

Evolutionarily stable strategies in competition for resource intake rate maximization

II. Oviposition behavior in *Tribolium confusum*

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Received June 23, 1988 / Accepted February 7, 1989

Summary. This paper presents an empirical study concerned with the question whether animals competing by resource exploitation can estimate the relative sizes of their opponents and modify their own behavior accordingly. Females of flour beetles *T. confusum* competed for limited oviposition sites. The problem addressed was: can the asymmetry in size and hence in the rate of egg laying determine the decisions of competitors about leaving or staying together? The results reveal that females of flour beetles do recognize their relative sizes and apply a “common sense” strategy, whereby smaller competitors withdraw. The procedure applied in the experiments allowed a standardization of the animals, where size was the sole phenotypic difference. It is possible that the ability to estimate opponent's size is innate, and, therefore, previous experience is not necessary.

Introduction

When a group of animals exploit a limited resource then every individual is faced with the question: is emigration a better alternative than joint exploitation? With the aid of a simple mathematical model (Korona 1989), I analyzed whether competition between unequal individuals promotes the evolution of the ability to estimate competitor size or other characteristics in order for the individual to apply this information to migration decisions. This model shows that the factors determining animals' decisions are (1) population density and (2) size differences between competitors. When the chance of finding a free patch of resource is high (low population density), the gains expected for each competitor after leaving a patch can be higher

than sharing the patch. If this holds true, there may be several ESS's, including conventional (e.g., based on ownership) and paradoxical ones (e.g., bigger competitors withdraw). In this case the existing asymmetry serves as information that is used to avoid less efficient joint exploitation. In a higher population density, when only poorer competitors would profit by leaving a patch, a unique “common sense” ESS exists, i.e., smaller competitors withdraw. Finally, with very high density, joint exploitation becomes the best solution for every individual. All these conclusions suggest that in competition by exploitation animals can be expected to take into account their relative sizes.

To test this hypothesis, I used pairs of females of *T. confusum* differing in size. They were left with a small amount of medium (later called a “patch”) in which they could lay eggs. The individual resource shares in joint exploitation were estimated by assuming them to be proportional to oviposition efficiency. The fitness of individuals was lowered both by the necessity to share resources and by egg cannibalism. At defined time intervals over a period of 4 days, I recorded which individuals occupied the oviposition place and which of them walked outside this patch of resource. The time that elapsed from the beginning was assumed to be a cue for the animals that it was becoming increasingly difficult to find a new oviposition site. The situation thus resembled an increase in population density.

From the theoretical model presented elsewhere (Korona 1989) and briefly described above, two results were expected. First, that females would be more and more inclined to occupy the patches during the experiment. Second, that bigger individuals would be more often recorded within patches. Should bigger competitors prevail during

the whole experiment (in different "densities") then this strategy would be called a size-based and "common sense" one (Korona 1989). The ecology and behavior of *T. confusum* are well known (Sokoloff 1974); aggressive behavior between adults has never been observed. This feature is a major advantage of using this species in such a study, because differences in migration decisions can be expected to be the result of the asymmetry in the rate of resource exploitation and not the result of fights.

The possible predomination by bigger females might, however, be explained in several alternative ways. The first explanation could be called "physiological". It assumes that smaller individuals do not occupy as much resources as bigger ones because they are underdeveloped or their requirements are lower. Another possibility is that smaller individuals tend to be more migratory in every competitive situation regardless of opponents' size. Still another alternative is that size does not correlate with competitive ability, i.e., bigger females do not lay more eggs or smaller females cannibalize the opponents' eggs more vigorously. All the mentioned hypotheses were tested in control experiments presented in this study.

Methods

Laboratory population

A laboratory population of *T. confusum* was established by hybridization of two laboratory strains and one strain taken from a bakery. Subsequently, beetles were kept in groups of several hundred (always over 500) for over 2 years in standard laboratory conditions: medium of 95% wheat flour and 5% baker's yeast, temperature $29 \pm 1^\circ \text{C}$, relative humidity $70\% \pm 3\%$. All experiments were carried out under the same conditions.

