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THE FECUNDITY AND DEVELOPMENT OF THE FLOUR BEETLES, *TRIBOLIUM CONFUSUM* AND *TRIBOLIUM CASTANEUM*, AT THREE CONSTANT TEMPERATURES [1]

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Data have been accumulated on the fecundity and rate of development of the flour beetles *Tribolium confusum* and *Tribolium castaneum* at three constant temperatures as part of an extensive investigation of interspecies competition now under way in this laboratory. Because these data seem to have some utility in their own right, apart from the major program, they are summarized in this brief paper.

MATERIALS AND METHODS

Temperature and humidity control.—All determinations were carried out in incubators set to run at 24°, 29°, and 34° C. The actual performance of these three incubators is shown in table I from which it is apparent that the average temperatures maintained during the assay periods are close to the desired values. The variability, as indexed by the standard deviations, is similar for each chamber and the daily deviations above and below the mean were evenly distributed in time. The readings were taken inside each incubator but measurements showed the temperature of the medium was similar to that of the surrounding air.

An attempt was made to keep the relative humidity of each incubator within the range of 70 to 75 per cent. Table I suggests that this was accomplished moderately well and it seems reasonable to conclude that no important differentials in terms of *relative* humidity were established between the different chambers. This, of course, does not hold for saturation deficit; these values increasing with temperature from 6.2 mm., to 7.5 mm., to 11.2 mm.

Techniques involved in the assay of fecundity.—Fecundity was measured by following the procedures outlined by Park and Davis ('45) which take advantage of the fact that infested flour can be screened through a bolting cloth sieve of such fine mesh that all eggs are retained for accurate counting.

One hundred and twenty shell vials were prepared by adding to each eight grams of a "standard laboratory medium" consisting of 95 per cent sifted whole-wheat flour and 5 per cent brewer's yeast powder. Forty of these vials were placed in the 24° incubator, 40 in the 29° incubator, and 40 in the 34° incubator. There they remained for six days in order to come into equilibrium with the obtaining temperatures and humidities, after which, one pair of beetles not exceeding two weeks of imaginal age was introduced into every vial. The replicates were evenly distributed so that, initially, there were 20 bottles containing *T. confusum* and 20 containing *T. castaneum* in each of the three temperature chambers.

After 72 hours, the beetles were gently removed and placed into vials with eight grams of fresh medium. The eggs were then counted and the numbers recorded vial-by-vial. This procedure was continued for the entire group of 120 samples for 10 egg censuses, or, until the rate of oviposition had been assayed for 30 days.

Techniques involved in the assay of rate of metamorphosis.—The objective was to determine the mean length of the egg, larval, and pupal stages of *Tribolium*

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TABLE I. *Mean temperatures and humidities maintained in the three incubators used in these experiments*

	Temperature, ° C.		Relative humidity		Saturation deficit (mm.)	N
	Mean ± P.E.	S.D.	Mean ± P.E.	S.D.		
Incubator No. 1	23.98±0.06	0.72	75.56±0.35	3.98	6.2	59
Incubator No. 2	29.06±0.08	0.68	75.10±0.70	5.75	7.5	31
Incubator No. 3	33.99±0.09	0.65	71.88±0.59	4.12	11.2	22

TABLE II. *Oviposition rate per female per 72 hour interval of* Tribolium confusum *and* Tribolium castaneum *at temperatures of 24, 29, and 34° C.*

