33.0	18.92	5.285	—	4.937
32.0	18.02	5.549	—	5.434
31.0	16.78	5.959	—	5.834
30.0	16.44	6.083	6.442	6.098
29.0	16.21	6.169	6.191	6.190
28.0	16.86	5.931	5.904	6.098
27.0	17.87	5.560	5.593	5.834
26.0	19.16	5.219	5.266	5.434
25.0	21.38	4.677	4.899	4.937
24.0	22.28	4.488	4.527	4.440
23.0	24.87	4.021	4.129	3.878
22.0	26.67	3.750	3.745	3.368
21.0	29.97	3.337	3.360	2.900
20.0	33.12	3.019	2.983	2.476
*19.08	38.01	2.631	2.655	2.135
*18.20	41.4	2.415	2.363	2.083
*17.15	48.7	2.053	2.029	2.043
*16.19	56.3	1.776	1.783	2.014
*14.95	67.9	1.473	1.449	1.961

* Data from Powsner (1935).

- 4) There seems to be no apparent pattern in the per cent of hatch nor in the standard deviation of the time necessary for hatching at the various temperature levels. (see Table 2). This is based on an examination of about 90 eggs at each temperature level.
- 5) The temperature at which no hatching occurred (lethal temperature) could be considered to lie within the interval of 33.5 — 34.0°C .
- 6) Attempts to fit the data of velocity (rate) of development vs. temperature to curves of normal and *t*-distribution were made. The results indicated that the deviation between observed and calculated values was so extreme as to exclude these types of relationships.

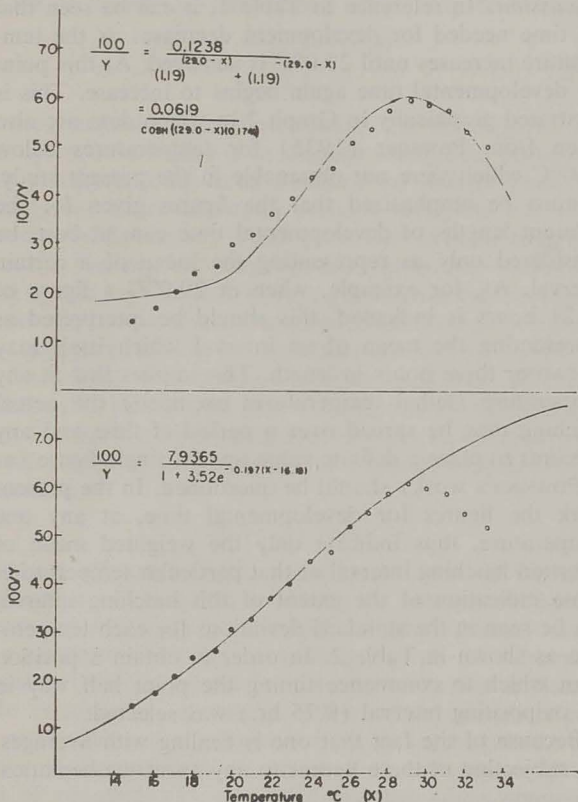
Discussion: In reference to Table 1, it can be seen that the time needed for development decreases as the temperature increases until 29.0°C is achieved. At this point the developmental time again begins to increase. This is illustrated graphically in Graph 2 in which data are also taken from Powsner (1935) for temperatures below 20.0°C which were not obtainable in the present study. It must be emphasized that the figures given for the different lengths of developmental time can, at best, be considered only as representing the mean of a certain interval. As, for example, when at 29.0°C a figure of 16.21 hours is indicated, this should be interpreted as representing the mean of an interval which itself may be two or three hours in length. This implies that at any temperature (lethal temperatures excluded) the actual hatching may be spread over a period of time and any attempts to place a definite value upon a single figure (as in Powsner's work) should be questioned. In the present work the figures for developmental time, at any one temperature, thus indicate only the weighted mean of a certain hatching interval at that particular temperature. Some indication of the extent of this hatching interval can be seen in the standard deviations for each temperature as shown in Table 2. In order to obtain a position from which to commence timing the point half way in the ovipositing interval (0.75 hr.) was selected.

Because of the fact that one is dealing with averages, the subjecting of these figures to any exact mathematical

TABLE 2. Comparison of Percent Hatch and Variability In Hatching Time.