Preparation of experimental material

About 300 adults of both sexes were taken from the main culture; they laid eggs within 24 h. These eggs were placed in the standard medium with a density of 1 egg/g. After 17 days, larvae were divided at random into two groups. One of these groups was placed in the medium to grow and pupate (later called "large"). The remaining larvae were placed separately into empty vials in order to obtain smaller pupae ("small"). Emerging imagines were collected and kept for 14 days in size-homogeneous groups at a density of 1 individual/g. Females of *T. confusum* need 9 days to complete maturation (Sokoloff 1974). Adults were sexed by detecting oviposition. In the experiment only those females were used that were able to lay eggs in normal numbers (4 and more per day) and were of normal appearance. Animals used in the main experiment and in the first control (C1) were taken at random from the same pool. These two experiments were carried out simultaneously, and the vials used in both experiments were placed at random in the same incubator. Therefore, C1 can be regarded as a control of the main experiment. Other experiments were carried out

later, but the same procedure was applied. These experiments will be also called "controls", because their purpose is to test alternative hypotheses.

Procedure of the main experiment

For this experiment I used glass vials, diameter 35 mm. Their bottoms were covered with an acrylic color and oak sawdust to make the surface rough, thus allowing the beetles to walk easily. A vertical paper tube, height 10 mm and diameter 6 mm, was placed in the center of each vial, and the medium (0.12 g) was put inside. In each of 128 experimental vials there were two randomly paired females, one "large" and one "small", which were used in the experiment only once. Each of two females had a dot of a different color in the center of its back. An individual was classified as being out of the medium when its dot was visible. The animals' positions inside and outside the medium were recorded every 12 h for 4 days. After the experiment, all eggs remaining in the medium and on the inside of walls of the paper tubes were counted in 30 randomly chosen vials. At the same time, 30 large and 30 small females from the experimental series C1 were weighed.

Procedures of control experiments

Single females (C1). Similar procedures as described above were applied also in controls C1 and C2. However, in C1 there was only one beetle per vial. In this experiment 60 large and 60 small females were used. Half of the individuals from each of these two groups were weighed at the end of the experiment, and the weights were pooled together with those from the main experiment. Eggs were counted in 30 vials with large and 30 vials with small females.

Pairs of similar-sized females (C2). In these series, 22 pairs of large females and 22 pairs of small ones were used. Animals were individually marked. After the experiment, all individuals were weighed, and eggs were collected from all paper tubes.

Oviposition rate (C3). In this control, 25 large and 25 small females were placed individually into glass vials, diameter 17 mm and height 35 mm, with 2.50 g of the medium for 4 days in order to estimate their maximum rate of egg production. Then the data on body weight as well as number of eggs and total weight of eggs were recorded for every vial.

Egg cannibalism rate (C4). Five eggs and one female predator were placed in a paper tube with medium (identical as in the main experiment) for 12 h. Half of the females used in this series, i.e., 16 large and 16 small ones, encountered their own eggs in the first trial; in the second trial, after one day pause, they encountered strangers' eggs. The remaining females were tested in the reverse order. Eggs were exchanged within pairs composed of one large female and one small female. After the experiment, all eggs (both remaining and newly laid) were collected and placed in an incubator. The eggs left to be cannibalized were 3 days old; therefore, it was possible to distinguish them from the predator's own eggs by the time of hatching.

Results

Experimental series

Figure 1 presents the oviposition behavior of experimental pairs during eight consecutive recordings. The number of vials where both competitors

