A STATISTICAL STUDY OF WINTER PAUSE IN WHITE LEGHORN PULLETS [1]

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INTRODUCTION

The character commonly referred to as winter pause has been recognized for a long time. However, its nature or the factors bringing about its expression are still largely unknown. Goodale (*1*, *2*) [3] considered that both hereditary and environmental factors were responsible. In a later report, Goodale and Sanborn (*3*) found that duration of pause could apparently be reduced by selection. On the other hand, indication of seasonal incidence was seen in the fact that 90 percent of the birds in their flock that started to lay in September exhibited winter pause, while of those that started to lay in December only 30 percent paused. Hays seems to be the only other worker who has pursued extensive studies on the subject. As early as 1924 he (*4*) suggested a single recessive factor for 7-day or longer pauses. In 1926 Hays and Sanborn (*7*) presented correlations between the length of winter pauses of 4 days or more and hatching date (−0.2480), date of first egg (−0.3205), age at first egg (−0.2329), and length of the laying period before the pause (−0.1385, the correlation ratio being 0.2199).

In 1936 Hays (*6*) presented similar correlations as well as correlations between winter-pause duration and a whole series of other production factors. Most of these, however, illustrate relations with post-pause characters. North (*8*) found that pausing caused an increase in body weight and two or more pauses an increase in egg weight.

The present study attempts to analyze statistically the nature of winter pause and its expression.

MATERIAL AND METHODS

In a study of such an ill-defined character as winter pause, a series of arbitrary definitions must be set up. Although any conclusions reached will of necessity apply only to the populations considered and to the factors defined at the outset, a better understanding may ensue from studies of this type. The writers believe that, while studies on experimental physiology will ultimately explain the mechanism of operation of the factors determining annual production, further preliminary biometric studies to point the way to experimental verification are needed.

Accordingly, two populations of Single-Comb White Leghorn pullets were selected from the station flock. The J population included 768 pullets hatched in 5 groups at intervals of 1 week, beginning March 20, 1934. The K population consisted of 626 pullets hatched in 4 groups

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[3] Italic numbers in parentheses refer to Literature Cited, p. 210.

at weekly intervals, beginning March 19, 1935. The basis of selection of both groups from pullet flocks numbering about 1,200 in the J series and 1,100 in the K series consisted of the following criteria, only birds answering these requirements being included:

Birds maturing before January 1.
Birds alive on July 1 of their second year of life.
Birds which did not exhibit broodiness before March 1.
Birds which were not floor layers at any time.
Birds which, if they paused before March 1, resumed laying before July 1.
Birds which had at least 19 sisters or half-sisters by a common sire, answering all of the above requirements.

Twenty sire families constituted the J series and 17 sire families the K population.

Winter pause is defined as a continuous nonlaying period of 7 days or longer beginning after at least one egg was laid, and before March 1. The factors studied were: (1) Percentage of the birds in a sire family, in a hatch, or in a series, which exhibited one or more winter pauses; (2) average duration of the pauses; (3) frequency of occurrance of pauses per pausing bird; (4) degree of pausing, which represents the loss in productive days due to pause in any given period; and (5) date and age on the first day of pause.

The degree of pausing, calculated as the percentage of pausing hen-days in any given period, is considered as an index expressing the extent of pausing in any of the groups considered. The degree of pausing was calculated for twelve 10-day periods from November 1 to February 28, inclusive. It is important to note that this includes all pauses as here defined irrespective of the causative factors involved, of which many may be in operation.

Prepause factors considered in this study include the date of hatch, the date of first egg, and the age at first egg of all the pullets in a sire family and of the pullets which later exhibited winter pause.

The total degree of pausing in the two populations differed markedly, the K series showing only somewhat over half the pausing observed in the J series. The data for the latter will be presented first, and only such K series data as do not show agreement with the observations on the J population will be given.