Temperature °C	Percent Hatch	Standard Deviation
33.0	75.00	2.868
32.0	93.18	1.079
31.0	86.67	0.660
30.0	92.11	0.704
29.0	77.78	1.024
28.0	80.00	0.746
27.0	91.11	0.550
26.0	75.56	0.461
25.0	84.44	1.459
24.0	93.33	1.564
23.0	83.33	0.711
22.0	81.82	2.501
21.0	77.27	5.094
20.0	82.30	2.559

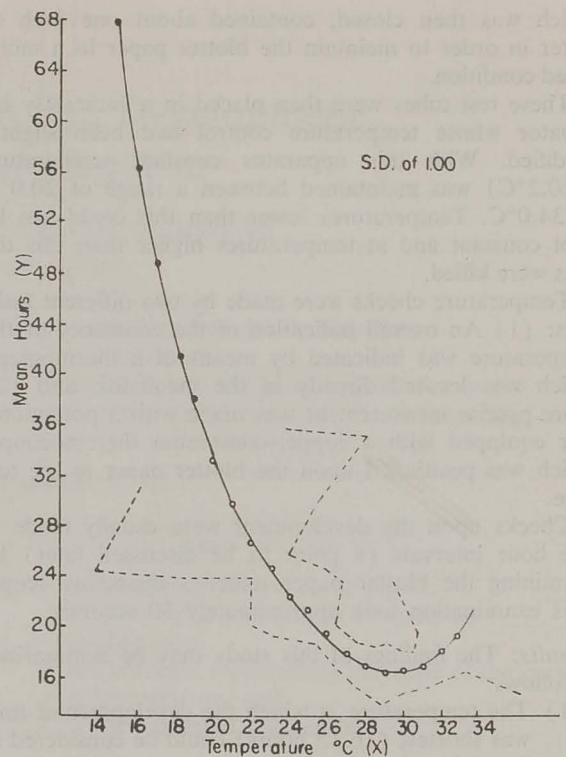
analysis may be open to question. Bearing this in mind, however, the reciprocals of developmental time, multiplied by 100 in order to obtain per cent of development per unit time (column 3 of table 1), were plotted against temperature. As seen in Graph 1, the fit of the observed values to the theoretical curve is better in the case of the logistic curve. It can be observed, however, that at temperatures above 29.0°C the logistic curve deviates from the observed results, and it was mainly for this reason that the catenary curve was originally suggested. Davidson (1942) pointed out, that the data beyond the optimum temperature are so limited that there can be no reasonable estimation as to the type of curve or equation describing the results. While the present authors do not completely agree with this assertion, no real attempt was made to investigate this further at this time.



GRAPH 1. Per cent of development per unit time plotted against temperature. Upper graph, catenary; lower graph, logistic. The dots (i.e., below 20°C) represent data taken from Powsner (1935) while the circles represent data from this study.

Consequently, considering only the temperatures up to 29.0°C it must be concluded that the logistic curve best describes the rate of hatching in *Drosophila* eggs, and that the catenary function can, at best, be considered a reasonable approximation.

At this point some mention should be made of the procedure followed in determining the various constants in both the logistic and the catenary equations. Without going into great detail, the constants for the logistic curve were determined by the method of selected points as stated in Kempthorne et al. (1954). The temperature



GRAPH 2. The mean hours of incubation plotted against the temperature at which the eggs were incubated. The dots (i.e., below 20°C) represent data taken from Powsner (1935) while the circles represent data from this study. The distance (normal to the curve) from each point to the broken line represents the standard deviation.

of 16.18°C was chosen as the origin temperature. In the case of the catenary, the values for optimum temperature and minimum developmental time were determined by inspection of the experimental data. The values of 29.0°C and 16.15 hours, respectively, were chosen. The value of a , the slope of the curve, is not readily calculated and though it can be computed directly for any specific temperature by solving the catenary equation, the value to be used should represent the average slope. Consequently, in the present study this slope was determined by averaging the velocities at all medial constant temperatures, converting to the corresponding time value, and then solving for the value of a of the catenary equation. This determination of the slope could be considered a possible source of error.

Powsner (1935) corrected for the effect of the temperature at which eggs were laid, but no such correction was made in the present study. The reasons for the latter being twofold: first, the intent of this work was more along comparative than absolute lines and thus what error was introduced remained constant throughout; secondly, in terms of hour degrees, the hour degree development at this hatching temperature represents, at the most, only about 1% of the total figure for hour degrees at each temperature. Nevertheless, this must also be considered as a possible source of error if one is interested in obtaining absolute values.

Huettner (1923) indicated that a female *Drosophila* may retain a fertilized egg for some time before it is laid. This may partially explain the large standard deviation in the hatching interval at certain temperatures (e.g. at 21.0°C) in the present work. Chiang and Hodson (1950) showed that increased fecundity was achieved by a combination of abundant food supply and decreased fly density. In keeping with this, culture bottles about 2 days old were used along with a reduced density of adults. In this way it was felt that the probability of obtaining eggs that had been retained by the female for a prolonged time was minimized.

Summary: The results of this study indicate that in the case of *Drosophila melanogaster* eggs, both the time for hatching and the velocity or rate of this hatching is best described by the logistic curve (3). The optimum temperature for hatching may be taken as being in the interval of 29.0—29.5°C at which temperature interval the hatching time interval had a mean of 16.15 hours. At temperatures above this point, hatching time increases until the lethal point is reached in the temperature interval of 33.5—34.0°C. No definite pattern could be established for percentile hatch nor for variability in incubation time at different temperatures.

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