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Tadeusz PRUS

EMIGRATIONAL ABILITY AND SURFACE NUMBERS OF ADULT
BEETLES IN 12 STRAINS OF *TRIBOLIUM CONFUSUM* DUVAL
AND *T. CASTANEUM* HERBST (COLEOPTERA, TENEBRIONIDAE)*

The analysis is given of emigrational abilities of adult beetles, males and females cultured separately, of 12 strains of *Tribolium* and of the incidence of adult beetles on the surface of the medium in confined groups of these strains. The strain and sex effects with regard to these two features were proved to be significant in both species examined. Specific comparisons are also given of these two features between each pair of the productivity-criterion strains and between wild strains and body-colour mutants of both species. The strain sequences according to the decreasing emigrational ability and decreasing surface numbers, are presented. The presumed correlation between surface numbers and emigrational abilities of these strains is also analyzed.

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*From the Institute of Ecology, Polish Academy of Sciences, Warszawa.

INTRODUCTION

There have been extensive studies in recent years of eight strains of *Tribolium*, bred for the purpose of exploring competitive phenomena. The eight strains were differentiated on the basis of their productivity. Park, Mertz and Petruszewicz (1961) have described how they were derived and presented data dealing with their primary characteristics such as fertility, fecundity, rate of development of each life stage and adult longevities. It was shown that the strains, differentiated according to productivity, also display differences with respect to primary characteristics. In many instances these differences are statistically significant. All four strains of *T. castaneum*, for example, differ significantly in fecundity. They also show clear differences in egg fertility at the same time that the strains of *T. confusum* show no significant differences in egg fertility. Significant differences were also observed in the duration of the developmental stages and average longevity of adults of these strains.

Besides the description of the primary characteristics of strains, there have also been studies of their cannibalistic relations (Park, Mertz, Grodziński and Prus 1965). The authors approached the problem analytically by considering all the cannibalistic behaviour which was manifested during the various developmental stages. It was reported that in many instances there are significant differences in predatory tendencies between strains at a given developmental stage in relation to members of its own or other species of *Tribolium* at different developmental stages.

The purpose of this paper is to study two other characteristics of *Tribolium* strains: 1) the emigrational ability of adult beetles¹ and 2) the incidence of adult beetles on the surface of the medium. Besides giving a general description of the "productivity" strains, wild strains and body-colour mutants of two species of *Tribolium* with regard to these two features, detailed comparisons will be made between each pair of strains of both species. Żyromska-Rudzka (1964), using the same method of study, has described differences in emigrational ability of adult beetles of two strains of *T. castaneum*, *cl* and *c*"jet", cultured in different media (fresh and conditioned flours, saw-dust).

It seems that these two features which are the subject of study play an essential part in the existence of *Tribolium* populations both in single species representations and in interspecies competitive units. By no means can one neglect the importance for a given population of the high or low ability its individuals to leave their environment. The second feature, the tendency of adult beetles to stay on the surface of their life environment, also appears to be very important for *Tribolium* populations. Their occurrence on the surface

¹The term emigrational ability is used to describe the tendency of adult beetles to leave their life environment if given the possibility.

or interior of the medium should basically affect the population and its organization since it is one of the aspects of spatial distribution of population. In the case of *Tribolium* populations it seems reasonable to divide them into two principal categories, namely: that group of individuals present on the surface of the culture medium – one might even say on the border of the life environment and the other group present within this environment, since this division of spatial occurrence is of utmost importance for life and for the existence of this population.

It has been reported that the adult beetles of *T. castaneum*, confined experimentally to the surface of medium, do not lay eggs or lay few eggs, thus considerably decreasing the total reproduction rate of the population (Sonleitner 1961). Such confinement to the surface of the medium has some delaying, restricting effect on fecundity of beetles, even, as shown by “alterative” experiments of Sonleitner (1961), when they are allowed to enter the medium. On the other hand, the beetles while on the surface of the medium do not contribute to the reduction of the population since they cannot exercise their cannibalistic tendencies to eat the immobile beetles present in the interior. As yet it is impossible to tell to what extent these two factors – the diminished fecundity and decreased cannibalism rate, both due to the appearance of beetles on the surface – are compensatory. What is certain is that the reduction in egg cannibalism with the increasing population density is entirely dependent on the prolonged time the adult beetles are spending on the surface of the medium (Sonleitner 1961).

A mass appearance of adult beetles on the surface of the medium, or even on the container wall, observed especially in overcrowded populations, can be considered as a kind of “defense” of the population against self-depletion. Due to this “defensive” reaction, a considerable part of gaseous excretion can evaporate, leaving the environment less contaminated, i.e., less conditioned.

From all that has been said, it is evident that the presumed varying incidence of adult beetles on the surface of the medium can, along with other studied characteristics of these strains, play a significant role in competitive situations in *Tribolium*, and that is why learning about this seems to be very important.

The last part of this paper will deal with the assumed correlation between surface numbers and emigrational ability of adult beetles of the examined strains. This is a methodical aspects of the paper. Such a correlation should exist since the device used to study the emigrational ability (Prus 1963) provides emigration possibilities to these beetles present on the surface of the medium only during the period when it is connected with the culture vial. The lack of such a correlation would indicate that although the adult beetles occur on the surface, they are not always inclined to leave their habitat. This

would be of some evidence in support of the effectiveness and validity of the applied method in studying the emigrational ability of adult beetles of the genus *Tribolium*.

MATERIAL AND METHODS

The material consisted of 12 strains of *Tribolium*: 4 productivity-criterion strains of *T. confusum* Herbst – *bl*, *bII*, *bIII*, *bIV*, 4 productivity-criterion strains of *T. castaneum* Duval – *cl*, *cII*, *cIII*, *cIV* (Park, Mertz, and Petruszewicz 1961), 1 wild strain of *T. confusum* – *b*“Chicago” standard, 1 homozygous body-colour mutant of *T. confusum* – *b*“ebony” (Park, Ginsburg, and Horwitz 1945), 1 wild strain of *T. castaneum* – *c*“Brazil” and 1 homozygous body-colour mutant of *T. castaneum* – *c*“jet” (according to the nomenclature by Park). All these strains come from the laboratory of Dr. Thomas Park of Chicago. They were brought to Poland in April 1963, and the experiments presented in this paper were performed in April and May 1964. Here it is necessary to mention that although the strains were originally the same as those studied by Park (Park, Mertz, and Petruszewicz 1961) they are evolving stocks, each of them somewhat different from the initial one, especially since they had been subjected to the rigore of an intercontinental voyage and a change in geographical and climatic conditions. Initially, strains *cl* and *c*“Brazil” were the same (Park, Mertz and Petruszewicz 1961), but with time, since they were cultured as separate stocks, they might have deviated from each other in their characteristics.

The beetles used in the experiment were cultured under more or less equal conditions of larval density and they were sexed as pupae (Park 1934a). The adult beetles were 15–25 days old at the beginning of the experiment, with the exception of strains *cII* and *bIII* where the adults were 7–25 days old. The considerable age differences were connected with difficulties in identifying a large number of pupae (over 20,000 individuals) within a short period of time. The adults of each sex were segregated both in the period preceding and during the experiment and kept at a constant density equal to 4 individuals per gram of medium.

The experiment consisted of two series. The first series was designed to define the emigrational ability of adult beetles, the second to define the surface numbers of adult beetles. There were 10 replicates for each sex, strain, and species in the first series, and 10 replicates – in the second one (except *cII*, where there were only 5 replicates in each series due to the inadequate number of pupae that were sexed). Thus, the whole experimental set consisted of 230 vials of the first series and of 230 vials of the second series, total of 460 vials (2 sexes × 12 strains × 10 replicates (5 for *cII*) × 2 series).

The procedure in starting the experiment was the same for both the series. Using glass vials with flat bottoms measuring 25 mm in diameter and holding 8 g of standard culture medium (95% of “wrocławska” wheat flour + 5% of

baker's powdered yeast), 32 adult beetles of a given strain were introduced (females or males alternately) onto the surface of the medium. The cultures were covered and placed in dark incubators with a mean temperature of $29.2^{\circ}\text{C} \pm 0.02$ and relative humidity of 70%² (this corresponds to the III climate in Park's (1954) competitive experiments) for the whole period of the experiment, i.e., 31 days.

In the first series, which sought to define emigrational ability, the beetles were allowed to leave the medium 24 hours after their introduction into the vials through a connection with an experimental set which consisted of a plastic tube, a cotton thread, and an empty vial (Prus 1963). The thread, passing through the tube linked the surface of the medium with the interior of the empty vial, without however touching its bottom. Beetles could get on the thread from the surface of the medium, pass through the tube, and eventually fall down to the bottom of the empty vial. The beetles which fell down could not return to the vial with flour. After 24 hours the whole set was disconnected, the beetles present on the bottom of the empty vial and those inside the tube were counted, and then they were reintroduced to the surface of the medium.

The number of beetles present in the empty vial plus the number of beetles lingering on the thread in the tube after 24 hours during which the culture vial was connected with the experimental set were accepted as an index of emigrational ability. The percentage index was calculated by relating this number to the initial density of 32 beetles. Elsewhere it was suggested that the number of beetles present in the empty vial is sufficient to measure emigrational ability (Prus 1963). However, due to uneven proportions of beetles lingering in the tube in both species, emigrational ability will be measured in the present paper by number of beetles which left the medium and its surface within 24 hours (thus, the number of beetles which were found on the thread in the tube and also on the bottom of the empty vial at the end of the 24-hour connection).

Emigrational ability was tested with this method on the 2nd, 10th, 20th, and 30th day of the experiment. In the intervals between these emigration tests, daily records were also taken of the surface numbers of beetles at 9:00 o'clock in the manner described below. These data were used when analyzing the correlation between the surface numbers and the emigration rates of beetles.

In the second series to study the tendency of beetles to appear in a certain proportion on the surface of the medium, numbers of beetles on the surface were recorded twice daily, at 9:00 and 15:00 o'clock (plus half an hour – the duration of the observation). In order to do this, vials were taken out of the incubator and, without removing their covers, the surface numbers were recorded by peering through the vial glass as quickly as possible. 40 vials at a time were taken out of the incubator. This appears to be the largest number of vials which can be checked at one time before an essential change occurs

²The relative humidity was measured and fixed at the level of 70% before the experiment was started since it was impossible to put a hygrometer into the incubator packed with vials; during the experiment only temperature was measured and eventually corrected.

in the distribution of beetles as a result of different surrounding conditions of temperature, humidity, and light.

To assess the possible effect of the change in surrounding conditions on the surface numbers of beetles, an additional experiment was carried out which involved the taking of 4 additional counts of the surface numbers. The first and second records were taken within the incubator, the third and fourth – out of the incubator, with 5 minute intervals between the counts. This experiment was performed with wild strains of *T. confusum* "Chicago" standard and *T. castaneum* "Brazil", setting up 5 replications for each strain. There were 21 observations made at intervals not shorter than one hour over a 3 day period. Differences in mean surface numbers between the third and fourth records (both out of the incubator) showed no statistical significance. On the other hand, differences between the first and third records (the first within the incubator and the first out of it) were statistically significant, at the probability level of 0.05.

Thus it can be inferred that although surface numbers obtained from the second series of the present experiment deviate to some extent from reality, they form a consistent set of data which can be used to characterize the strains.

In order to maintain constant numbers of beetles in the vials, dead beetles found on the surface were replaced with live ones of a corresponding sex, strain, or species, derived from the same initial stocks.

Throughout the entire experiment, the medium in the vials was left unsifted except for cultures of *c*"Brazil" females where, in spite of careful segregation of sexes, a few males must have got in. Some large larvae were found in these cultures which were removed by sifting the medium at the end of the experiment. It should be kept in mind that in this case the characteristics of emigrational ability and surface numbers refer to fertilized females, accompanied by growing larvae – their progeny. Thus it seems probable that the increase in emigrational ability of *c*"Brazil" females observed on the 20th day of the experiment and the increase in their surface numbers observed especially on 18–22 days of the experiment might have been brought about by the presence of a considerable number of large larvae in these cultures. The presence of large larvae in the cultures was indeed found to have significantly increased the surface numbers of adult beetles (unpublished data).