DATA ON THE J SERIES

Data on the J series were analyzed from two standpoints: (1) As one population, irrespective of descent, and (2) as 20 separate sire families in order to determine the genetic implications of the relation between the different factors studied.

Table 1 presents the pausing characteristics of this population with respect to date of hatch. The degree of pausing is highest in the earliest hatches and decreases regularly in the later hatches. The same trend may be noted with respect to the percentage of pausing birds. However, the frequency of pausing and the average duration of pause seem to have no relation to the date of hatch. From the average age at pause onset, which tends to decrease with the date of hatch, it may be seen that in this population the factor bringing on pause operated approximately at the same time. This is borne out by the average date of pause onset, which fell within a period of 14 days in the five hatches studied. Apparently seasonal and age effects are both responsible for the condition of winter pause. Once the birds

pause, however, their age has no effect on the length of time they stay out of production.

Table 2 presents an analysis of variance of degree of pausing between and within the 10-day periods between November 1 and February 28. This analysis, made by pooling the variances for the sire families, indicates significant differences between periods in degree of pausing. Furthermore, the table also shows that there are differences between the families of the different sires and gives the variance between hatches and periods, thus indicating three significant factors in the degree of pausing: (1) Season (between periods), (2) age (between hatches), and (3) inheritance (between sire families). A triple criterion analysis (hatch, period, sire) was not attempted because the numbers in the subclasses are disproportionate, and some of the subclass numbers would be so small as to render the determination of degree of pausing inaccurate.

TABLE 1.—*Characteristics of the J series with respect to date of hatch*

Date of hatch	Total birds	Proportion of birds pausing	Total pauses	Pauses per pausing bird (frequency)	Average age at pause onset	Average date at pause onset	Average duration of pause	Degree of pausing
	Number	*Percent*	*Number*		*Days*		*Days*	
Mar. 20	237	84.0	323	1.62	257	Dec. 2	28.2	28.6
Mar. 27	130	71.5	125	1.34	253	Dec. 5	31.1	23.4
Apr. 3	124	62.1	123	1.60	257	Dec. 16	25.1	19.0
Apr. 10	193	64.2	180	1.45	240	Dec. 6	24.9	18.9
Apr. 17	84	48.8	58	1.41	239	Dec. 12	25.3	13.2
All hatches	768	69.5	809	1.51	252	Dec. 6	27.2	21.9

TABLE 2.—*Analysis of variance of degree of pausing, J series, between and within 10-day periods from November 1 to February 28*

Source of variance	Degrees of freedom	Sum of squares	Mean square
Total	2,399	496,339	
Between periods	11	460,771	41,888
Within periods	2,388	35,568	15
Total	239	56,546	
Between sire families	19	10,593	558
Between periods	11	35,156	3,196
Remainder	209	10,797	52
Total	59	9,671	
Between hatches	4	1,655	414
Between periods	11	6,283	571
Remainder	44	1,733	39

The trend of degree of pausing by the 10-day periods can be seen from table 3, which gives the distribution by sires and periods. The family showing the highest degree of pausing is that of sire G36 with a degree index of 37.7; the lowest degree observed is 11.8 for sire F15, the other sire families falling within this range. The significant point in this table is that 14 out of the 20 sire families show the mode of pausing in the same period (December 1–10); 4 families have a mode in the neighboring periods. Only 2 of the families show modes in other periods and only 1 of these differs significantly

from the degree of pausing in the December 1–10 period. The significance of differences between any 2 cells may be ascertained from the values given in the footnote to the table. Table 3 thus presents further evidence for the interpretation of table 2 so far as sire family and period differences are concerned.

Table 4 supplies similar evidence with respect to the effect of hatch. The mode for the whole of the population falls in the period of December 1–10, three earlier hatches showing the highest degree of pausing during that period. The two later hatches have modes in the preceding period which, however, are not significantly higher than the degree-of-pausing values for these hatches for the modal period of the whole population.