Interval (days)	Mean ± P.E. (eggs)	S.D. (eggs)	C.V. (%)	N	Interval (days)	Mean ± P.E. (eggs)	S.D. (eggs)	C.V. (%)	N
Tribolium confusum at 24° C.					*Tribolium castaneum* at 24° C.				
0–3	10.8±0.36	2.4	22.2	20	0–3	17.4±0.68	4.5	25.9	20
3–6	15.2±0.63	4.2	27.6	20	3–6	22.5±0.69	4.6	20.4	20
6–9	17.2±0.63	4.2	24.4	20	6–9	21.2±1.13	7.5	35.4	20
9–12	15.9±0.93	6.2	39.0	20	9–12	18.6±1.34	8.9	47.8	20
12–15	16.1±0.87	5.8	36.0	20	12–15	19.3±1.13	7.5	38.9	20
15–18	16.1±0.79	5.1	31.7	19	15–18	18.2±1.24	8.2	45.0	20
18–21	14.2±0.79	5.1	35.9	19	18–21	19.3±1.16	7.7	39.9	20
21–24	14.5±0.94	6.1	42.1	19	21–24	17.8±1.21	8.0	44.9	20
24–27	13.0±0.97	6.3	48.5	19	24–27	18.3±1.02	6.8	37.2	20
27–30	13.7±1.02	6.6	48.2	19	27–30	18.0±1.09	7.2	40.0	20
0–30	14.7±0.27	5.6	38.1	195	0–30	19.1±0.35	7.3	38.2	200
Tribolium confusum at 29° C.					*Tribolium castaneum* at 29° C.				
0–3	25.0±0.72	4.8	19.2	20	0–3	42.7±1.70	11.3	26.5	20
3–6	38.0±1.06	7.0	18.4	20	3–6	53.4±1.57	10.4	19.5	20
6–9	38.0±1.16	7.7	20.3	20	6–9	53.5±1.69	11.2	20.9	20
9–12	42.6±1.48	9.8	23.0	20	9–12	61.0±2.13	14.1	23.1	20
12–15	43.0±1.69	11.2	26.0	20	12–15	57.8±1.82	12.1	20.9	20
15–18	40.3±0.88	5.7	14.1	20	15–18	49.6±1.64	10.9	22.0	20
18–21	43.3±1.04	6.7	15.5	20	18–21	52.6±2.76	18.3	34.8	20
21–24	38.8±1.18	7.6	19.6	20	21–24	47.6±2.05	13.6	28.6	20
24–27	35.9±1.01	6.5	18.1	20	24–27	45.6±2.34	15.5	34.0	20
27–30	36.8±1.41	9.1	24.7	20	27–30	40.8±2.14	14.2	34.8	20
0–30	38.2±0.45	9.3	24.4	200	0–30	50.5±0.70	14.7	29.1	200
Tribolium confusum at 34° C.					*Tribolium castaneum* at 34° C.				
0–3	32.9±1.45	9.4	28.6	20	0–3	43.9±1.81	11.7	26.6	19
3–6	42.5±1.19	7.7	18.1	20	3–6	63.1±2.23	14.8	23.4	20
6–9	43.6±1.44	9.3	21.3	20	6–9	58.6±2.07	13.7	23.4	20
9–12	49.7±1.38	8.9	17.9	20	9–12	64.6±1.64	10.9	16.9	20
12–15	48.0±1.58	10.2	21.2	20	12–15	63.9±1.66	11.0	17.2	20
15–18	44.7±1.21	7.8	17.4	19	15–18	55.9±1.86	12.0	21.5	19
18–21	46.0±1.33	8.6	18.7	19	18–21	58.7±2.09	13.5	23.0	19
21–24	41.9±1.93	12.5	29.8	19	21–24	56.4±1.67	10.8	19.1	19
24–27	41.3±1.92	12.4	30.0	19	24–27	57.6±1.67	10.8	18.7	19
27–30	36.5±2.26	14.6	40.0	19	27–30	48.5±2.40	15.5	32.0	19
0–30	42.7±0.56	11.4	26.7	195	0–30	57.2±0.68	14.0	24.5	194

confusum and *T. castaneum* at the three temperatures with a maximal range of error of ± 3 hours.

A mass culture consisting of several thousand *T. confusum* imagoes was established in a large jar containing fresh medium. After six hours, the newly laid eggs were collected and from this group three batches, each containing 56 eggs, were selected at random and placed into empty syracuse dishes. These dishes were put into the incubators at 24°, 29°, and 34°. Such a procedure initiates three cohorts whose later development can be followed and dated in terms of their individual members. As the first instar larvae emerge, the fact is noted and the elapsed time in hours between collecting the eggs and their hatching is taken as the duration of the egg stage. The larvae were then placed singly into vials containing two grams of medium and immediately returned to the respective temperatures at which they developed as eggs. These larvae were not disturbed until they had pupated, and the recording, by vials, of the time of pupation measures the length of the larval period for each larva. The pupal stage is timed in the same way, namely: the interval from pupation to eclosion is determined. Precisely similar procedures were followed simultaneously for *T. castaneum*.