EMIGRATIONAL ABILITY

The emigration rate index as defined in the previous Chapter was used to characterize the emigrational ability of strains and their sexes of both species. To recapitulate: the number of beetles which left their environment and its surface during 24 hours of connection with the experimental set was accepted as such an index. The percentage index was calculated as the ratio of this number to the initial number of 32 beetles.

In giving a general description of the strains, the results obtained during the initial period of the experiment were excluded from the analysis since they deviated considerably from the more or less uniform data of the later period, and since both species studied differed diametrically in their responses to a new medium. Characteristics of strains, both with regard to emigrational abilities and surface numbers, were based on the results obtained in a later period (10–31 days of the experiment); they concern the beetles present in a slightly conditioned, unchanged medium. This latter remark is very essential since the conditioning of the medium, depending among other factors on excretion of harmful substances by beetles (Alexander and Barton 1943, Roth 1943, Loconti and Roth 1953), has a strong impact on a number of population characteristics such as fecundity (Park 1934b, 1935, 1936; Park and Woollcott 1937; Birch, Park, and Frank 1951, Sonleitner 1961, Prus 1961), the rate of egg cannibalism (Park 1934a, Sonleitner 1961, Park, Mertz, Grodziński, and Prus 1965), the duration of the developmental stages of larvae and pupae (Park, Miller, and Lutherman 1939), mortality (Lloyd and Park 1962) or finally, surface numbers (Sonleitner 1961, Żyromska-Rudzka 1964) and emigration rate (Żyromska-Rudzka 1964). The emigrational ability and surface numbers of adult beetles for the initial period following the introduction of beetles to the fresh medium will be discussed elsewhere in this paper. The general description of emigrational abilities of strains was based on the indices obtained on 10th, 20th, and 30th days of the experiment, pooled together. The characterization of the emigrational differentiation as well as that of surface numbers was based on the analysis of variance (statistics F). Statistical tables by Czechowski et al. (1957) were used. The detailed comparisons between strains were carried out separately for the productivity strains and for wild strains and body-colour mutants.

General regularities

A general regularity observed was that both sexes of all the strains of *T. confusum* and *T. castaneum* show a tendency to leave their life environment if given the possibility (Tab. I). This tendency measured by the percentage indices, differs: in the conditions of the present experiment it ranges from 5.2% (in *bIV* ♀♀) to 87.3% (in *b* "Chicago" ♂♂) for *T. confusum*, and from 38.0% (in *cIII* ♀♀) to 86.6% (in *cI* ♂♂) for *T. castaneum* (Tab. I).

The analysis of variance proved that in *T. confusum* and in *T. castaneum* the emigration rates differ between strains and sexes in a significant way ($P < .01$) (Tab. II).

The second universal regularity that was observed is that the emigrational

The emigration rates of adult beetles: numbers of beetles leaving their medium within 24 hrs. Means cover 3 subsequent censuses on 10th, 20th, and 30th day of the experiment. Percentage of the initial number: 32 adults in 8 g of medium

Tab. I

Strain	<i>T. confusum</i>					
	♂♂		♀♀		(♂♂ + ♀♀) : 2	
	Emigration rates		Emigration rates		Emigration rates	
	number	per cent	number	per cent	number	per cent
<i>bI</i>	24.73	77.3	13.40	41.9	19.07	59.6
<i>bII</i>	18.76	58.6	8.17	25.5	13.47	42.1
<i>bIII</i>	23.47	73.3	8.83	27.6	16.15	50.5
<i>bIV</i>	18.93	59.1	1.67	5.2	10.30	32.2
<i>b</i> "Chicago"	27.93	87.3	16.67	52.1	22.30	69.7
<i>b</i> "ebony"	26.43	82.6	12.80	40.0	19.61	61.3
<i>T. castaneum</i>						
<i>cI</i>	27.73	86.6	19.90	62.2	23.82	74.4
<i>cII</i>	26.86	83.9	24.20	75.6	25.53	79.8
<i>cIII</i>	14.27	44.6	12.17	38.0	13.22	41.3
<i>cIV</i>	19.40	60.6	19.40	60.6	19.40	60.6
<i>c</i> "Brazil"	25.03	78.2	22.27	69.6	23.65	73.9
<i>c</i> "jet"	26.30	82.2	21.50	67.2	23.90	74.7

Analysis of variance of data in Table I. Strain and sex effects on surface numbers

Tab. II

<i>T. confusum</i>					
Source of variation	Sum of squares	D.F.	Mean squares	F	Probability
Between strains	5,806.80	5	1,161.36	52.9576	< .01
Between sexes	15,492.10	1	15,492.10	706.4341	< .01
Interaction	490.50	5	98.10	4.4733	< .01
Residual	7,631.09	348	21.93		
<i>T. castaneum</i>					
Between strains	5,762.10	5	1,152.42	41.1285	< .01
Between sexes	964.95	1	964.95	34.4379	< .01
Interaction	532.20	5	106.44	3.7987	< .01
Residual	8,909.90	318	28.02		

abilities of males are, as a rule, higher than those of females (*cIV* is exception to this rule, with equal emigration rates for males and females). Considerably greater differences were observed between the male and female emigration

Probability values for statistics F (analysis of variance) of emigration rates of adult beetles: between sexes (on diagonal), between strains: males (above diagonal), females (below diagonal)

Tab. III

<i>T. confusum</i>							<i>T. castaneum</i>						
	<i>bI</i>	<i>bII</i>	<i>bIII</i>	<i>bIV</i>	<i>b</i> "Chi- cago"	<i>b</i> "ebo- ny"		<i>cI</i>	<i>cII</i>	<i>cIII</i>	<i>cIV</i>	<i>c</i> "Bra- zil"	<i>c</i> "jet"
<i>bI</i>	< <u>.01</u>	< .01	> .05	< .01	< .02	> .05	<i>cI</i>	< <u>.01</u>	> .05	< .01	< .01	< .02	> .05
<i>bII</i>	< .01	< <u>.01</u>	< .01	> .05	< .01	< .01	<i>cII</i>	< .05	> <u>.05</u>	< .01	< .01	> .05	> .05
<i>bIII</i>	< .01	> .05	< <u>.01</u>	< .01	< .01	< .01	<i>cIII</i>	< .01	< .01	> <u>.05</u>	< .01	< .01	< .01
<i>bIV</i>	< .01	< .01	< .01	< <u>.01</u>	< .01	< .01	<i>cIV</i>	> .05	< .01	< .01	> <u>.05</u>	< .01	< .01
<i>b</i> "Chi- cago"	< .05	< .01	< .01	< .01	< <u>.01</u>	< .05	<i>c</i> "Bra- zil"	< .05	> .05	< .01	> .05	> <u>.05</u>	> .05
<i>b</i> "ebo- ny"	> .05	< .01	< .01	< .01	< .02	< <u>.01</u>	<i>c</i> "jet"	> .05	> .05	< .01	> .05	> .05	< <u>.01</u>

rates in the strains of *T. confusum* than were observed between those of *T. castaneum*. These differences, compared by means of analysis of variance, are statistically significant (Tab. III). When ranking the strains according to the extent of differences between emigration rates of females and males, from maximum to minimum, the following strain sequence is obtained in *T. confusum*: *bIV* – *bIII* – *b*“ebony” – *bI* – *b*“Chicago” – *bII*. The differences in *T. castaneum* strains are much smaller; they are statistically significant (as compared by analysis of variance) only for *cl* and *c*“jet” (Tab. III). The strain sequence is: *cl* – *c*“jet” – *c*“Brazil” – *cII* – *cIII* – *cIV*.

Differences in emigrational ability of strains

High indices of emigration rates were found in males of *T. confusum* and *T. castaneum* strains (of the rank of 58.3–87.3% and 44.6–86.6%, respectively), lower ones for females of *T. castaneum* strains (ranging from 60.6–75.6%), and the lowest for females of *T. confusum* strains (5.2–52.1% within 24 hours) (Tab. I).

In the first place, comparisons were made of the strains for each sex separately, e.g., *bI* ♂♂ were compared with *bII* ♂♂ and *bI* ♀♀ with *bII* ♀♀, etc. Comparisons were also made between strains when sex was ignored. It is futile to compare the productivity-criterion strains between two species, e.g., *bI* with *cl*, etc., since these strains are not equivalent, *bI* is not an equivalent of *cl*; the strains are biologically real only within species (Park, Mertz, and Petruszewicz 1961; Park, Mertz, Grodziński, and Prus 1965).

The detailed analysis of differences between the strains of two species was also based on analysis of variance. The probability of 0.05 was accepted as the level of significance, and all the cases with probability 0.02 and 0.05 were considered as borderline ones. Although all possible combinations of strain pairs within one species were compared, discussion will be limited to comparisons of productivity strains, and of wild strains and body-colour mutants. The comparison of wild strains and colour mutants with the productivity strains will serve merely to ascertain to which of the genetic strains these strains are most similar with regard to emigrational ability.

Productivity strains

For an overall illustration of the significance of differences in emigrational ability of genetic strains, it can be said that of 24 comparisons between pairs of productivity strains within each sex and species, based on analysis of variance, only 5 differences were statistically insignificant (Tab. III).

In *T. confusum*, of 6 possible comparisons between males of the productivity strains, 4 differences were statistically significant (Tab. III). Insignificant differences were those between males of the following pairs of strains: *bI* – *bIII* and *bII* – *bIV*. Of the analogous 6 comparisons between females of the productivity strains of this species, 5 differences were significant; an insignificant difference was that between females *bII* and *bIII*. In *T. castaneum*, of 6 comparisons possible between males of productivity strains, 5 were statistically significant (Tab. III). There was an insignificant difference between males of *cI* and *cII*. Similarly, of 6 comparisons between females of this species, 5 differences were statistically significant, *cI* with *cII* being the borderline case. There was an insignificant difference between females of *cI* and *cIV*.

In *T. confusum*, the sequences of strains for males and females, arranged according to diminishing rates of emigration (given in parentheses), and marked with symbols: > – significant, ~ – insignificant, are as follows:

$$\text{♂♂ } bI (24.73) \sim bIII (23.50) > bIV (18.93) \sim bII (18.76),$$

$$\text{♀♀ } bI (13.40) > bIII (8.83) \sim bII (8.17) > bIV (1.67).$$

In *T. castaneum*, the analogous sequences of strains are as follows:

$$\text{♂♂ } cI (27.73) \sim cII (26.36) > cIV (19.40) > cIII (14.27),$$

$$\text{♀♀ } cII (24.20) > cI (19.90) \sim cIV (19.40) > cIII (12.17).$$

The differentiation of the emigrational ability in the productivity strains can be better illustrated by a percentage presentation of emigration rates. Accepting the highest mean values of emigration rates to be 100% and relating to them the remaining rates, the following percentages are obtained for *T. confusum* strains:

males: *bI* – 100%, *bII* – 75.9%, *bIII* – 95.0%, *bIV* – 76.5%,

females: *bI* – 100%, *bII* – 61.0%, *bIII* – 65.9%, *bIV* – 12.5%,

and for *T. castaneum* strains:

males: *cI* – 100%, *cII* – 96.9%, *cIII* – 51.5%, *cIV* – 70.0%,

females: *cI* – 82.2%, *cII* – 100%, *cIII* – 50.3%, *cIV* – 80.2%.

The above percentage presentation points to the highest differentiation of emigration rates in females of productivity strains of *T. confusum*, to considerably lower and similar rates, for males and females in the productivity strains of *T. castaneum*, and to the lowest one for males of productivity strains of *T. confusum*.

Because of the design accepted in this experiment, the emigrational ability of each strain is characterized by two indices: the emigration rate for females and that for males. It would be most interesting to know the emigrational ability of a population composed of both sexes in an even proportion. Results of another, supplementary experiment permit the supposition that the emigration rate for such a population can be defined by the arithmetical mean of the emigration rates calculated for males and females cultured separately providing there are no large larvae in the population. This qualification is very important since it is known (from unpublished data of the author) that the presence of large larvae in the medium considerably enhances the emigration of adult beetles.