Degree of pausing was broken down into its constituents: (1) Percent of birds exhibiting pause, (2) frequency or number of pauses per pausing bird, and (3) average duration of each pause. These, together with date of pause onset, were analyzed with respect to differences between hatches and to differences due to variation in the date of first egg. To facilitate the analysis of variance, the periods of maturity here selected (September 18 to November 17) were such as to have representatives of all hatches in each of the four 15-day periods. This included 718 of the 768 birds in the J series.

TABLE 3.—*Distribution of degree of pausing by sires and by periods, J series* [1]

Period	Degree of pausing classified by sire and number of daughters as indicated									
	F15, 29	H58, 35	H62, 48	G14, 65	H42, 29	H79, 78	H8, 42	H90, 66	H91, 39	H39, 24
Nov. 1–10	20.0	13.9	5.3	5.2	4.8	13.8	2.1	6.0	12.3	0
Nov. 11–20	15.4	14.9	13.7	15.9	4.0	15.7	13.5	11.1	22.0	15.3
Nov. 21–30	*51.8*	27.9	27.4	35.5	13.7	29.6	35.9	17.9	39.4	42.9
Dec. 1–10	29.2	*53.4*	*51.2*	*41.5*	28.2	*53.2*	*42.7*	30.5	*51.3*	*40.5*
Dec. 11–20	14.7	22.4	19.9	31.2	28.2	28.0	32.4	*30.7*	39.0	36.0
Dec. 21–30	5.0	17.8	14.1	21.3	28.8	25.5	28.1	23.4	24.0	38.1
Dec. 31–Jan. 9	12.2	8.7	16.0	19.2	*37.9*	24.0	27.4	26.3	24.0	31.9
Jan. 10–19	8.2	4.2	14.8	13.8	32.1	20.6	22.3	24.5	15.6	30.7
Jan. 20–29	2.4	.3	7.2	6.0	21.9	17.0	16.0	21.8	8.9	16.5
Jan. 30–Feb. 8	2.1	.9	5.8	1.5	10.5	11.8	10.0	17.9	3.6	2.8
Feb. 9–18	0	2.1	5.8	4.5	8.5	9.2	5.7	17.6	5.6	0
Feb. 19–28	0	1.2	4.8	3.1	8.7	4.7	5.0	19.7	3.8	0
Total degree of pausing	11.8	12.3	13.8	16.6	18.9	19.4	20.1	20.6	20.8	21.2

Period	Degree of pausing classified by sire and number of daughters as indicated								
	G52, 50	G5, 27	H60, 29	H64, 30	H43, 34	H46, 31	H37, 20	H25, 23	H33, 38	G36, 31
Nov. 1–10	14.4	4.5	15.8	15.6	9.0	2.1	4.5	19.6	27.2	15.5
Nov. 11–20	27.0	26.0	24.1	15.8	10.8	13.0	10.0	20.3	23.7	25.0
Nov. 21–30	41.6	46.9	*55.6*	39.5	32.7	33.8	33.8	55.5	41.5	41.5
Dec. 1–10	*45.0*	*58.8*	41.0	*48.3*	*58.5*	*55.0*	*51.0*	*56.2*	48.2	55.8
Dec. 11–20	39.8	40.8	33.1	43.1	43.3	45.2	47.5	47.8	*50.0*	58.9
Dec. 21–30	32.2	30.0	31.2	34.9	32.0	43.2	28.5	50.0	41.3	55.9
Dec. 31–Jan. 9	26.0	27.2	27.3	32.8	41.6	44.7	45.0	43.0	43.7	*60.9*
Jan. 10–19	16.4	18.2	17.9	30.8	31.7	30.9	44.5	33.5	39.4	55.8
Jan. 20–29	13.2	14.6	9.8	23.0	26.3	21.8	34.0	22.5	31.9	40.1
Jan. 30–Feb. 8	9.0	10.1	14.7	20.3	21.5	13.0	20.0	9.3	22.5	22.7
Feb. 9–18	4.6	.8	8.9	10.0	9.6	22.4	15.5	15.4	19.2	11.8
Feb. 19–28	3.8	0	2.8	5.5	5.1	14.0	11.0	4.1	9.8	8.0
Total degree of pausing	22.8	23.2	23.5	26.6	26.8	28.3	28.8	31.4	33.2	37.7

[1] 6.7 constitutes a significant, and 9.2 a highly significant difference between any 2 cells.