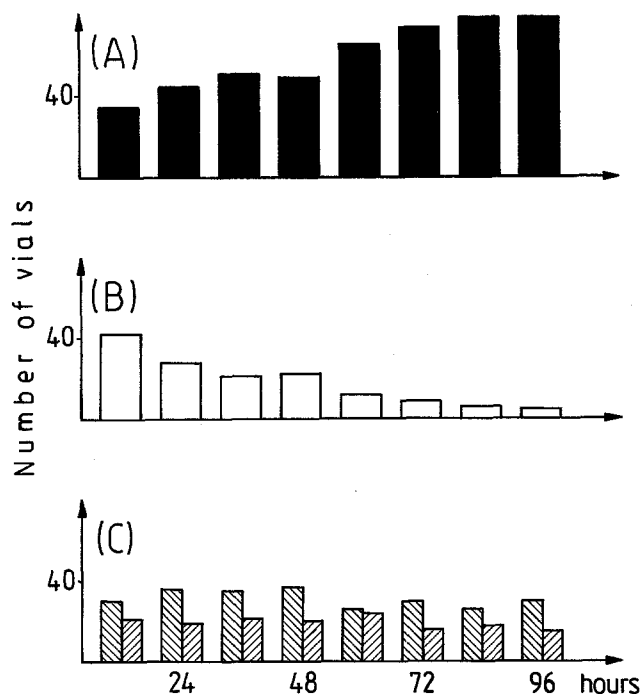


Fig. 1. Every 12 h the state of 128 vials with pairs of females was recorded. The bars represent the sums of consecutive scores for four possible events: both females occupy the oviposition site (A), both of them are outside (B), and when only one individual is inside (C) this can be a "large" one (the left hand bars in pairs) or a "small" one (the right bars)

stay together within the oviposition site increases with time ($r_s = 0.997$, $n = 8$, $P < 0.001$). Conversely, the number of vials where both females are outside the patch decreases ($r_s = -0.976$, $n = 8$, $P < 0.001$). It is noteworthy that during the whole experiment, the number of large females (2.79 ± 0.21 mg) occupying the medium alone is higher than that of small ones (1.99 ± 0.29 mg), as is shown in Fig. 1C. A simple test, two-tailed binomial distribution, reveals that such an event could hardly be produced by chance ($p = 0.5$, $n = 8$, $P = 1/128$).

The last finding, i.e., that large females occupy resource patches more frequently than small ones can be examined quantitatively. In order to verify it, I counted how many times (a maximum of 8) each individual was inside the oviposition site, and I compared these numbers for all 128 pairs. Large are more often recorded as being inside ($F = 15.586$, $df = 1$, 126 , $P < 0.001$, two-way ANOVA).

Control experiments

Single females (C1). When large and small females were placed separately into the vials, size did not affect the frequency of being found inside the medi-

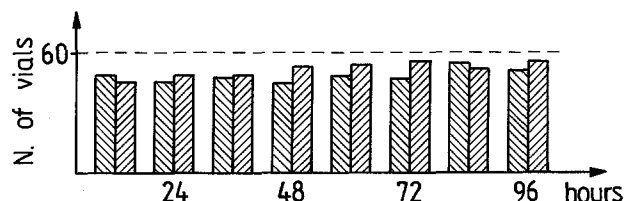


Fig. 2. In control C1, each female was placed separately into the experimental vial. In every pair of bars, the left one shows how many large females (out of 60) were inside a medium. Analogous score for small ones is given by the right bar

um ($F = 1.23$, $df = 1$, 118 , NS, ANOVA). The intensity of medium occupation was almost constant and similar for these two groups (Fig. 2).

The numbers of eggs found after the main experiment and control C1 series were compared. There were three classes: experimental "pairs" (2.13 ± 1.81 eggs), single "large" from C1 (5.60 ± 3.44) and single "small" from C1 (6.43 ± 3.41). Differences are significant ($F = 16.71$, $df = 2$, 87 , $P < 0.001$). Pairs leave fewer eggs than either large ($LSR = 1.56$, $P < 0.05$, Student-Newman-Keuls test) or small females alone ($LSR = 1.87$, $P < 0.05$). Thus, the presence of an opponent considerably reduces number of eggs found. There are no differences within the control between large and small individuals ($LSR = 1.56$, NS), thus the patches seem to be of similar value to them.

In experiment C1, 41% of large females and 50% of small ones were found inside the medium in all eight recordings. The corresponding figures for large and small females from experimental pairs were 9.3% and 3.9%, respectively.

Pairs of similar-sized females (C2). Similar to the main experiment, here I counted how many times (a maximum of 8) each individual was found inside a patch. Females from large pairs (2.62 ± 0.28 mg) were on average 3.48 times inside the medium while females from small pairs (1.79 ± 0.25 mg) were 4.91 times inside. This difference in occupation intensity was significant ($F = 10.877$, $df = 1$, 86 , $P < 0.01$). Large pairs left more eggs than small ones (2.14 and 0.96, respectively, Kruskal-Wallis, $H = 6.580$, $P < 0.02$).