The supplementary experiment, carried out on the wild strain, *c* "Brazil" of *T. castaneum*, was designed as follows: there were 3 series in the experiment with 5 replicates in each: 1) males, 2) females, and 3) males + females in ratio 1:1. The beetles used in the experiment were 14 days old, initial density - 32 individuals in 8 g of standard medium, temperature - 29°C, relative humidity - 75%. To test emigration, the experimental sets were kept connected with the cultures for 10 days and every 24 hours the beetles that were found in the empty vials and in the connecting tubes were counted and then reintroduced on the surface of the medium in the culture vials. Thus, for each series of the experiment there were 50 values of the emigration index (5 replicates × 10 days). The mean emigration rates (mean number of adult beetles that left their environment within 24 hours during the 10 day test period) for these 3 series are as follows: (1) males - 23.4 ± 0.46 , (2) females - 15.4 ± 0.58 , and (3) males + females - 18.2 ± 0.69 . The arithmetic mean, calculated from series (1) and (2), i.e., from the emigration rates of males and females cultured separately, is 19.4 ± 0.54 . There is no significant difference between this calculated mean and the empirical value obtained for series (3), that is, for males and females cultured together. The lack of significant difference between the arithmetical mean from the indices for males and females and the empirical value of the emigration rate obtained for the mixed population, with sex ratio 1:1, permits the supposition that the emigrational ability of the mixed population is, indeed, a kind of product of the emigrational abilities of males and females. It should be emphasized, however, that this experiment has been carried out on one strain only and it is impossible to predict to what extent, if any, its results can be extended to the remaining strains examined.

Describing the emigrational ability of the productivity strains with sex differences ignored, on the basis of means of emigration rates of males and females, the following strain sequences, from maximum to minimum, are obtained:

T. confusum: *bI* (19.07) ~ *bIII* (16.15) ~ *bII* (13.47) > *bIV* (10.30),

Lack of significant differences between strain pairs: *bI-bIII* and *bII-bIII* (Tab. IV) is purely of statistical manipulation reason, since by pooling very diverse material for females and males, rather high variances were obtained which strongly affected the empirical *F* values.

Probability values of statistics *F* (by analysis of variance) of emigration rates of adult beetles, with sex ignored, between strains of *T. confusum* (above diagonal) and *T. castaneum* (below diagonal).

Tab. IV

		<i>T. confusum</i>						
		<i>bI</i>	<i>bII</i>	<i>bIII</i>	<i>bIV</i>	<i>b</i> "Chicago"	<i>b</i> "ebony"	
<i>T. castaneum</i>	<i>cl</i>		< .01	> .05	< .01	< .05	> .05	<i>bI</i>
	<i>cII</i>	> .05		> .05	< .05	< .01	< .01	<i>bII</i>
	<i>cIII</i>	< .01	< .01		< .01	< .01	< .01	<i>bIII</i>
	<i>cIV</i>	< .01	< .01	< .01		< .01	< .01	<i>bIV</i>
	<i>c</i> "Brazil"	> .05	> .05	< .01	< .01		> .05	<i>b</i> "Chicago"
	<i>c</i> "jet"	> .05	> .05	< .01	< .01	> .05		<i>b</i> "ebony"
		<i>cl</i>	<i>cII</i>	<i>cIII</i>	<i>cIV</i>	<i>c</i> "Brazil"	<i>c</i> "jet"	

In the latter presentation of emigration rates one can easily note that the emigrational tendencies of strains of *T. castaneum* are generally higher than those of *T. confusum*.

Generalizing, the emigrational abilities of the productivity strains, as measured by all the foregoing indices, can be described as follows:

T. confusum. Strain *bI*, both males and females, shows the highest emigrational tendency (Tab. I).

Strain *bIII* comes second. The emigrational ability of males in this strain does not differ statistically from that of males *bI*, whereas females of these two strains show significant difference (Tab. III). A relatively high difference was observed between males and females in this strain as regards emigration ability (second in turn) (Tab. III).

Strain *bII* comes third. Its males show the smallest emigrational ability, almost equal to that of males *bIV*. The emigration rate of its females is very close to that of females *bIII* (Tab. III). In this strain, the difference between males and females, although statistically significant, is the smallest (Tab. III).

Strain *bIV* shows the smallest emigrational ability. Females of this strain have an extremely low emigration index (1.7 or 5.3%) (Tab. I), and the difference between males and females is highest as compared with the rest of productivity strains (Tab. III).

T. castaneum. Of the productivity strains, *cII* and *cI* are strains with the highest emigrational abilities (Tab. I). The emigration rates of males of these two strains show no significant difference, but the emigration rate of females *cII* is significantly higher than that of females *cI* (Tab. III). The emigration rates of females and males in strain *cI* differ significantly, and those of strain *cII* show no significant difference (Tab. III).

Strain *cIV* comes third as regards emigrational ability. Males in this strain differ significantly from males of the three remaining productivity strains, but the emigration rate of females is almost identical with that of females *cI* while it differs significantly with the rates of the two remaining strains (Tab. III). With sex ignored, this strain differs significantly from the strains: *cI*, *cII*, and *cIII* (Tab. IV). Strain *cIV* is the only one whose emigration rates for males and females are equal.

The smallest emigration tendency is characteristic for strain *cIII*; its emigration rates, both for females and males, differ significantly from the analogous rates of the remaining productivity strains of this species (Tab. III).

Wild strains and body-colour mutants

From studies conducted it can be said that the wild strains and body-colour mutants of *T. confusum* and *T. castaneum* show rather high emigrational abilities (Tab. I). Comparisons were made of the strain pairs: *b* "Chicago" – *b* "ebony" of *T. confusum* and *c* "Brazil" – *c* "jet" of *T. castaneum*.

The emigrational ability of *b* "Chicago", both of its males and females, is higher than that of *b* "ebony". The emigration rates of males, females, and males and females pooled together, of these two strains show borderline differences, with the *F* value for the last comparison shifted somewhat towards insignificance (Tab. III and IV).

It is interesting to compare the emigrational ability of these strains with that of productivity strains of *T. confusum*. Strain *b* "Chicago" (males and females) shows the highest emigration rates, differing significantly from the analogous rates of the four productivity strains in this species (only the difference with *bI* is borderline) (Tab. I and III). Thus, of the strains of *T. confusum*, strain *b* "Chicago" is most similar to strain *bI* in terms of emigrational ability (Tab. III and IV).

Strain *b* "ebony" also shows a rather high emigrational tendency, although not as high as *b* "Chicago". The emigration rates of its males and females differ significantly from the analogous rates of *bII*, *bIII*, and *bIV*, but are

similar to those of *bl* (Tab. III). Thus, strain *b* "ebony", resembling strain *b* "Chicago" in its emigrational tendency is most similar to strain *bl* (insignificant difference – Tab. IV). This is a very important finding since these two strains, differing in body-coloration, can be used in further experiments on migration in *T. confusum*, with *b* "ebony" constituting a naturally marked material.

When comparing strains *c* "Brazil" and *c* "jet" of *T. castaneum*, it was found that these two strains, both their males and females, do not differ significantly in the values of emigration rates (Tab. III). The emigration rate of males *c* "Brazil" is significantly lower than that of males *cl*, insignificantly lower than that of males *cII*, and significantly higher than the rates of males *cIII* and *cIV*. The emigration rate of females *c* "Brazil" is insignificantly lower than that of *cII* females, insignificantly higher than those of *cl* and *cIV*, and significantly higher than that of *cIII* (Tab. I and III). When ignoring sex differences, strain *c* "Brazil" is similar in its emigrational ability to strains *cl* and *cII*, but significantly higher than *cIII* and *cIV* (Tab. I and IV).

In strain *c* "jet" the emigration rate of males is insignificantly lower than the rates of males *cl* and *cII*, but significantly higher than those of males *cIII* and *cIV*. Females of this strain have the emigration rate insignificantly lower than that of females *cII*, insignificantly higher than those of *cl* and *cIV*, and significantly higher than that of females *cIII* (Tab. I and III). Ignoring sex, strain *c* "jet" does not differ significantly from strains *cl* and *cII*, but it differs from strains *cIII* and *cIV* (Tab. IV).

The observed lack of a significant difference in emigrational ability between strains *c* "jet" and *cl* conflicts with the literature data. Żyromska-Rudzka (1964), using the same method of investigation, studied differences in emigrational ability of those two strains and found that strain *c* "jet" has a considerably higher (several times higher) tendency to emigrate than strain *cl*. This apparent incongruency of results may be possibly explained by differences in the application of the method. In the paper by Żyromska-Rudzka, emigrational ability was characterized by emigration rates obtained just after the beetles were introduced to a fresh medium (the emigration test sets were connected with cultures after 24 hours following the introduction of beetles), which would correspond with the results obtained on the second day of the present experiment. The data for this period really point to an initially higher emigration ability of strain *c* "jet" rather than of *cl*. The emigration rates on the second day of the experiment are as follows: *cl* ♂♂ – 18.50, ♀♀ – 7.20, *c* "jet" ♂♂ – 22.60, ♀♀ – 14.60.

Differences in emigrational ability between the sexes of wild strains and body-colour mutants have been discussed earlier.

Time changes in emigrational ability

We will now consider changes in the emigrational ability of *Tribolium* strains in relation to the time which beetles have spent in the medium and/or to their age. As has been mentioned earlier, the results obtained on the 2nd day of the experiment differed considerably from those obtained later.

The data obtained on the second day of the experiment were concerned with the period directly following the introduction of beetles into a new habitat, the fresh medium. It is known that both species of *Tribolium* differ diametrically in their responses to such a change (Gent 1960, Bond 1961). *T. confusum*, when faced with an alternative of fresh and conditioned media, always chooses the conditioned one, and the opposite holds for *T. castaneum*: it always chooses the fresh medium (Gent 1960).

When starting up this experiment, it was observed that the beetles of *T. confusum* strains, when introduced to the surface of the fresh medium, were not inclined to enter its interior; a large proportion remained on the surface of the medium for some time (Fig. 1B and 3B). This apparently was responsible for the higher emigration of *T. confusum* strains, a much higher emigration in the later period (Fig. 1A and 3A).

On the other hand, the beetles of *T. castaneum* strains, when introduced onto the surface of fresh medium, entered its interior rather quickly, and only a few individuals were found remaining on the surface at this time (Fig. 2B and 3B). Correspondingly, the emigration rates of *T. castaneum* strains were very low at this time (Fig. 2A and 3A).

The period of an altered distribution of beetles in the medium is relatively short, it barely lasts several days following the introduction of beetles to the new medium, and the emigration rates obtained for this period differ considerably from more or less uniform rates for the later, much longer, time. For this reason the emigration rates for the second day of the experiment were considered as inadequate for characterizing the general emigrational abilities of strains. The different behaviour patterns of both species in the fresh medium probably have some important bearing on time-specific changes in emigrational abilities of adult beetles. In *T. confusum* strains, the highest values of emigration rates were chiefly those observed at the beginning of the experiment (2nd day); later, on the 10th, 20th, and 30th day, a slight decreasing tendency in emigrational ability was noticed (Fig. 1A and 3A). In *T. castaneum* strains, besides clearly low emigration rates observed on the second day of the experiment (the lowest for the entire experimental period), maximum values were recorded on 10th and 20th day of the experiment, followed also by a slight decrease in the emigrational tendency (Fig. 2A and 3A).