The reduction in numbers within the N-columns of table V is accounted for by death of members of each cohort during larval development. It is evident that there was negligible mortality at the two lower temperatures for both species. At 34°, the mortality was higher, being approximately 20 per cent.

Fecundity

The data concerned with fecundity are presented in table II, that reports mean fecundity rate by intervals for both species of beetles at the three temperatures; in table III that compares selected mean differences in these rates in ratio to their probable errors, and in table IV, that shows the percentage differences in rates both between species at the same temperatures and within species at different temperatures.

From these tables the following points are to be noted:

(1) Regardless of the temperatures involved, *T. castaneum* has a higher rate of oviposition than does *T. confusum*. This point has been suggested before on the basis of studies conducted at 29° (Park, '48; Park and Davis, '45) but it has not been proved up to this time by fecundity assays under identical conditions at a series of temperatures. Since the present data were collected under the favorable circumstances of no crowding, negligible egg cannibalism, renewed and nutritious medium, and a modicum of handling, it is reasonable to conclude that the rates reported are close to the maximum possible for the beetles maintained in the particular experimental conditions described. Further, it seems to follow that the difference between the two *Tribolium* is primarily a *species* difference which leads to the generalization that *T. castaneum* possesses an innately higher reproductive potential than does *T. confusum*.

The differences between the means for the entire period of study (0 to 30 day interval), when compared by species for each of the three temperatures, are all highly significant statistically as borne out in table III. These differences decrease with temperature: *T. castaneum* oviposits, on the average, 14.5 more eggs per female per 72 hours than does *T. confusum* at 34°; 11.8 more eggs at 29°, and 4.4

Table III. *Selected statistical comparisons of the oviposition rates for the 0–30 day interval reported in table II*

Comparison	Mean difference ± P.E.
T. castaneum–T. confusum, at 24°	4.4±0.44
T. castaneum–T. confusum, at 29°	11.8±0.83
T. castaneum–T. confusum, at 34°	14.5±0.87
T. confusum, 29°–24°	24.0±0.52
T. confusum, 34°–29°	4.0±0.72
T. castaneum, 29°–24°	31.4±0.78
T. castaneum, 34°–29°	6.7±0.98

TABLE IV. *Per cent that smaller oviposition rates are of larger oviposition rates (from the data reported in table II for the 0–30 day interval)*

The fraction	Quotient
Between species and within temperatures:	
100 *T. confusum*, 24° ÷ *T. castaneum*, 24°	77.0%
100 *T. confusum*, 29° ÷ *T. castaneum*, 29°	76.6%
100 *T. confusum*, 34° ÷ *T. castaneum*, 34°	74.6%
Within species and between temperatures:	
100 *T. confusum*, 24° ÷ *T. confusum*, 29°	38.0%
100 *T. confusum*, 24° ÷ *T. confusum*, 34°	34.4%
100 *T. confusum*, 29° ÷ *T. confusum*, 34°	90.6%
100 *T. castaneum*, 24° ÷ *T. castaneum*, 29°	37.8%
100 *T. castaneum*, 24° ÷ *T. castaneum*, 34°	33.4%
100 *T. castaneum*, 29° ÷ *T. castaneum*, 34°	88.3%

at 24° In terms of percentages (table IV), *T. castaneum* has approximately a 25 per cent higher fecundity rate although there is a suggestion that the egg production of *T. confusum* relative to *T. castaenum* increases slightly with decrease in temperature.