Modes in italic figures.

TABLE 4.—*Distribution of degree of pausing with respect to date of hatch in the J series* [1]

Period	Data for date of hatch indicated					
	Mar. 20	Mar. 27	Apr. 3	Apr. 10	Apr. 17	All hatches
Nov. 1–10	12.2	7.3	8.0	10.1	13.8	10.3
Nov. 11–20	16.3	10.9	14.8	20.8	20.6	16.6
Nov. 21–30	45.3	33.6	21.9	*35.2*	*24.4*	34.4
Dec. 1–10	*59.2*	*47.6*	*30.6*	32.4	20.9	*41.9*
Dec. 11–20	50.3	43.4	25.6	23.3	17.7	34.9
Dec. 21–30	42.5	33.2	20.1	18.2	18.4	28.4
Dec. 31–Jan. 9	36.5	31.0	27.8	24.4	12.8	28.5
Jan. 10–19	27.1	30.5	22.8	19.1	12.7	23.4
Jan. 20–29	19.9	19.9	16.7	11.6	10.7	16.8
Jan. 30–Feb. 8	15.7	10.1	14.3	8.0	2.9	11.5
Feb. 9–18	11.2	8.7	14.5	6.0	1.3	9.3
Feb. 19–28	7.0	5.1	11.0	5.1	1.7	6.6
Total degree of pausing	28.6	23.4	19.0	17.9	13.2	21.9

[1] Modes in italic figures.

Table 5 presents this analysis and indicates that date of first egg has more influence on the date of pause onset and on duration of pause than has date of hatch, while the latter has a greater influence in determining the percentage of birds in a population exhibiting pause. Frequency of pause or occurrence of repetitional pausing by the same bird seems to be independent of either date of hatch or date of first egg.

TABLE 5.—*Analysis of variance of pausing characters in the J series*

Source of variance	Degrees of freedom	Date of pause onset		Percentage of birds pausing		Frequency of pause		Duration of pause	
		Sum of square	Mean square	Sum of square	Mean square	Sum of square	Mean square	Sum of square	Mean square
Total	24	3,373		72,106		16.15		1,303	
Between hatches	4	315	78.8	28,564	[1] 7,141	3.46	0.865	260	65.0
Between dates of first egg	4	1,874	[2] 468.5	7,271	1,818	2.28	.570	708	[2] 177.0
Remainder	16	1,184	74.0	36,721	2,267	10.41	.651	335	20.9

[1] Significant. [2] Highly significant.

Although the date of first egg apparently bears no relation to the proportion of birds in the population which pause, this does not hold true within sire families. Thus, the date of first egg of pausing half-sisters is 9.85 days earlier than that of the nonpausing birds in the same family. The *t* value for 19 degrees of freedom is 6.5405, which indicates that this difference is highly significant.

The genetic implications involving the factors discussed were analyzed by means of correlations between the characteristics exhibited by sire families. With 20 sires represented in this population, 18 degrees of freedom for the zero-order correlations were available. Table 6 gives the coefficients of correlation and indicates that:

1. Frequency of pauses is not correlated with any of the other factors studied.

2. Date of pause onset is not correlated with any of the other factors studied.

3. Date of first egg of pausing birds is correlated with the percentage of birds in the sire family which exhibit pause, the correlation coefficient being 0.5127.

4. Percentage of pausing birds in the sire family is not correlated with average duration of pause.

5. The degree of pausing shows the greatest correlation with the percentage of pausing birds (0.7421), followed by the correlation with duration of pause (0.5869).