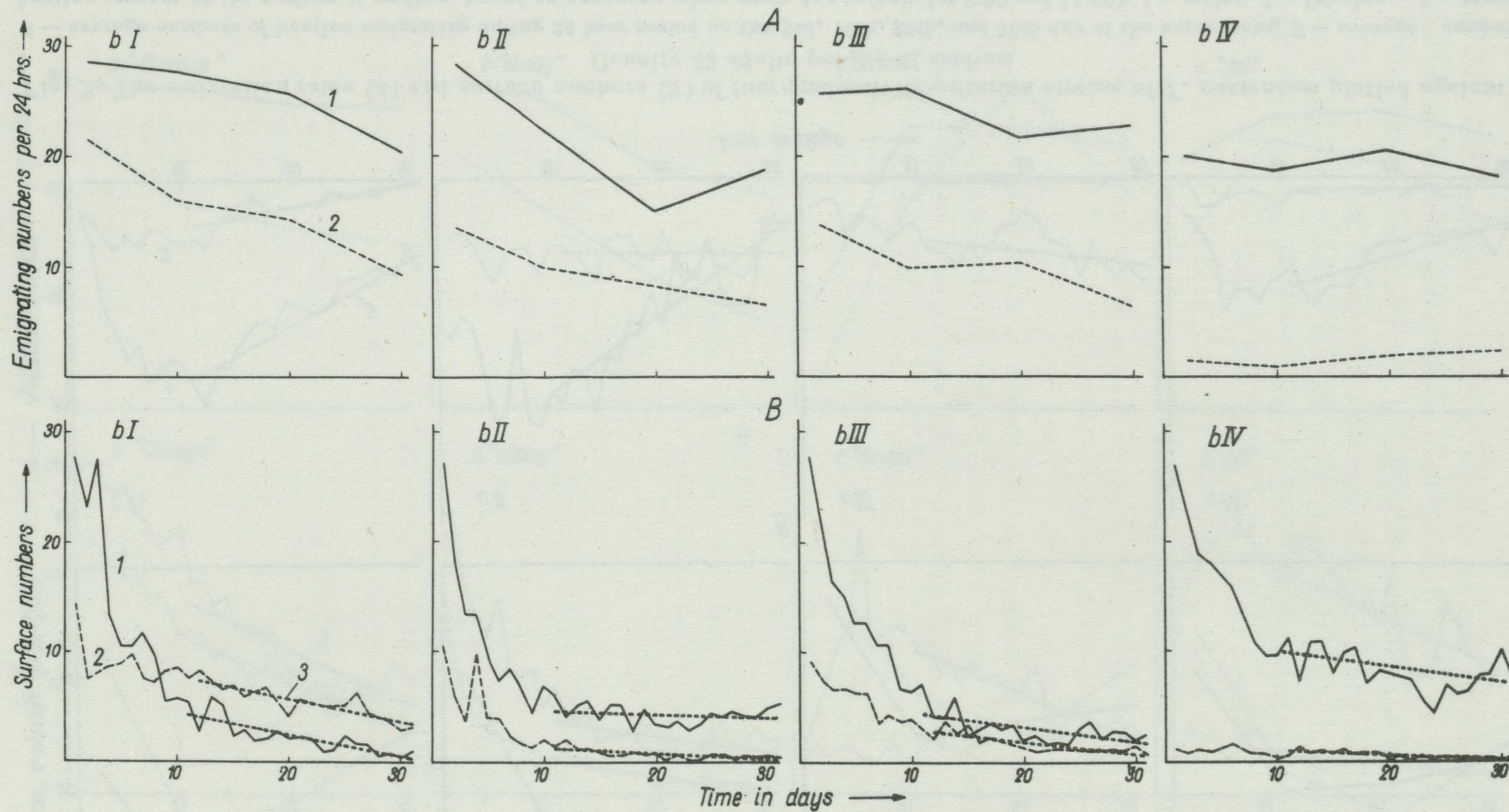


Fig. 1. The emigration rates (A) and surface numbers (B) of four productivity-criterion strains of *T. confusum* plotted against time.

Density 32 adults per 8 g of medium

A — average numbers of beetles emigrating during 24 hour period on the 2nd, 10th, 20th, and 30th day of the experiment, B — average numbers of beetles present on the surface of medium, based on censuses taken every day twice (at 9:00 and 15:00); 1 — males, 2 — females, 3 — regression lines of surface numbers for 11–31 day of the experiment

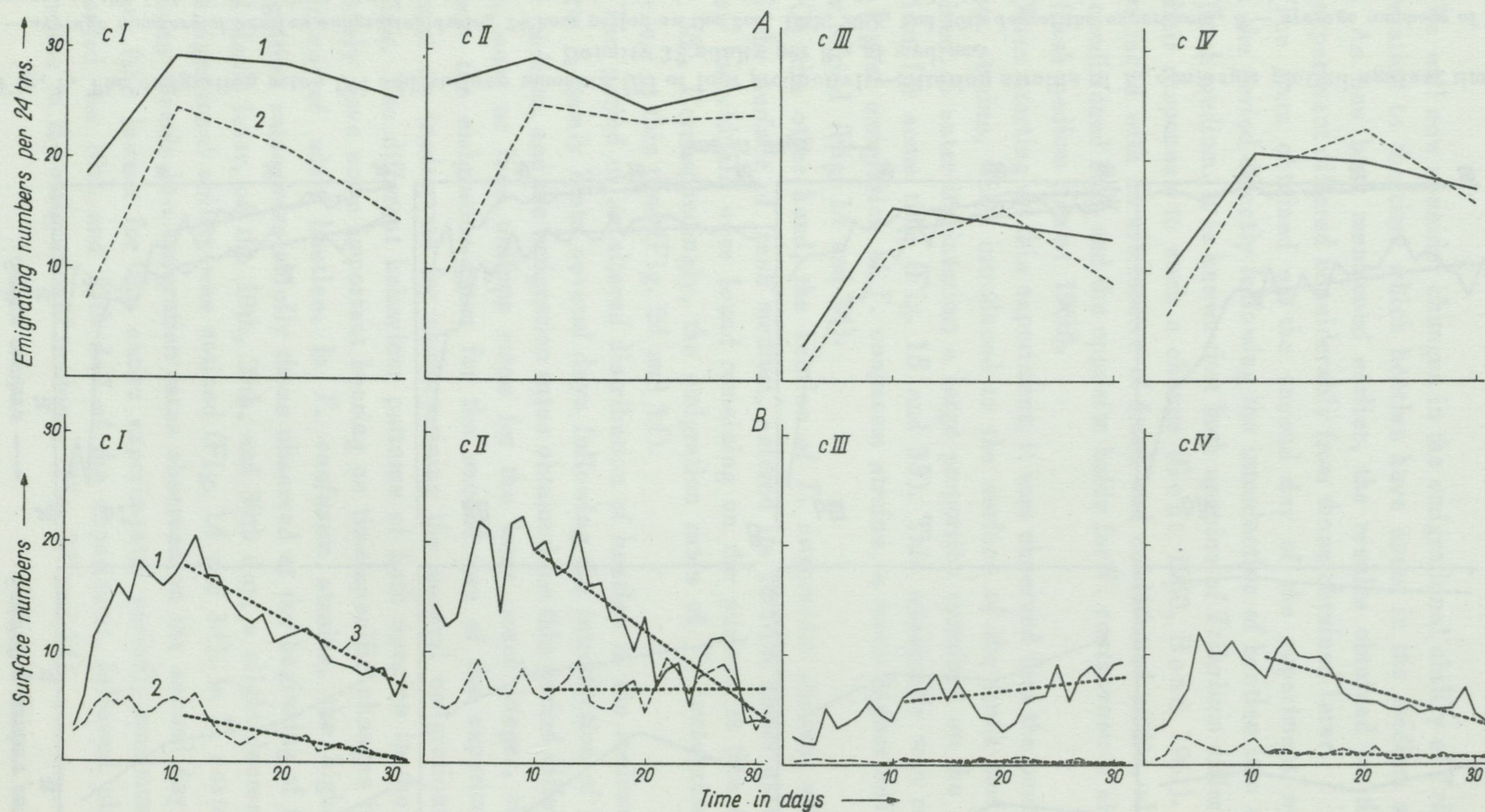


Fig. 2. The emigration rates (A) and surface numbers (B) of four productivity-criterion strains of *T. castaneum* plotted against time. Density 32 adults per 8 g of medium

A — average numbers of beetles emigrating during 24 hour period on the 2nd, 10th, 20th, and 30th day of the experiment, B — average numbers of beetles present on the surface of medium, based on censuses taken every day twice (at 9:00 and 15:00); 1 — males, 2 — females, 3 — regression lines of surface numbers for 11–31 day of the experiment

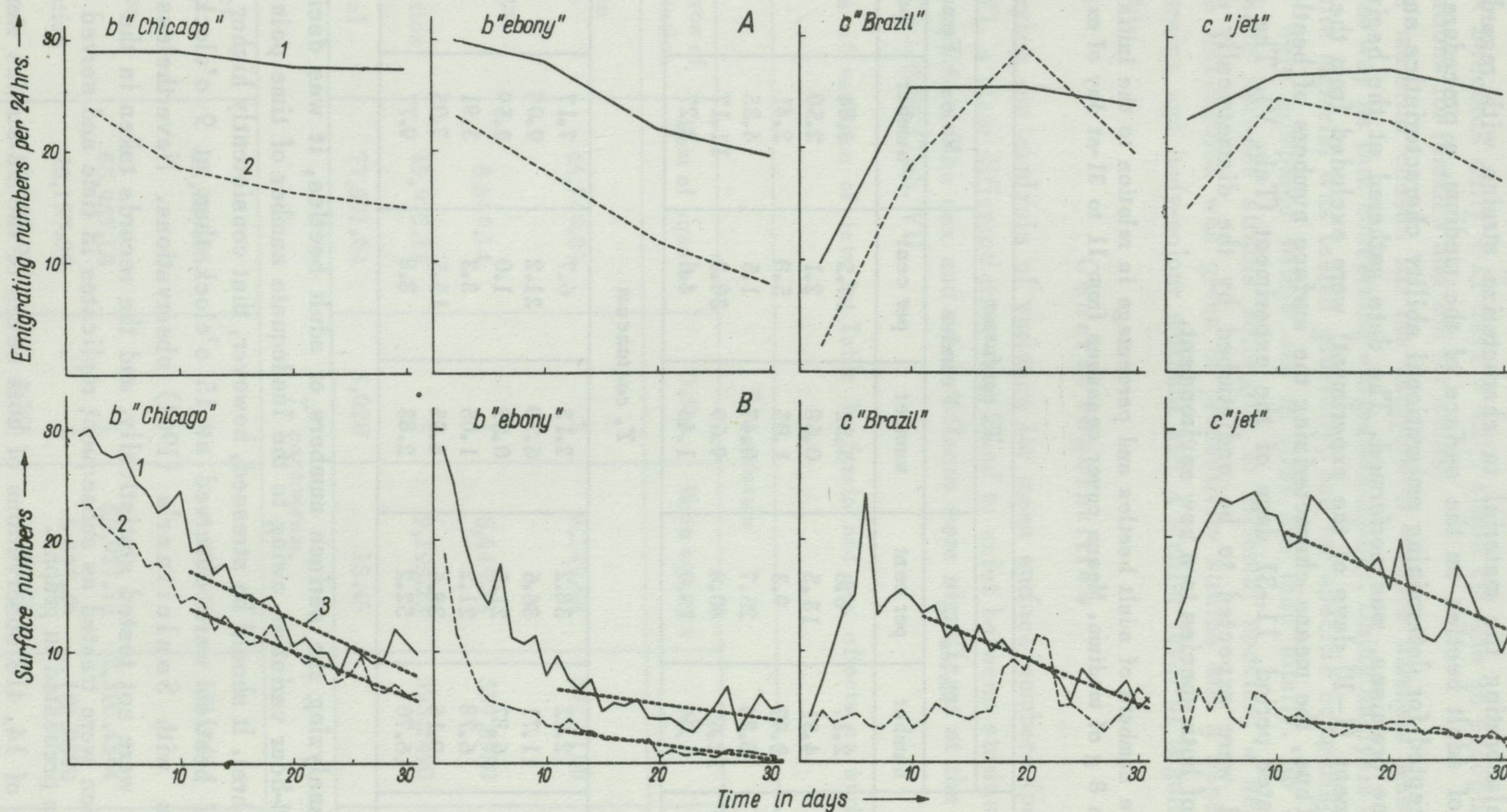


Fig. 3. The emigration rates (A) and surface numbers (B) of wild strains and body-colour mutants, *T. confusum* and *T. castaneum* plotted against time. Density 32 adults per 8 g of medium

A — average numbers of beetles emigrating during 24 hour period on the 2nd, 10th, 20th, and 30th day of the experiment; B — average numbers of beetles present on the surface of medium, based on censuses taken every day twice (at 9:00 and 15:00); 1 — males, 2 — females, 3 — regression lines of surface numbers for 11–31 day of the experiment

SURFACE NUMBERS

When elaborating the material to characterize strains with regard to the incidence of adult beetles on the surface of the medium, a procedure similar to that accepted for determining emigrational ability characteristics and based on the same premises, was performed. The data gathered at the beginning of the experiment (1–10 days of the experiment) were excluded from the general analysis. Thus, the means characterizing the surface numbers of beetles comprise a later period, 11–31 days of the experiment (Tab. V). The data for this period were expected to be undisturbed by the diametrically different responses of both species to a new environment.