(2) As would be expected for median thermal ranges, the rate of oviposition becomes higher with increasing temperature. This is true for both beetles. At 24°, *T. confusum* exhibits a mean rate of 14.7 eggs per 72 hours; at 29°, 38.7 eggs, and at 34°, 42.7 eggs. Comparable means for *T. castaneum* are 19.1, 50.5, and 57.2. These differences in fecundity at different temperatures are all highly significant statistically (table III). The acceleration

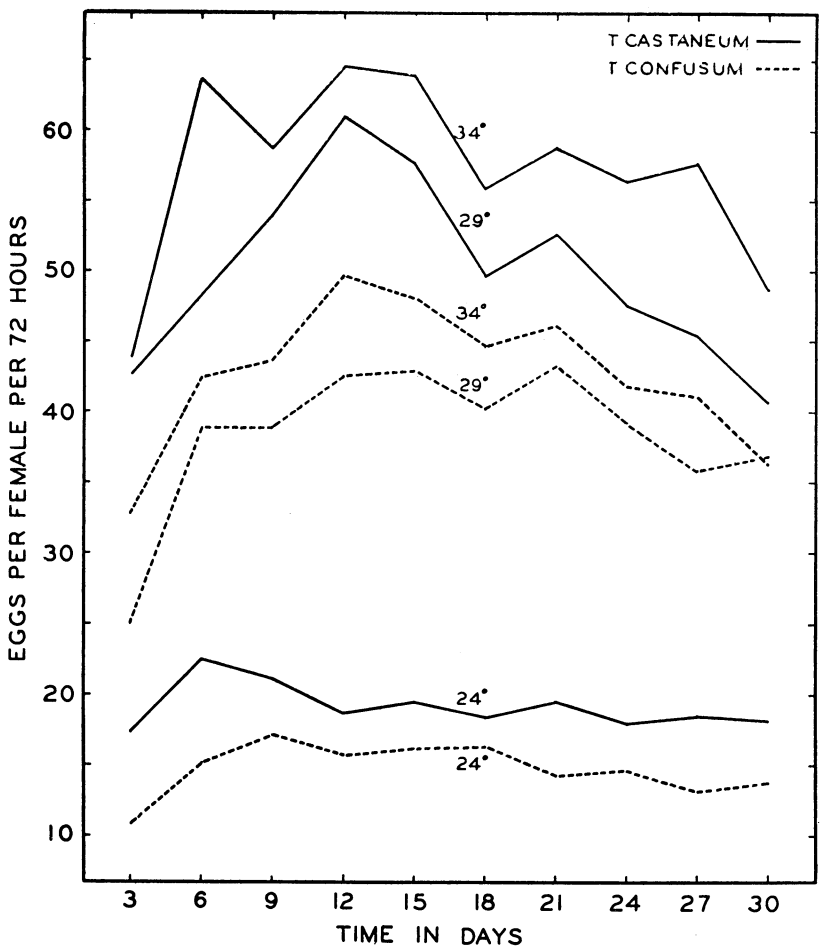

FIG. 1. Rate of oviposition graphed against time for *Tribolium confusum* and *T. castaneum* maintained at temperatures of 24°, 29°, and 34° C.

of oviposition is much greater when the temperature increases by 5° from 24° to 29° than when the increase is from 29° to 34° as seen in table IV. For example, at 24° the fecundity of *T. confusum* is only 38 per cent that of the fecundity at 29°, while the latter is 90 per cent of that obtaining at 34°. The same relations hold for *T. castaneum* with the possible exception that this species is slightly more favored at 34° relative to 29° than is *T. confusum*.

(3) Figure 1 depicts the pattern of oviposition by intervals. It is clear (a) that the first count is uniformly low; (b) that a peak in egg production characteristically occurs during the 6 to 15 day interval, and (c) that the decline in fecundity with time is more pronounced at the two higher temperatures than at 24°. In all curves, except that for *T. confusum* at 24°, there is a noticeable decline at 18 days with reference to the preceding 15 day count. This decline is of borderline significance for *T. castaneum* at 34° and 29° (P = 0.0309 and 0.0218 respectively) but is completely without significance in the other instances (P> 0.05).

(4) There are no especially important patterns as regards variability. The standard deviations (table II) increase with temperature primarily because the means become larger, and, for the same reason, the standard deviations are somewhat higher for *T. castaneum* than for *T. confusum*. The coefficients of variability (table II) are largest at 24° for both species with negligible differences exhibited between the 29° and 34° samples.

Rate of Development

The data concerned with rate of development are presented in table V, that lists the duration of the egg, larval, and pupal stages of both *T. confusum* and *T. castaneum* at three temperatures; in table VI, that compares selected mean differences in these rates, and in table VII, that shows the percentage time spent in the various immature stages. Figure 2 graphs the essential information contained in table V.