TABLE 6.—*Zero-order correlation coefficients between characteristics of sire families in the J series* [1]

Character studied	B	C	D	E	F	G
A. Date of first egg of all birds	0.9309	0.3762	0.1355	−0.2852	0.3043	0.0947
B. Date of first egg of pausing birds		.3825	.0302	−.2233	.5127	.2356
C. Date of pause onset			−.2815	.4200	.1935	.2950
D. Frequency of pause				−.3226	−.1733	−.0265
E. Duration of pause					.1476	.5869
F. Percentage of birds pausing						.7421
G. Degree of pausing						

[1] r at $P=0.05$ is 0.444; r at $P=0.01$ is 0.561.

The coefficient of multiple correlation, with degree of pausing as the dependent variable and frequency of pause, duration of pause, and percentage of pausing birds as the independent variables, was found to be 0.9225, giving 85 percent determination. Complete determination of degree of pausing by these three independents is not attained, since the measurement of degree is confined to the period between November 1 and February 28, while some of the pauses started before, and others continued beyond these dates.

TABLE 7.—*Characteristics of the K series with respect to date of hatch*

Date of hatch	Total birds	Proportion of birds pausing	Total pauses	Pauses per pausing bird (frequency)	Average age at pause onset	Average date at pause onset	Average duration of pause	Degree of pausing
	Number	*Percent*	*Number*		*Days*		*Days*	
Mar. 19	127	55.1	109	1.56	246	Nov. 20	26.2	11.8
Mar. 26	166	48.8	141	1.74	246	Nov. 27	28.6	13.2
Apr. 2	179	46.4	127	1.53	249	Dec. 7	26.4	12.3
Apr. 9	154	34.4	74	1.40	249	Dec. 14	24.5	8.3
All hatches	626	45.8	451	1.57	248	Dec. 2	26.7	11.4

DATA ON THE K SERIES

The characteristics of the K series of birds are presented in table 7. A comparison of this table with table 1 shows considerable differences in the pausing characters of the two populations. Thus, the degree of pausing in the J series is nearly twice that exhibited by the K pullets. The trend in the latter with respect to date of hatch is not so uniform as that found in the J birds, although the last hatch shows the least amount of pause. The percentage of pausing birds is considerably higher in the J series, while pause frequency and pause duration are not markedly different in the two populations. The most significant

differences between the J and the K series lie in the average age and the average date of pause onset in the different hatches, although when each population is considered irrespective of hatching dates, these differences are not marked. While the pauses in the different hatches of the J series occurred at approximately the same date, the K population showed increasingly later onset of pause with the later date of hatch. As a consequence, in the J series the pausing birds in the late hatches were younger than those in the early hatches at the time of pause onset, whereas in the K series a uniformity in age of pausing birds, irrespective of date of hatch, obtained.

TABLE 8.—*Distribution of degree of pausing with respect to date of hatch in the K series* [1]

Period	Data for date of hatch indicated				
	Mar. 19	Mar. 26	Apr. 2	Apr. 9	All hatches
Nov. 1–10	10.6	14.3	9.1	4.9	10.0
Nov. 11–20	12.9	11.5	13.7	9.6	11.6
Nov. 21–30	13.1	13.2	16.7	10.6	13.4
Dec. 1–10	10.0	*16.3*	*20.9*	*18.4*	*16.4*
Dec. 11–20	13.4	15.6	19.4	11.5	15.3
Dec. 21–30	12.6	9.7	11.7	8.8	10.5
Dec. 31–Jan. 9	12.2	12.0	7.7	3.3	8.7
Jan. 10–19	*15.8*	14.1	10.5	7.0	11.7
Jan. 20–29	14.6	15.8	11.8	8.6	12.7
Jan. 30–Feb. 8	9.0	11.9	10.1	11.2	10.8
Feb. 9–18	7.7	12.4	9.3	6.4	9.0
Feb. 19–28	9.2	11.7	6.7	4.8	8.0
Total degree of pausing	11.8	13.2	12.3	8.3	11.4

[1] Major modes in italic figures.