Mean surface numbers of adult beetles and percentage in relation to the initial number 32 adults in 8 g of medium. Means cover censuses from 11 to 31-st day of experiment

Tab. V

Strain	<i>T. confusum</i>					
	Males		Females		Males + Females	
	number	per cent	number	per cent	number	per cent
<i>bI</i>	2.17	6.8	5.52	17.2	3.84	12.0
<i>bII</i>	4.31	13.5	0.68	2.1	2.50	7.8
<i>bIII</i>	2.97	9.3	1.85	5.8	2.41	7.5
<i>bIV</i>	8.24	25.7	0.47	1.5	4.35	13.6
<i>b"Chicago"</i>	12.65	40.8	9.69	30.3	11.17	34.9
<i>b"ebony"</i>	5.09	15.9	1.46	4.6	3.27	10.0
	<i>T. castaneum</i>					
<i>cI</i>	12.22	38.2	2.13	6.7	7.17	22.4
<i>cII</i>	11.71	36.6	6.79	21.2	9.07	28.3
<i>cIII</i>	6.87	21.5	0.32	1.0	3.59	11.2
<i>cIV</i>	6.78	21.2	1.05	3.3	3.91	12.2
<i>c"Brazil"</i>	9.16	28.6	4.95	15.5	7.05	22.0
<i>c"jet"</i>	16.70	52.2	2.83	8.8	9.77	30.5

When analyzing the surface numbers of adult beetles, it was decided not to study 24-hour variation owing to the inadequate number of time points (only two per 24 hrs). It should be stressed, however, that consistently higher surface numbers of beetles were observed at 15 o'clock than at 9 o'clock, which corresponds with Sonleitner's (1961) observations. Nevertheless, these differences were not tested statistically, and the records taken in the morning and afternoon were treated as subsequent replicates in time and served to draw daily means presented in graphs.

A total of 14, 418 observations of both sexes of the 12 strains were made

during the entire experiment in the second series. The averages of surface numbers for each sex of a given strain are based on 420 observations (10 replicates \times 2 records daily \times 21 days = 420); strain *cII* was an exception with 310 observations for females and 268 for males.

The material chosen for the analysis of surface numbers was handled in a similar way as that concerning emigration ability. Using analysis of variance, the entire material was tested generally, and for specific comparisons pairs of strains were compared within sex at first and then totally. No comparisons were made between strains belonging to different species; a separate comparative description was given of productivity strains and a separate one of wild strains and body-colour mutants and a similar level of significance was accepted.

General regularities

Carrying out analysis of variance for mean surface numbers (presented in Table V), a clear differentiation was found to exist between strains and sexes of both species. The sex and strain effects were significant at the probability level of $\alpha = 0.05$ (Tab. VI).

Analysis of variance of data in Table V. Strain and sex effects on surface numbers

Tab. VI

<i>T. confusum</i>					
Source of variation	Sum of squares	D.F.	Mean squares	<i>F</i>	Probability
Between strains	45,749.89	5	9,149.98	592.3198	< .01
Between sexes	8,649.14	1	8,649.14	559.8980	< .01
Interaction	45,976.14	5	9,195.23	595.2490	< .01
Residual	77,671.04	5,028	15.45		
<i>T. castaneum</i>					
Between strains	25,039.06	5	5,007.81	181.2454	< .01
Between sexes	65,937.18	1	65,937.18	2,386.4344	< .01
Interaction	25,137.08	5	5,027.40	181.9500	< .01
Residual	131,705.91	4,766	27.63		

The surface numbers of adult beetles range for the analyzed period (11th–31st days of the experiment) from 1.5% of beetles (in *bIV* ♀♀) to 40.8% (in *b* “Chicago” ♂♂) for both sexes of *T. confusum* strains and from 1.0% (in *cIII* ♀♀) to 50.1% (in *c* “jet” ♂♂) for both sexes of *T. castaneum* strains. The extremes of surface numbers when sex is ignored range from 7.5% (in *bIII*) to 34.9% (in *b* “Chicago”) for *T. confusum* strains and from 11.2% (in *cIII*) to 29.5% (in *c* “jet”) for *T. castaneum* strains (Tab. V).

A comparison of these results with meager data available from the literature is difficult because of different conditions in which the experiments were carried out. Nevertheless, some data of the present experiment can be compared with Sonleitner's (1961) observations.

This author reported that in *c* “Brazil” cultures with 32 density and 1:1 ratio, kept in temperature and humidity conditions similar to those in the present experiment, the number of adult beetles on the surface of the medium comprised 20% of the total on the 14th day of his experiment. In the present experiment with the same strain, 6.7% of females and 34.1% of males were on the surface of the medium on the 14th day for an average percentage of 20.4. The mean averages recorded from the 11th to 31st day are 28.6% (males) and 15.5 (females), or a combined mean average of 22.0% (Tab. V). The rather close similarity of these results suggests a conclusion on the recurrence of the observed phenomenon and, at the same time, proves the reliability of the method employed in the present paper despite the fact that it is a much simpler although perhaps a less precise method than Sonleitner's which involved the taking of pictures of the culture surface.

Another general regularity is that males of all the strains of both species appear on the surface of the medium in higher numbers than females (*bI*, where the opposite was observed, is an exception to this rule). This regularity is more clearly expressed in *T. castaneum* strains than in *T. confusum* strains (Tab. VII). In the case of emigrational ability, higher sex-specific differences were observed in *T. confusum* strains.

A comparison of surface numbers of males with those of females by analysis of variance showed significant differences in all the strains examined (Tab. VII). Ranking strains according to the decreasing differences between surface numbers of males and females, the following sequences are obtained: *T. confusum*: *bIV* – *bII* – *b* “ebony” – *b* “Chicago” – *bIII* (*bI* excluded). *T. castaneum*: *c* “jet” – *cI* – *cIII* – *cIV* – *cII* – *c* “Brazil”.

Summing up, it can be said that males of almost all strains of both species show higher emigration rates as well as higher surface numbers than those of females of corresponding strains. From this it can be inferred that in the two species of *Tribolium*, and also in their strains, males show higher general locomotory activity than females as regards emigrational ability and the incidence of surface numbers in the confined populations. This is in

Probability values for statistics F (by analysis of variance) of surface numbers of adult beetles: between sexes (on diagonal), between strains: males (above diagonal), females (below diagonal)

Tab. VII

	<i>T. confusum</i>						<i>T. castaneum</i>						
	<i>bI</i>	<i>bII</i>	<i>bIII</i>	<i>bIV</i>	<i>b</i> "Chicago"	<i>b</i> "ebony"	<i>cI</i>	<i>cII</i>	<i>cIII</i>	<i>cIII</i>	<i>cIV</i>	<i>c</i> "Brazil"	<i>c</i> "jet"
<i>bI</i>	< <u>.01</u>	< .01	< .01	< .01	< .01	< .01	<i>cI</i>	< <u>.01</u>	> .05	< .01	< .01	< .01	< .01
<i>bII</i>	< .01	< <u>.01</u>	< .01	< .01	< .01	< .01	<i>cII</i>	< .01	< <u>.01</u>	< .01	< .01	< .01	< .01
<i>bIII</i>	< .01	< .01	< <u>.01</u>	< .01	< .01	< .01	<i>cIII</i>	< .01	< .01	< <u>.01</u>	> .05	< .01	< .01
<i>bIV</i>	< .01	< .01	< .01	< <u>.01</u>	< .01	< .01	<i>cIV</i>	< .01	< .01	< .01	< <u>.01</u>	< .01	< .01
<i>b</i> "Chicago"	< .01	< .01	< .01	< .01	< <u>.01</u>	< .01	<i>c</i> "Brazil"	< .01	< .01	< .01	< .01	< <u>.01</u>	< .01
<i>b</i> "ebony"	< .01	< .01	< .01	< .01	< .01	< <u>.01</u>	<i>c</i> "jet"	< .01	< .01	< .01	< .01	< .01	< <u>.01</u>

accord with the literature data, e.g., those by Surtees (1963a, 1963b, 1963c). Studying the mobility of beetles of the *Curculionidae*, *Silvanidae*, *Tenebrionidae*, and *Cucujidae* families, and basing himself on other premises, Surtees reported higher activity of males compared with females of *Sitophilus granarius* (L.), *Oryzaephilus surinamensis* (L.), *Tribolium castaneum* (Herbst), and *Cryptolestes ferrugineus* (Steph.).

Differences in surface numbers

Productivity strains

In order to characterize the significance of differences of surface numbers among the productivity strains it can be said that of 24 comparisons made between pairs of strains by analysis of variance within each sex and species, only 2 differences are statistically insignificant: in males of *T. castaneum* strains (Tab. VII). In *T. confusum*, of 12 comparisons of mean surface numbers between strains carried out for males and females, all differences are statistically significant (Tab. VII).

In *T. castaneum*, of 12 analogous comparisons, 10 differences are statistically significant. Males of *cl* with *cII* and *cIII* with *cIV* differ insignificantly (Tab. VII).

In *T. confusum*, the strain sequences for males and females, ranked according to the diminishing mean surface numbers (given in parentheses) and marked with symbols: > – significant, ~ – insignificant, are as follows:

$$\delta\delta \text{ } bIV \text{ (8.24)} > bII \text{ (4.31)} > bIII \text{ (2.97)} > bI \text{ (2.17)},$$

$$\varphi\varphi \text{ } bI \text{ (5.52)} > bIII \text{ (1.85)} > bII \text{ (0.68)} > bIV \text{ (0.47)}.$$

In *T. castaneum*, such strain sequences for males and females of these strains are:

$$\delta\delta \text{ } cI \text{ (12.22)} \sim cII \text{ (11.71)} > cIII \text{ (6.87)} \sim cIV \text{ (6.78)},$$

$$\varphi\varphi \text{ } cII \text{ (6.79)} > cI \text{ (2.13)} > cIV \text{ (0.98)} > cIII \text{ (0.32)}.$$

For the period considered, the surface numbers of adult beetles observed were highest in males of *T. castaneum* productivity strains; they were lower in males of *T. confusum*, still lower in females of *T. castaneum*, and lowest in females of *T. confusum*.

In surface numbers of *T. confusum* strains the sequence of males is precisely the reverse of the sequence of females and it is also practically the reverse of the strain sequence according to diminishing productivity. In sur-

face numbers of *T. castaneum* the strains follow exactly the productivity sequence; this relation is also maintained in females, at least to the extent that two more productive strains show higher surface numbers than the two remaining ones. The accord of diminishing surface numbers of females of strains with the diminishing productivity strain sequence can probably suggest that the productivities of strains of both species are to certain extent dependent on the incidence of females present in the flour, and by this reversely dependent on the incidence of the female surface numbers.

To illustrate more clearly the differences between the productivity strains in surface numbers, percentage presentation is useful. Taking the highest mean values of surface numbers as 100%, the following percentages are obtained: in *T. confusum*

males: $bl - 26.3\%$, $bII - 52.3\%$, $bIII - 36.0\%$, $bIV - 100\%$;

and females $bl - 100\%$, $bII - 12.3\%$, $bIII - 33.5\%$, $bIV - 8.5\%$.

In strains of *T. castaneum*, the analogous percentages are as follows:

for males: $cl - 100\%$, $cII - 95.8\%$, $cIII - 56.2\%$, $cIV - 55.5\%$;

and females: $cl - 31.4\%$, $cII - 100\%$, $cIII - 4.7\%$, $cIV - 14.4\%$.

These percentages suggest that the highest differentiation as regards surface numbers is that among females of *T. confusum* and *T. castaneum* productivity strains, lower differentiation was found among males of *T. confusum*, and the lowest among males of *T. castaneum*.

Analyzing surface numbers of adult beetles of productivity strains with sex-specific differences ignored, the following sequences of strains are obtained ranking mean surface numbers (given in parentheses) from maximum to minimum, with significance of differences marked:

T. confusum $bIV (4.35) > bl (3.84) > bII (2.50) \sim bIII (2.41)$,

T. castaneum $cII (9.07) > cl (7.17) > cIV (3.88) \sim cIII (3.59)$.

Generally, it can be said that under the conditions of the present experiment, the strains of *T. castaneum* show a tendency to appear more abundantly on the surface of the medium than the strains of *T. confusum*.