Centering attention first on the dura-

Table V. *Biometric constants for rate of development of* Tribolium confusum *and* Tribolium castaneum *at temperatures of 24, 29, and 34° C.*

Stage	Mean duration ± P.E. (hours)	S.D. (hrs.)	C.V. (%)	N	Mean duration ± P.E. (hours)	S.D. (hrs.)	C.V. (%)	N
	Tribolium confusum at 24° C.				*Tribolium castaneum* at 24° C.			
Egg	205.3±0.38	4.2	2.0	55	162.0			53
Larval	824.6±6.78	74.6	9.0	55	796.9±3.89	42.0	5.3	53
Pupal	260.0±7.00	7.7	3.0	55	249.2±0.97	10.5	4.2	53
Total	1289.9±7.19	79.1	6.1	55	1208.1±4.31	46.6	3.9	53
	Tribolium confusum at 29° C.				*Tribolium castaneum* at 29° C.			
Egg	127.0			54	93.6±0.11	1.2	1.3	55
Larval	396.1±3.87	42.2	10.7	54	398.6±3.13	34.4	8.6	55
Pupal	138.9±1.54	16.8	12.1	54	121.7±1.89	20.8	17.1	55
Total	662.0±4.96	54.0	8.1	54	613.9±4.41	48.5	7.9	55
	Tribolium confusum at 34° C.				*Tribolium castaneum* at 34° C.			
Egg	93.9±0.21	2.1	2.2	44	66.0±0.13	1.3	2.0	46
Larval	415.6±3.55	35.0	8.4	44	372.9±5.20	52.3	14.0	46
Pupal	118.4±0.99	9.8	8.3	44	99.4±0.81	8.1	8.2	46
Total	627.9±5.60	55.0	8.8	44	538.3±5.46	55.0	10.2	46

TABLE VI. *Selected statistical comparisons of the rates of development reported in table V*

Comparison	Egg stage		Larval stage		Pupal stage		Total period	
	Mean diff. ± P.E.	P.	Mean diff. ± P.E.	P.	Mean diff. ± P.E.	P.	Mean diff. ± P.E.	P.
T. confusum–*T. castaneum*, 24°	43.3		27.7±7.8	.0182	10.8±1.2	.0000	81.8±8.4	.0000
T. confusum–*T. castaneum*, 29°	33.4		*2.5±5.0	>.5	17.2±2.4	.0000	48.1±6.6	.0000
T. confusum–*T. castaneum*, 34°	27.9±0.25	.0000	42.8±6.3	.0000	19.0±1.3	.0000	89.7±7.8	.0000
T. confusum, 24°–29°	78.3		428.5±7.8	.0000	121.1±1.7	.0000	627.9±8.7	.0000
T. confusum, 29°–34°	33.1		**19.5±5.2	.0126	20.5±1.8	.0000	34.1±7.5	.0024
T. castaneum, 24°–29°	68.4		398.3±5.0	.0000	127.5±2.1	.0000	594.2±6.2	.0000
T. castaneum, 29°–34°	27.6±0.17	.0000	25.8±6.1	.0046	22.3±2.1	.0000	75.7±7.0	.0000

* The mean for *T. castaneum* higher.
** The mean for 34° higher than that for 29°.

tion of the total period of metamorphosis (the interval from laying of the egg to imaginal eclosion), it is evident that, at each of the three temperatures, *T. castaneum* passes through this development at a significantly faster rate than does *T. confusum*. It is equally evident from table V that development accelerates with increases in temperature. These two findings are similar to those already described for fecundity. There is also the suggestion that, in terms of rate of development, *T. confusum* is slightly favored *relative* to *T. castaneum* at 24° while at 34° the reverse is true. In other words, an increase in temperature speeds up metamorphosis somewhat more for *T. castaneum* than would be expected on the hypothesis that both species have identical temperature optima. This physiological point may well be correlated with the geographical distribution of the two species discussed by Good ('36) who remarks: "Records in the United States indicate