A further difference in the behavior of the 2 series may be observed from the comparison of tables 4 and 8, which give the distribution of the degree of pausing in the respective series by periods. Whereas the J series in general gives a unimodal type of distribution, the K series invariably shows 2 or more peaks for each hatch. The reasons for these observed differences are somewhat obscure. It is not certain that the reduction in number of pauses (809 pauses in a flock of 768 birds or 1.05 per bird in the J series; 451 pauses in a flock of 626 birds or 0.72 per bird in the K series) did not lead to the differential behavior observed.

TABLE 9.—*Zero-order correlation coefficients between pause characters of sire families in the K series* [1]

Character studied	B	C	D	E	F	G
A. Date of first egg of all birds	0.8334	0.2920	−0.0997	−0.2726	0.1695	0.1545
B. Date of first egg of pausing birds		.2782	−.0754	−.3582	.2491	.1853
C. Date of pause onset			.0940	−.3552	.1389	.0929
D. Frequency of pause				−.4336	.7492	.6796
E. Duration of pause					−.4840	−.1023
F. Percentage of birds pausing						.8786
G. Degree of pausing						

[1] r at P=0.05 is 0.482; r at P=0.01 is 0.606.

Some differences may be also noted between the two populations with respect to the magnitude of the correlation coefficients between the different pause characters of sire families in the two populations. Table 9 lists the coefficients for the K population corresponding to those for the J series in table 6. There is agreement between the two tables as far as the majority of the correlation coefficients is concerned. There are, however, a few notable differences. Thus, while frequency of pause shows no correlation with percentage of birds pausing (−0.1733) or with degree of pausing (−0.0265) in the J series, in the K population the respective coefficients are 0.7492 and 0.6796. This changed relation also brings about differences in the coefficients of correlation between duration of pause and percentage of birds pausing (−0.4840 for the K series as compared to 0.1476 for the J) and between duration of pause and degree of pausing (−0.1023 for the K series and 0.5869 for the J). The coefficient of multiple correlation between degree of pausing on the one hand and frequency of pause, duration of pause, and percentage of birds pausing on the other is somewhat higher in the K series (0.9560) than in the J (0.9225), the former yielding 91 percent determination. Percentage of birds pausing seems to be the factor of major importance in accounting for differences in the degree of pausing in both of the series. This suggests that in breeding against occurrence of winter pausing the percentage of pausing birds, rather than duration or frequency in a family might be used as the standard of selection.

The general picture obtained from analysis of the J series is not particularly changed by the addition of the data for the K population. The fact that some of the relations between pause characters of sire families are different in the two populations argues for the point of view that the relations vary with the degree of pause observed.

The results from repetitional matings in the 2 years for which the data are considered may be of some interest. Table 10 presents the pause characteristics of the progeny of males mated in both years, as well as the performance of full sisters hatched in the 2 years. Only those matings which produced five or more sisters in each of the series are listed. It is apparent from this table that while the degree of pausing is higher in the J series, there is no consistent difference in either frequency or duration of pause between the J and K pullets. The percentage of birds pausing is, however, invariably greater in the J series sires' progeny and in full-sister families. This confirms the interpretation placed on the correlation coefficients. The same is true for all but one of the full-sister families with respect to degree of pausing.

It may be noted that for all of the repetitional matings the incidence of pausing birds is reduced 35.7 percent in the K over the J series. For the whole flock the reduction is 34.1 percent. This suggests that the major factors responsible for a lower percentage of pausing birds in the K series are environmental in nature, rather than genetic.

In absence of controlled experimental results it is not possible to say what these factors may be. However, by comparison of the performance of birds from the repetitional matings presented in table 10 and from other available information, some of the possible reasons for the observed differences in pause behavior may be considered.