In the productivity strains of *T. confusum*, an inverse relation can be easily noted between mean surface numbers of males and females. In other words: the higher the surface numbers of males in a given strain, the lower the surface numbers of females in this strain. For example, strain *bIV* in comparison with the other strains shows the highest mean surface numbers of males and, simultaneously, the lowest mean surface numbers of females. On

the other hand, strain *bI* shows the opposite relation: mean surface numbers of males are lowest as compared with the remaining strains, and those of females are highest. In the latter case this inverse relation prevails over the other regularity noted that males occur on the surface more abundantly than females.

It is difficult to give any biological interpretation of the above described relation. It seems, however, that it may represent a compensatory interaction between two component elements of the population, females and males, in their spatial utilization of the life environment.

In the light of the above described inverse relation between surface numbers of males and females in productivity strains of *T. confusum*, general characteristics of these strains which do not distinguish sex-specific differences, are of necessity somewhat artificial.

Probability values for statistics *F* (by analysis of variance) of surface numbers of adult beetles, with sex ignored, between strains of *T. confusum* (above diagonal) and of *T. castaneum* (below diagonal)

Tab. VIII

		<i>T. confusum</i>						
		<i>bI</i>	<i>bII</i>	<i>bIII</i>	<i>bIV</i>	<i>b</i> "Chicago"	<i>b</i> "ebony"	
<i>T. castaneum</i>	<i>cI</i>		< .01	< .01	< .01	< .01	< .01	<i>bI</i>
	<i>cII</i>	< .01		> .05	< .01	< .01	< .01	<i>bII</i>
	<i>cIII</i>	< .01	< .01		< .01	< .01	< .01	<i>bIII</i>
	<i>cIV</i>	< .01	< .01	> .05		< .01	< .01	<i>bIV</i>
	<i>c</i> "Brazil"	> .05	< .01	< .01	< .01		< .01	<i>b</i> "Chicago"
	<i>c</i> "jet"	< .01	> .05	< .01	< .01	< .01		<i>b</i> "ebony"
		<i>cI</i>	<i>cII</i>	<i>cIII</i>	<i>cIV</i>	<i>c</i> "Brazil"	<i>c</i> "jet"	

Among the productivity strains of *T. confusum*, strain *bIV* shows the highest mean surface numbers, differing in that from the remaining strains. The males determine the high rank of this strain since the females show the minimum surface numbers. Hence, the difference between females and males of this strain in surface numbers is the highest one (Tab. V, VII, and VIII).

Strain *bI* comes second and differs significantly from other genetic strains. It occupies second place owing to the very high surface numbers of females, the highest as compared with those of the remaining strains, while the surface numbers of males are very small, the smallest. This strain is an exception to a general rule that males appear more abundantly on the surface than females (Tab. V, VII and VIII).

Strain *bII* is third in turn. It does not differ significantly from *bIII* although separate comparisons of males and females between these two strains do show significant differences. This arises from the fact that strain *bII* is characterized by relatively high surface numbers of males and relatively low surface numbers of females, and this is the opposite in strain *bIII*. Strain *bII* shows relatively high difference in surface numbers between sexes, and in strain *bIII* this difference is the smallest one (Tab. V, VII and VIII).

Among the productivity strains of *T. castaneum*, *cII* beetles exhibit the highest tendency to stay on the surface of the medium and the mean surface numbers of *cII* differ significantly from those of other strains. Males of this strain hold second position as regards their surface numbers; they differ significantly in that from males of *cIII* and *cIV*, are similar to males of *cI*. Females of strain *cII* show the highest surface numbers, differing significantly from females of the remaining strains of this species. The difference between males and females is lowest in this strain as compared with other productivity strains of this species (Tab. V, VII, and VIII).

Strain *cI* ranks second, differing significantly from the other productivity strains; its males occur on the surface most abundantly, differing in that from males of strains *cIII* and *cIV*. It shows no significant difference, however, when compared with males of *cII*. Strain *cI* reveals the highest difference in surface numbers between males and females of all the productivity strains of *T. castaneum* (Tab. V, VII, and VIII).

Strains *cIV* and *cIII* show similar tendencies to appear on the surface although females of these two strains differ significantly. Females of *cIII* have the smallest surface numbers. The differences between surface numbers of both sexes in these two strains are of average value (Tab. V, VII, and VIII).

Wild strains and body-colour mutants

Comparison has been made between *b*"Chicago" and *b*"ebony" of *T. confusum*, and between *c*"Brazil" and *c*"jet" of *T. castaneum*. Strain *b*"Chicago" reveals a much higher tendency to occur on the surface of the medium than strain *b*"ebony" (Tab. V). The differences between these two strains, and also between their males and females, are significant (Tab. VII and VIII).

It is most interesting to compare these strains with the productivity strains. In strain *b*"Chicago" surface numbers, both of males and females, are higher than those of the *T. confusum* productivity strains, differing from them significantly. Here are also significant differences between the surface numbers of *b*"ebony" compared with those of the productivity strains. At the same time there is a general resemblance to strain *bI*, although its males show the closest resemblance to *bII*, its females to *bIII* (Tab. V, VII, and VIII).

Strain *c* "jet" shows a significantly higher tendency to stay on the surface of the medium as compared with *c* "Brazil" (Tab. V and VIII). The preponderance of this strain over the other is mostly due to very high surface numbers of its males (the highest of all the strains examined), since surface numbers of females are significantly lower than those of *c* "Brazil" females (Tab. V and VII).

Strain *c* "Brazil" is most similar to *cl*, although males *c* "Brazil" show significantly lower surface numbers and females *c* "Brazil" significantly higher surface numbers compared with the respective sexes of strain *cl* (Tab. V, VII, and VIII). When sex is ignored, however, there is no significant difference in surface numbers between these two strains (Tab. VIII). Although strains *c* "Brazil" and *cl* were the same initially, they apparently deviated from one another in this characteristic examined. Strain *c* "Brazil" (males, females, and also both sexes pooled together) differs significantly in surface numbers from the remaining productivity strains (Tab. VII and VIII).

Strain *c* "jet" shows the highest difference between surface numbers of both sexes, strain *c* "Brazil" – the lowest one. Males of *c* "jet" are most similar (although statistically different) to males of *cl* and *cII* and its females are most similar to those of *cl*. Generally, this strain is most similar (insignificant difference) to strain *cII* (Tab. V, VII and VIII).

Time changes in surface numbers

As is the case with emigrational ability, the surface numbers of strains of one species differ diametrically in their behaviour from those of the other species in the initial period of the experiment (Fig. 1B, 2B, and 3B).

In males of *T. confusum* strains, surface numbers of beetles were extremely high accounting sometimes to 100% of the total abundance during the first day following their introduction to a fresh medium. A rather rapid decrease in surface numbers followed within several (up to ten) days. Then the period of uniform level of surface numbers occurred with a slightly decreasing tendency. Only strain *b* "Chicago", both its males and females, shows a constant, rather clear, diminishing tendency in surface numbers lasting throughout the entire experiment (Fig. 1B and 3B).

Females of *T. confusum* strains after their introduction onto the surface of the medium also occur more abundantly on the surface at the beginning of the experiment, but their numbers usually do not exceed 50% of the total number introduced. Hence, in females there is a division of the diminishing emigration tendency into two periods: an initial period of a fast decrease followed by a later period of a slow, barely perceptible decrease in all but the *b* "ebony" and *bII* strains. In the remaining strains of this species, a uniform rate of disappearance of females from the surface of the medium is observed (Fig. 1B and 3B).

In *T. castaneum* strains, there are only small numbers of beetles on the surface of the medium at the beginning of the experiment, that is 24 hours after their introduction to the medium. Later on, the surface numbers of males increase considerably reaching their maximum between the 5th to 15th day of the experiment, at which time there begins a uniform decrease. Strain *cIII* is an exception, where a constant, uniform increase in surface numbers was noted throughout the entire of the experiment (Fig. 2B and 3B).

In females of *T. castaneum* strains, there is no maximum period of surface numbers except in two cases when the maxima coincide with those of the males (Fig. 2B and 3B).

The general trend of changes in surface numbers plotted against time (shape of the curve) follows that of changes reported by Sonleitner (1961) for strain *c* "Brazil" (64 pairs in 8 g of medium). The author in that study dealt with the correlation between decreasing real fecundity, interpreted as an effect of crowding, and surface numbers of adult beetles in relation to aging of beetles. He ascribed the vanishing of beetles from the surface with the elapse of time to adaptational changes found in conditions of overcrowding as well as to aging of beetles which was accompanied by decreasing mobility and general sensibility of these organisms. These two latter phenomena probably result in decreasing secretion of etylquinone by beetles (Sonleitner 1961).

Since the medium was not changed throughout the duration of the present experiment, it is impossible to separate the aging effect from the effect of

Equations for regression lines of surface numbers of adult beetles against time as drawn in Fig. 1B, 2B, and 3B (3)

Tab. IX

Strains	$y = ax + b$	
	males	females
<i>T. confusum</i>		
<i>bI</i>	$y = -0.2083x + 6.6143$	$y = -0.2136x + 9.9956$
<i>bII</i>	$y = -0.0267x + 4.8707$	$y = -0.0496x + 1.7312$
<i>bIII</i>	$y = -0.1386x + 5.8806$	$y = -0.1176x + 4.1496$
<i>bIV</i>	$y = -0.1372x + 11.3238$	$y = -0.0302x + 1.1242$
<i>b</i> "Chicago"	$y = -0.4845x + 22.8245$	$y = -0.4092x + 18.2532$
<i>b</i> "ebony"	$y = -0.1409x + 8.0789$	$y = -0.1376x + 4.3596$
<i>T. castaneum</i>		
<i>cI</i>	$y = -0.5435x + 23.6035$	$y = -0.1992x + 6.3132$
<i>cII</i>	$y = -0.7336x + 26.9556$	$y = -0.0196x + 6.3684$
<i>cIII</i>	$y = -0.1075x + 4.6125$	$y = -0.0109x + 0.5549$
<i>cIV</i>	$y = -0.2997x + 13.1237$	$y = -0.0205x + 1.4105$
<i>c</i> "Brazil"	$y = -0.4171x + 17.6791$	$y = -0.6173 + 0.4769x + 0.0028x^2 - 0.0004x^3$
<i>c</i> "jet"	$y = -0.4503x + 25.4563$	$y = -0.0845x + 4.5545$

Probability values of statistical comparisons (by t-student test) of regression coefficients "a" for surface numbers: between sexes (on diagonal), between strains: males (above diagonal), females (below diagonal)

Tab. X

	<i>T. confusum</i>						<i>T. castaneum</i>						
	<i>bI</i>	<i>bII</i>	<i>bIII</i>	<i>bIV</i>	<i>b</i> "Chicago"	<i>b</i> "ebony"		<i>cI</i>	<i>cII</i>	<i>cIII</i>	<i>cIV</i>	<i>c</i> "Brazil"	<i>c</i> "jet"
<i>bI</i>	< <u>.01</u>	< .01	< .01	> .05	< .01	> .05	<i>cI</i>	< <u>.01</u>	> .05	< .01	< .02	< .01	> .05
<i>bII</i>	< .01	> <u>.05</u>	< .05	> .05	< .01	> .05	<i>cII</i>	< .05	< <u>.01</u>	< .01	< .01	< .01	> .05
<i>bIII</i>	< .01	< .05	< <u>.01</u>	< .01	< .01	< .01	<i>cIII</i>	< .01	> .05	> <u>.05</u>	< .01	< .01	< .01
<i>bIV</i>	< .01	> .05	< .01	> <u>.05</u>	< .01	> .05	<i>cIV</i>	< .01	> .05	> .05	< <u>.01</u>	< .01	> .05
<i>b</i> "Chicago"	< .01	< .01	< .01	< .01	< <u>.01</u>	< .01	<i>c</i> "Brazil"	—	—	—	—	—	< .01
<i>b</i> "ebony"	> .05	< .01	< .01	< .01	< .01	< <u>.01</u>	<i>c</i> "jet"	< .05	> .05	< .02	> .05	—	< <u>.01</u>

increasing conditioning of the medium on the course of surface numbers. It appears, however, that the slight decrease in surface numbers observed in the later period speaks in favour of Sonleitner's interpretation, especially if one notes that it occurs in both species which differ diametrically in their responses to the conditioning of medium.