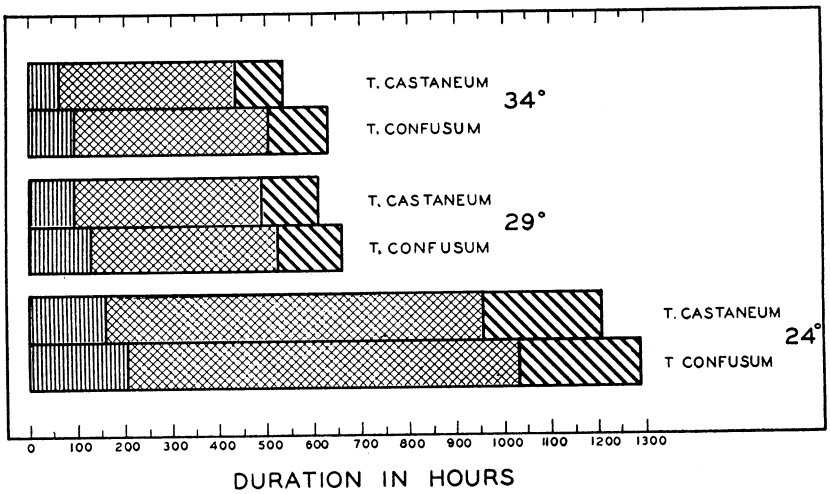

FIG. 2. Duration of the embryonic and post-embryonic stages of *Tribolium confusum* and *T. castaneum* at 24°, 29°, and 34° C. Left-hand boxes represent the egg stage; middle boxes the larval stage, and right-hand boxes the pupal stage.

that temperature has quite an effect on distribution. *T. castaneum* is essentially an insect of warm climates, and, although sometimes recorded from Canada and other northern countries, it is evidently not a permanent resident north of the fortieth parallel in eastern United States except in heated buildings. *T. confusum,* on the other hand, is more frequently found in the northern part of the United States than in the southern part. From 37° to about 40° N. both species occur commonly, while south of 37° *confusum* gradually become less common and in the Gulf States is largely replaced by *castaneum.*"

At all three temperatures it takes longer for the egg and pupal stages of *T. confusum* to develop than it does for those of *T. castaneum.* The larval stages of the two species respond in similar fashion at 24° and 34°, namely: *T. confusum* larvae develop more slowly. At 29°, however, a deviation from this trend occurs—the two species requiring about the same number of hours to complete larval development. Thus, the greater total time spent in metamorphosis by *T. confusum* reflects at the lowest and highest temperatures significantly longer egg, larval, and pupal periods, while at 29° this greater time is to be accounted for by the egg and pupal stages only.

Table VII records the percentage time spent in the three stages. It can be stated in summary (a) that the larval stage consumes about two-thirds of the total developmental period; (b) that the egg stage is relatively longer for *T. confusum* at all temperatures and that the length of this stage relative to the total metamorphic period is greatest at 29°, and (c) that the pupal stage is essentially similar for both species as regards its percentage duration.

Several points worth noting can be made from scrutiny of the coefficients of variability listed in table V. Firstly, it is apparent that the relative variation descriptive of development is considerably less than that for fecundity (table II). The latter coefficients characteristically have values in the 20 to 40 per cent range; the former are all below 20 per cent with modal values occurring below 10 per cent. A second point is that the egg stage is temporally less variable than the larval and pupal stages for both species. In fact, in two instances as indicated in table V, all eggs hatched within a single period of observation so that standard deviations and coefficients of variability could not be computed. Thirdly, there is some suggestion that variation is less at 24° than at 29° and 34°, the last two being quite similar in this respect. And finally, no important differences between species are evident.

Summary

Data are presented on fecundity and rate of development of the flour beetles *Tribolium confusum* and *Tribolium castaneum* maintained at the three constant temperatures of 24°, 29°, and 34° C. It is shown for both species that fecundity increases and length of metamorphosis decreases as the temperature rises. It is further shown that *T. castaneum* has, as a species, a higher fecundity and a faster development than does *T. confusum* at all temperatures studied. There is a suggestion that the lowest temperature is relatively more favorable for *T. confusum* and the highest temperature relatively more favorable for *T. castaneum.* The larval mortality of both beetles is increased by about 20 per cent when this stage is kept at 34°.

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