TABLE 10.—*Pause characteristics of repeat matings*

Sire or mating	Series	Total birds	Proportion of birds pausing	Pauses per pausing bird (frequency)	Average duration of pauses	Degree of pausing
		Number	*Percent*		*Days*	
G14	J	65	66.2	1.33	23.8	16.6
	K	35	37.1	1.38	28.6	6.9
G52	J	50	74.0	1.57	24.0	22.8
	K	29	44.8	1.38	28.4	10.8
H33	J	38	81.6	1.55	34.4	33.2
	K	32	43.8	1.57	35.7	14.1
H60	J	29	82.8	1.83	15.8	23.5
	K	42	78.6	1.67	18.2	18.8
H90	J	66	63.6	1.31	35.4	20.6
	K	59	39.0	1.43	23.2	9.0
G14♂F424	J	6	33.3	1.50	14.3	5.7
	K	6	16.7	1.00	25.0	3.6
G14♂G738	J	9	55.6	1.60	25.5	17.5
	K	5	20.0	2.00	9.0	1.5
G14♂G742	J	12	58.3	1.29	12.6	5.1
	K	7	42.9	1.00	44.8	7.3
G52♂H590	J	11	81.8	1.56	27.6	25.4
	K	6	66.7	1.75	9.3	8.1
H90♂G312	J	7	57.1	1.25	20.4	12.6
	K	6	33.3	1.50	20.7	6.8

As reported elsewhere (*9*), each of the two series was divided approximately evenly, so that one-half of the pullets of each mating were on one ration, and one-half on another. The difference between these rations was in the percentage of wheat bran in substitution for whole wheat, the percentage of protein and minerals being adjusted by other slight changes. One ration was common to both series. Despite differences in age at sexual maturity between the groups on different rations in the J series, there was no difference in the extent of winter pause. The K series on the whole exhibited earlier sexual maturity than the J series, though no difference was found in age at first egg of pullets on the two rations used in the K series. However, sexual maturity cannot be considered as a differential factor between the two series, since as shown in table 5 it has little bearing on the characters determining the degree of pausing. The difference in maturity between pausing and nonpausing birds within families existing above, if effective between series, would operate in the direction of increasing rather than decreasing the proportion of pausing birds in the K series above that of the J series.

There was no difference in extent or type of chick mortality in the repetitional matings of the two series, but the rate of growth was higher for the pullets of the K series. The average weight at 6 weeks of age in the repetitional matings was nearly 100 grams higher in the K series (342.1 grams against 248.1 grams in the J series). What bearing this observation may have on the nature of winter pausing cannot be determined from the data on hand.

So far as repetitional pausing of the same bird is concerned, there seems to be no consistent or significant difference between the duration of the first pause and that of the second (table 11). This was true for both the J and K series. There seems to be no evidence indicating that the second pause in birds pausing twice differs in any appreciable way from the first pause.

CLIMATOLOGICAL OBSERVATIONS

Seasonal curves for the total degree of pausing between November 1 and February 28 were drawn for each of the series and compared with the curves for precipitation, humidity, and maximum, minimum, and mean daily temperatures. These were drawn from data [4] recorded on the south bank of the canyon. The poultry plant is located on the north bank. No apparent relation between these climatological observations and the degree of pausing was apparent from these curves. Similarly, no apparent relation of the degree of pausing in the K series to daily hours of sunshine could be noted. The sunshine observations were made on the university campus about half a mile from the poultry plant.[5] No sunshine data for the year of hatch of the J series were available.

As far as the length of day is concerned, the degree of pausing in the J series varies inversely with the length of day up to the first period in December (December 1–10). In the mid-December period the degree of pausing begins to decrease while the length of day reaches its minimum. In general, the fluctuations in degree of pausing follow the changes in day length in a none-too-regular curvilinear fashion. This does not hold true for the K series, in which it appears that the degree of pausing fluctuates fortuitously as far as the length of day is concerned.