A mathematical analysis was carried out of the time-specific variation in surface numbers by calculating adequate regression lines for particular strains. The regression lines were determined by a method of minimum squares for the period from the 11th to 31st day of the experiment (Fig. 1B, 2B, 3B, and Tab. IX). In this period, there is a linear dependence between time function and surface numbers in all strains of two species (Fig. 1B, 2B, 3B, and Tab. IX). Only females of *c*"Brazil" show a curvilinear dependence of the third degree. The curvilinear character of this function can be explained by the presence of large larvae in these cultures on account of methodical error (Fig. 3B).

Differences in regression coefficients of the calculated lines are, in the majority of cases, statistically significant, both between sexes within each strain, and between strains within each sex of each species, which points to the unparallelled courses of these lines (Tab. X).

In *T. confusum*, of 6 comparisons of regression coefficients between sexes of strains, 4 differences are statistically significant, insignificant differences being those between males and females of strains *bII* and *bIV* (Tab. X). Of 5 analogous comparisons in *T. castaneum*, 4 differences are statistically significant. Only in strain *cIII*, the coefficients for females and males differ insignificantly (Tab. X).

When comparing the regression coefficients of surface numbers of males of productivity strains of *T. confusum*, out of 6 cases examined, 4 differences are statistically significant (with one borderline difference). Insignificant differences are those between males of the strain pairs: *bI* - *bIV* and *bII* - *bIV*. Of analogous 6 comparisons between females of productivity strains of *T. confusum*, 5 differences are statistically significant (with one borderline case). The coefficients for females *bII* and *bIV* do not differ significantly (Tab. X).

In *T. castaneum*, out of 6 comparisons of regression coefficients between males of productivity strains, 5 differences are statistically significant. An insignificant difference is that between males of *cI* and *cII*. Of 6 analogous comparisons between females of productivity strains of *T. castaneum*, 3 differences are significant. Insignificant differences are those between the coefficients for females of the following strain pairs: *cII* - *cIII*, *cII* - *cIV*, and *cIII* - *cIV* (Tab. X).

When checking the significance of differences between regression coefficients for wild strains and body-colour mutants, a significant difference was observed between strains *b*"Chicago" and *b*"ebony" (both between their males and females) as well as between males of *c*"Brazil" and *c*"jet" (Tab. X). The

regression coefficients, both for males and females of strain *b* "Chicago", are significantly different, being higher than the coefficients of all 4 productivity strains of *T. confusum*. On the other hand, the regression coefficient for males of *b* "ebony" differs significantly only from that of males of *bIII*, and the analogous coefficient for females of *b* "ebony" is significantly different from those of females *bII*, *bIII*, and *bIV*. The coefficient for males *c* "Brazil" differs significantly from analogous coefficients for males of all four productivity strains of *T. castaneum* (females *c* "Brazil" were excluded from this comparison). The coefficient for males of *c* "jet" differs significantly only from that of males of *cIII*, and the regression coefficient for females *c* "jet" differs significantly only from those of females *cI* and *cIII* at the borderline level (Tab. X).

The results of comparative analysis of regression coefficients given above lead to a conclusion that the productivity strains and also the wild strains and body-colour mutants of both species examined differ in one more feature, namely, in the rate of disappearance of adult beetles from the surface of the medium, expressed as a function of time. However, the linear character of the dependence between time function and surface numbers is a common feature for both sexes of all strains examined.

CORRELATION BETWEEN SURFACE NUMBERS AND EMIGRATION RATES

The next aim of this paper was to study presumed correlation between surface numbers and emigration rates of adult beetles. Calculations were based only on the material of the first series of the experiment. On account of earlier discussed premises, the initial period of the experiment (2nd day) was excluded from the analysis; this period, when taken into consideration, would have obscured the presumed correlation that can exist in the later continuation of the experiment.

Correlation was searched in the material arranged in two levels: firstly, at the strain level (separately for males and females), and secondly, at the species level (also separately for males and females) (Tab. XI). In the first case, there were 30 numerical values for each sex of a given strain (15 values for *cII*) — denoting surface numbers which corresponded to 30 values of emigration rates (10 replicates x 3 time points: 10th, 20th, and 30th day of the experiment). Surface numbers were characterized by averages from two consecutive morning observations taken on the day preceding installation of the emigration sets and just before the sets were connected with the cultures. Thus, the correlation at this level concerns numerical (10) and time (3) replications within each sex of each strain.

Coefficients of correlation between surface numbers and emigration rates of adult beetles

Tab. XI

	<i>n</i>	<i>r</i> correl. index	<i>P</i> Probability	<i>n</i>	<i>r</i> correl. index	<i>P</i> Probability
♂ ♂				♀ ♀		
<u>Correlation at the strain level</u>						
<i>T. confusum</i>						
<i>bI</i>	30	.509	< .01	30	.447	< .02
<i>bII</i>	30	.192	> .05	30	.059	> .05
<i>bIII</i>	30	.394	< .05	30	.590	< .01
<i>bIV</i>	30	.313	> .05	30	-.037	> .05
<i>b</i> "Chicago"	30	.595	< .01	30	.619	< .01
<i>b</i> "ebony"	30	.178	> .05	30	.713	< .01
<i>T. castaneum</i>						
<i>cI</i>	30	.298	> .05	30	.487	< .01
<i>cII</i>	15	.239	> .05	15	.488	> .05
<i>cIII</i>	30	.118	> .05	30	.216	> .05
<i>cIV</i>	30	.187	> .05	30	.091	> .05
<i>c</i> "Brazil"	30	.337	> .05	30	.759	< .01
<i>c</i> "jet"	30	.000	> .05	30	.564	< .01
<u>Correlation at the species level</u>						
<i>T. confusum</i>	18	.369	> .05	18	.729	< .01
<i>T. castaneum</i>	18	.404	> .05	18	.772	< .01

In the second case, the correlation between surface numbers and emigration rates was tested jointly for six strains of each species, though separately for males and females. By this means it could be determined whether the strains with lower surface numbers also show a lower emigrational ability and vice versa. To calculate this correlation, the averages from 10 replicates considered in the previous correlation were used for 3 time points (10th, 20th, and 30th day of the experiment). Thus, for each sex of each species, 18 pairs of values were obtained (3 time points x 6 strains). Sixteen classes, 0-2, 2.1-4, etc., were accepted both for surface numbers and for emigration rates. The correlation indices were then calculated and their significance was estimated according to the *t* values calculated from the formula:

$$t = \sqrt{\frac{n-2}{1-r^2}}$$

Probability values of statistical comparisons (by t-student test) of significant correlation indices, between sexes (on diagonal) and between strains: males (above diagonal), females (below diagonal)

Tab. XII

	<i>T. confusum</i>							<i>T. castaneum</i>					
	<i>bI</i>	<i>bII</i>	<i>bIII</i>	<i>bIV</i>	<i>b</i> "Chicago"	<i>b</i> "ebony"		<i>cI</i>	<i>cII</i>	<i>cIII</i>	<i>cIV</i>	<i>c</i> "Brazil"	<i>c</i> "jet"
<i>bI</i>	> <u>.05</u>	—	> .05	—	> .05	—	<i>cI</i>	> <u>.05</u>	—	—	—	—	—
<i>bII</i>	—	—	—	—	—	—	<i>cII</i>	> .05	> <u>.05</u>	—	—	—	—
<i>bIII</i>	> .05	—	> <u>.05</u>	—	> .05	—	<i>cIII</i>	—	—	—	—	—	—
<i>bIV</i>	—	—	—	—	—	—	<i>cIV</i>	—	—	—	—	—	—
<i>b</i> "Chicago"	> .05	—	> .05	—	> <u>.05</u>	—	<i>c</i> "Brazil"	> .05	> .05	—	—	> <u>.05</u>	—
<i>b</i> "ebony"	> .05	—	> .05	—	> .05	< <u>.05</u>	<i>c</i> "jet"	> .05	> .05	—	—	> .05	< <u>.05</u>

where: r – correlation index, n – number of observations. This statistic has a t-student distribution with $(n - 2)$ degrees of freedom. The probability level of 0.05 was accepted as significant. Further, the significance was tested of the differences in the correlation indices between males and females for the strains as well as between pairs of strain (within sexes) whose correlation indices proved to be significant (Tab. XII).

All but one (females *bIV*) of the correlation indices have positive values. Hence, there seems to be a certain positive correlation between surface numbers and the emigrating numbers of adult beetles. However, this correlation is not always significant. In males and females of 6 strains of *T. confusum*, 7 correlation indices out of 12 showed statistical significance. Significant indices were obtained for males of *bI*, *bIII* (borderline), *b*“Chicago” and for females of *bI* (borderline), *bIII*, *b*“Chicago” and *b*“ebony”. The correlation indices for females were usually higher than those for males (Tab. XI).

In males and females of 6 strains of *T. castaneum* out of 12 indices calculated, only 3 are significant. All indices calculated for males proved to be insignificant. The significant correlation was found for females *cI*, *c*“Brazil”, and *c*“jet”. The correlation index for females *cII* shows almost borderline significance (Tab. XI).

When considering the second type of correlation, at the species level, a significant, positive correlation was observed for females of both species, whereas the correlation indices for males of both species proved to be insignificant (Tab. XI).

The comparison of the significant correlation indices of males and females within each strain (Tab. XII) showed that they do not differ significantly in 6 cases out of 8 tested. Borderline significance was observed in strains *b*“ebony” and *c*“jet”. The comparison of the significant correlation indices between strains (within each sex) of both species showed insignificant differences (Tab. XII). These two facts are evidence that if there is a positive correlation between surface numbers and emigration rates, it is a rather similar one for males and females as well as for different strains.

Summing up, it can be said that under the conditions of the present experiment, a certain, positive correlation between surface numbers and emigrating numbers was found to exist. This correlation however is usually significant only in females.

The finding of a positive correlation between surface numbers of females and their emigrational tendencies along with generally very low emigrational abilities of females, and also the lack of such a correlation in males, suggest the following reasoning and statements. The appearance of adult beetles on the surface of the medium is a feature less typical for females than males. Females, kept in mono-sex cultures, come up to the surface of the medium with

an apparent inclination to leave the surface which they do whenever a possibility arises. The appearance of males on the surface of the medium is something typical for this sex. Although they do appear on the surface of the medium, they are not always inclined to leave it.

The above reasoning supports the effectiveness of the method employed in this paper to study emigrational abilities of the strains.

CONCLUSIONS

1) Both sexes of all the strains examined of *T. confusum* and *T. castaneum* show a tendency to leave their life environment, provided that they have a possibility to do so.

2) Under conditions of this experiment, both males and females of all the strains examined occur continuously on the surface of the medium in certain proportions.

3) The emigrational rate is differentiated and for the conditions of the present experiment it ranges from 5.2% per 24 hours to 87.3% in males and females of *T. confusum* strains, and from 38.0% to 86.6% in males and females of *T. castaneum* strains. The emigrational rate when sex is ignored ranges from 32.2% to 69.7% for *T. confusum* strains, and from 41.3% to 79.8% for *T. castaneum* strains.

The overall analysis of variance proved that there were significant strain and sex effects in emigrational ability of *T. confusum* and *T. castaneum*.

4) The occurrence of adult beetles on the surface of the medium is also differentiated by strains and sexes and for the period examined it ranges from 1.5% to 40.8% for both sexes of *T. confusum* strains and from 1.0% to 50.1% for both sexes of *T. castaneum* strains. The differentiation of surface numbers when sex is ignored ranges from 7.6% to 34.9% for *T. confusum* strains and from 11.2% to 29.5% for *T. castaneum* strains.

The overall analysis of variance showed that in *T. confusum* and in *T. castaneum* both the strain and sex effects were significant.

5) Males of all but one strain (*cIV*) of both species show higher emigration rates than females of corresponding strains, the differences in emigrational ability observed between males and females in strains of *T. confusum* being higher (all differences statistically significant) than in strains of *T. castaneum* (only two differences significant).