TABLE 11.—*Duration of pauses of birds pausing twice*

Series	Double-pausing birds	Duration of pause		First pause longer	Second pause longer	Two pauses of equal length
		First	Second			
	Number	*Days*	*Days*	*Number* [1]	*Number* [1]	*Number* [1]
J	136	23.1	20.2	73	58	5
K	55	22.3	24.5	27	26	2
Both	191	22.9	21.4	100	84	7

[1] Cases.

DISCUSSION

From evidence presented by Hays (*5*) and by the present writers, winter pause appears to be a character dependent upon both genetic and environmental conditions for its expression. The environmental agents producing a pause are seasonally determined but do not seem to be directly associated with any seasonal changes in the climatological factors studied. Evidence is available that pullet offspring from the same matings in different years respond differently with respect to pause. Since the genetic constitution of such groups of offspring would be expected to be very similar, the difference in incidence of pause might be presumed to be related to differences in environmental conditions between the years.

However, the intrinsic susceptibility of birds to pause does not seem to be constant. With increasing age at the season of the modal pausing period (effect of hatching date) and with increasing time in production preceding this period, there appears to be induced in the bird a physiological condition causing it to respond more readily to

[4] Supplied through the courtesy of C. J. Kraebel, of the California Forest Experiment Station.

[5] The sunshine observations were made available to the writers by Prof. John B. Leighly, of the Department of Geography of the University of California.

the environmental stimuli by pausing. Birds with different genetic constitutions show different responses to the same age, production, and environmental effects.

It is possible to conceive of winter pause as being induced by adverse environmental conditions which overcome the resistance of the bird to such external influences. The threshold of response varies with different birds at the same time and under the same conditions, and within the same bird at different times. Once induced, the pause proceeds for a period of time that does not seem to be related to the incidence of pausing in the flock or to the frequency of pausing in the bird. In the case of repetitional pausing, the course of the second pause does not seem to differ from that of the first pause. The duration of extremely long pauses might conceivably express the action of either repeated or continuous periods in which the effect of the adverse environment was above the threshold of response for the individual bird.

The distribution of pauses by 10-day periods between November and February indicated, in the case of the population with the high degree of pause, a uniform modal pausing period irrespective of the date of hatch. In the case of the population with a low degree of pausing, multimodal distribution prevailed, but the major modes in three out of four hatches fell in the same period as did the modes in the other population.

The seasonal distribution of pausing in the progenies of different sires showed considerably uniformity.

Date of pause onset and duration of pause depended largely on the date of first egg in the population as a whole, though no such relation is observed when sire families are considered.

Percentage of birds pausing depended to the greatest extent on date of hatch.

In birds pausing twice, there was no apparent difference between the duration of the first and of the second pauses.

The variation within the year in climatological factors studied did not seem to bear any direct relation to the degree of pausing in either population.

If the foregoing assumptions are true, the character of winter pause, observable only by its presence or absence, may in fact be genetically or physiologically governed by a wide range of variation in response thresholds. It is not likely that this concept of the basis of production of winter pauses can be proved by study of the production records of birds. Physiological studies identifying the changes in the birds associated with changes in thresholds of response would seem to be a more likely means of solution of the problem.

GENERAL CONCLUSIONS

Degree of winter pausing as defined here (percentage of hen-days from November to February spent in pauses of 7 days' duration or longer) is determined by the percentage of birds pausing in a population, by the frequency of pauses, and by duration of pause.

Percentage of birds pausing is of major influence in determining the degree of pausing in a population.

In a population with 21.9 as the degree of pausing, duration of pause was significantly correlated with degree of pausing, while in a popu-

lation with 11.4 as the degree of pause, frequency of pause was of greater importance than duration of pause.

Percentage of pausing birds in a family is suggested as a standard of selection in breeding against occurrence of winter pause.

Degree of pausing depends also on the genetic constitution of the birds (as shown by variance between sires), on the date of hatch, and on the season.

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