6) Similarly, surface numbers of males are higher than those of females of corresponding strains (*bI* is an exception).

The differences are slightly higher in *T. castaneum* strains than in *T. confusum* strains, although statistically significant in all strains of both species.

7) The two latter findings indicate that in two species of *Tribolium* genus examined, and also in their strains, males show higher general locomotory activity than females, as measured by emigrational ability and the incidence of surface numbers in the confined populations.

8) Males and females of the productivity strains, ranked according to decreasing mean values of emigration rates, with the significance of differences marked with symbols, give the following strain sequences: *T. confusum*, males: $bI \sim bIII > bIV \sim bII$, females: $bI > bIII \sim bII > bIV$; *T. castaneum*, males: $cI \sim cII > cIV > cIII$, females: $cII > cI \sim cIV > cIII$. When sex is ignored the sequences are the following: *T. confusum*: $bI \sim bIII \sim bII > bIV$, *T. castaneum*: $cII \sim cI > cIV > cIII$.

9) Similar strain sequences can be presented when ranking males and females of the productivity strains according to their surface numbers, from maximum to minimum, with symbols denoting significance of differences: *T. confusum*, males $bIV > bII > bIII > bI$, females: $bI > bIII > bII > bIV$; *T. castaneum*, males: $cI \sim cII > cIII \sim cIV$, and females: $cII > cI > cIV > cIII$.

10) In surface numbers of *T. confusum* strains, the sequence of males is precisely the reverse of the sequence of females, and it is also practically the reverse of the strain sequence arranged according to diminishing productivity. In surface numbers of males of *T. castaneum*, the strains follow exactly the productivity sequence; this relation is also maintained in females, at least to the extent that two more productive strains show higher surface numbers than the two remaining ones. Besides, in productivity strains of *T. confusum*, the following relation was noted: the higher the surface numbers of males in a given strain, the lower the surface numbers of females in that strain, and vice versa, which may be interpreted as a compensating action of two population elements, males and females, in spatial utilization of the environment by these strains.

11) Wild strains and body-colour mutants show rather high emigrational abilities and also high surface numbers as compared with the other strains of the corresponding species.

12) Analyzing emigrational abilities and surface numbers of strains against time, different patterns of time-specific changes were observed for both species in the initial period of the experiment, followed by a similar trend for both species in a later period (10th–31st day of the experiment), when a uniform level with a slightly decreasing tendency was noted (with some exceptions). Different responses of the two species to a new medium seem to account for different patterns of time-specific changes in surface numbers and emigrational abilities observed in the period following directly the introduction of adult beetles to the fresh medium.

13) Calculating regression lines for the period of the 11th–31st day of the experiment, a linear dependence was found between time function and surface

numbers of adult beetles in the strains of both species examined. In the majority of cases, significant differences were observed between coefficients of regression lines between sexes and strains. Hence, the steepness of the regression lines of surface numbers, as measured by regression coefficients is still one more feature which differs the genetic strains examined.

14) Examining the dependence between surface numbers and the intensity of emigration at two levels (strain, species), a positive correlation was ascertained between these two parameters. The correlation indices for females were generally higher than those for males. A higher number of significant cases of correlation was noted for females and males of *T. confusum* strains than those of *T. castaneum*, where for males all correlation indices were insignificant. At the species level, a positive correlation was found only for females of both species, while the correlation indices for males proved to be insignificant.

SUMMING UP

The work has been carried out on the material of 12 strains of *Tribolium confusum* Duval and *T. castaneum* Herbst. These were the following: 4 productivity strains of *T. confusum*: *bI*, *bII*, *bIII*, *bIV*, 1 wild strain *b* "Chicago", 1 homozygous body-colour mutant of this species – *b* "ebony" as well as 4 productivity strains of *T. castaneum*: *cI*, *cII*, *cIII*, *cIV*, 1 wild strain – *c* "Brazil", and 1 homozygous body-colour mutant of this species, according to the nomenclature by Park (Park, Mertz, and Petruszewicz 1961; Park, Leslie, and Mertz 1964).

The objective of the paper was to study emigrational tendencies of adult beetles, males and females, of the above listed strains of *T. confusum* and *T. castaneum* as well as to characterize the incidence of adult beetles on the surface of the medium in the confined populations of these strains, represented by each sex separately. The further objective was to analyze a presumed correlation between surface numbers and emigrational tendencies of the strains examined.

The emigrational tendency was taken as the ability of adult beetles to leave their life environment, flour, provided that such a possibility was open to them. This was achieved by temporal connection (24 hrs) with a simple device – an emigration testing set which consisted of an empty vial connected with a culture vial by means of a plastic tube with a cotton thread passing through it.

The number of adult beetles that left their life environment and its surface within 24 hrs, (the environment consisting of 8 g of wheat flour and powdered yeast with a 95:5 weight ratio) was accepted as an index of emigrational ability. The percentage index of emigrational ability was calculated as the ratio of this number to the initial number of beetles which was always 32 individuals.

The emigrational tendencies of beetles were tested 4 times in ten-day intervals during the experiment which lasted 31 days.

Surface numbers of adult beetles were characterized by number of beetles present on the surface of the medium during two direct observations of cultures taken daily at 9 and 15 o'clock.

The experiment was carried out in an almost dark incubator at a temperature of $29.0^{\circ}\text{C} \pm 0.02$, and relative humidity of about 70%.

A detailed description was given of the productivity strains concerning the intensity of emigrational ability of males and females of these strains. A conspicuous differentiation in emigrational ability was ascertained between sexes and among strains of both species. Males of almost all strains examined showed higher emigrational tendencies than females.

A detailed analysis was given of the surface numbers of productivity strains by comparing them within each sex and species. Significant differences were found in surface numbers of adult beetles between sexes and among strains of both species. Males occur more abundantly on the surface of the medium than females.

Analyzing time variation of surface numbers, different patterns of time-specific changes were observed for both species in the initial period of the experiment, followed by a similar trend for both species in a later period, when a uniform level of surface numbers was noted with a slightly decreasing tendency.

An analysis was also made of the correlation between surface numbers and the intensity of emigration at two levels: the strain and species level, and separately for both sexes. A positive correlation was ascertained, significant chiefly for females.

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TENDENCJE EMIGRACYJNE CHRZĄSZCZY DOROSŁYCH ORAZ PRZEBYWANIE ICH
NA POWIERZCHNI SUBSTRATU HODOWLANEGO U 12 SZCZEPÓW GATUNKÓW:
TRIBOLIUM CONFUSUM DUVAL I *T. CASTANEUM* HERBST
(COLEOPTERA, TENEBRIONIDAE)

Streszczenie

Prace wykonano na materiale 12 szczepów *Tribolium confusum* Duval i *T. castaneum* Herbst. Były to: 4 szczepy *T. confusum* charakteryzujące się różną produktywnością: *bI*, *bII*, *bIII*, *bIV*, dziki szczep – *b*“Chicago”, homozygotyczny czarny mutant tego gatunku – *b*“ebony” oraz 4 szczepy *T. castaneum* wyróżnione również w oparciu o kryterium produktywności: *cI*, *cII*, *cIII*, *cIV*, szczep dziki – *c*“Brazil” i homozygotyczny czarny mutant tego gatunku – *c*“jet”, wg nomenklatury Parka (Park, Mertz, Petruszewicz 1961; Park, Leslie, Mertz 1964).

Zbadano tendencje emigracyjne chrząszczy dorosłych, samców i samic wyżej wymienionych szczepów *T. confusum* i *T. castaneum* oraz scharakteryzowano ich stopień przebywania na powierzchni substratu hodowlanego w hodowlach zamkniętych, reprezentowanych przez każdą płć oddzielnie. Dalszym celem pracy było szukanie korelacji między liczbą chrząszczy przebywających na powierzchni substratu hodowlanego a nasileniem tendencji emigracyjnych szczepów.

Przez tendencje emigracyjne chrząszczy określono zdolność chrząszczy dorosłych do opuszczenia swojego środowiska życiowego, o ile umożliwi im się wychodzenie z zamkniętej hodowli. Opuszczanie środowiska życiowego, będącego mieszaniną mąki pszennej i drożdży (w stosunku wagowym 95:5), umożliwiano chrząszczom przez okresowe, na czas 24 godzin, zakładanie prostego urządzenia, składającego się z dodatkowej pustej próbki połączonej z hodowlą za pomocą rurki plastikowej z przechodzącą przez nią nitką. Za wskaźnik tendencji emigracyjnej przyjęto liczbę chrząszczy, które w ciągu 24 godzin opuściły środowisko i jego powierzchnię. Procentowy wskaźnik tendencji emigracyjnej stanowił stosunek tej liczby do wyjściowej liczby chrząszczy, wynoszącej zawsze 32 osobniki jednej płci. Tendencje emigracyjne chrząszczy badano czterokrotnie w odstępach czasowych dziesięciodniowych podczas eksperymentu trwającego 31 dni.

Przebywanie chrząszczy dorosłych na powierzchni substratu hodowlanego charakteryzowano liczbą chrząszczy znajdujących się na powierzchni substratu w czasie dwukrotnych w ciągu dnia (o godz. 9 i 15) bezpośrednich obserwacji.

Doświadczenie przeprowadzono w termostacie w temperaturze $29,2^{\circ}\text{C} \pm 0,02$ i wilgotności względnej około 70%.

Podano szczegółową charakterystykę szczepów pod względem nasilenia tendencji emigracyjnych samców i samic tych szczepów (tab. I). Stosując metodę analizy wariancyjnej wykazano w oparciu o test Fishera istotność wpływu płci i szczepu na tendencje

emigracyjne badanych chrząszczy obu gatunków (tab. II). Samce niemal wszystkich badanych szczepów wykazywały większe tendencje emigracyjne niż samice (tab. I i III). Stwierdzono istnienie wyraźnego zróżnicowania tendencji emigracyjnych pomiędzy poszczególnymi szczepami w obrębie każdej płci i gatunku (tab. III i IV).

Podano szczegółową charakterystykę szczepów pod względem przebywania na powierzchni substratu (tab. V). Za pomocą analizy wariancyjnej i testu Fishera wykazano silny, istotny wpływ płci i szczepu na liczebność chrząszczy przebywających na powierzchni hodowlanego substratu (tab. VI).

Porównując między sobą szczepy w obrębie każdej płci i każdego gatunku, stwierdzono wyraźną różnicę w liczebności chrząszczy dorosłych przebywających na powierzchni substratu między płciami i szczepami u obu gatunków (tab. VII i VIII). Samce występują na powierzchni substratu znacznie liczniej niż samice (tab. VII).

Analizując zmienność czasową liczby chrząszczy przebywających na powierzchni substratu, stwierdzono różny jej przebieg w zależności od gatunku w początkowym okresie eksperymentu i wspólny dla szczepów obu gatunków, polegający na wystąpieniu dość wyrównanego poziomu liczebności z lekką tendencją spadkową w późniejszym okresie eksperymentu (fig. 1B, 2B i 3B).

Wyznaczając funkcję prostych regresji metodą najmniejszych kwadratów, stwierdzono liniową zależność między funkcją czasu a liczbą chrząszczy dorosłych, przebywających na powierzchni substratu hodowlanego u obu płci niemal wszystkich szczepów obu gatunków (fig. 1B, 2B, 3B i tab. IX). Wyniki porównawczej analizy współczynników nachylenia kąтового wyznaczonych prostych regresji wskazują, iż szczepy wyróżnione na podstawie kryterium produktywności, jak również szczepy dzikie i barwne mutanty, różnią się między sobą pod względem jeszcze jednej cechy, tj. pod względem przedstawionego w funkcji czasu tempa zanikania chrząszczy na powierzchni substratu hodowlanego (Tab. X).

Dokonano również analizy korelacji między liczbą chrząszczy występujących na powierzchni substratu a nasileniem tendencji emigracyjnych oddzielnie dla obu płci na dwu poziomach: szczepu i gatunku. Stwierdzono istnienie dodatniej korelacji, istotnej głównie u samic (tab. XI), o podobnej wartości wskaźników korelacji u obu płci szczepów obu gatunków (tab. XII).

AUTHOR'S ADDRESS:

M.Sc. Tadeusz Prus
Institute of Experimental Biology
Warszawa, ul. Pasteura 3, Poland.