In this experiment I also noted if migrating individuals were found on the bottom of a vial or on top of the medium. Top positions were observed rarely, and there were no clear differences between the two phenotypes (6.0% for large and 4.8% for small).

Oviposition rate (C3). Under conditions much better than in the main experiment, large females

(2.92 ± 0.23 mg) can lay 8.05 eggs per day and small ones (1.83 ± 0.19 mg) 5.58 eggs ($F=29.64$, $df=1$, 48, $P<0.001$). The mean egg weight for large females is 0.053 mg and for small ones 0.048 mg; this difference is significant ($F=18.566$, $df=1$, 48, $P<0.001$).

Egg cannibalism rate (C4). Females cannibalized their own eggs at a similar rate as strangers' eggs ($F=0.702$, $df=1$, 60, NS). There was no difference in the cannibalism rate between large females (56.8% of eggs cannibalized) and small ones (60.1%; $F=0.145$, $df=1$, 60, NS). Eggs left in an incubator as a control hatched at 97.5% and at 98.2%, respectively.

Discussion

The results of experiment C3 (oviposition rate) support the simple expectation that size differences determine the maximum efficiency of oviposition. I expected that this difference could cause higher migration rate of small individuals, which are less efficient in competition by exploitation. The results of the main experiment seem to be consistent with this prediction.

From the beginning of the experiment, competitors were aware of sharing the patch with the other. Perhaps, they postponed egg laying for better opportunities. As time passed and no alternative places were found, more and more individuals decided to share the patch. This effect was not detected in C1 (single females) where, in addition, individuals occupied patches much more often. During the whole main experiment, larger females were found more frequently in the medium despite the passing time, i.e., decreasing chances for successful emigration. Therefore, this strategy can be regarded as the common sense one, although there was the hypothetical possibility of a paradoxical solution (Korona 1989).

A question may be asked about the hypothetical role of ownership. The fact that individuals in pairs changed between occupation and migration much more often than in single oviposition (C1) indicates that any effects of ownership can hardly be suggested in these contests. If such ownership had taken place, some individuals (owners) would have been more persistent in the presence of opponents.

Some particular aspects of animal competition were studied in this experiment. Individuals were standardized in all their features except size. All were of the same age and social experience. In particular, we can assume that the characteristic (in

this case body size) determining the role is not genetically linked with strategies. Of course, a rule "when you are small behave as..." could be innate, but this conditional strategy would be present in a genotype regardless of the phenotype. This lack of the linkage is a basic assumption of the ESS theory, and it was secured here by artificial creation of body size differences. Another important point is that before pairing, both small and large females were reared in size-homogeneous groups under very good conditions. Therefore, it was the first time they were faced with the necessity to compete for drastically limited resources. Moreover, they had had no previous opportunities to meet opponents of significantly different size. This strongly suggests that females of *T. confusum* need no prior experience to detect size differences. It can be postulated, therefore, that this is their innate ability.

A really difficult question is how these beetles can acquire the relevant information about an opponent's size. Outside the medium I often observed that they touched or even climbed on each other. Although it looked like accidental events, it might have served as an information exchange. Sounds or vibrations could be another hypothetical means of information. But, it is probably not easy to recognize opponent's size inside a medium such as flour. A considerable "noise" (i.e. not always the larger occupying and the smaller migrating) is probably caused by this difficulty.

Let us examine other possible hypotheses that could explain the observed prevalence of bigger females within patches. The absence of references about aggression among *T. confusum* in the literature was, in this study, corroborated by behavioral observations and the lack of any apparent injuries suffered by competitors. Hence, a factor such as the cost of fight cannot be applied to explain the results. Similarly, we cannot suppose that the value of a patch is higher for bigger females, because both phenotypes laid similar numbers of eggs in experiment C1 (single females).

Physiological differences between large and small individuals might serve as another plausible interpretation of the outcome in the main experiment. Differences in behavior should be noticed in the absence of any competition when, for instance, different-sized individuals have had unequal nutritional requirements or abilities to migrate. Similarly, if smaller females were less mature, despite equal age in days, they would tend to disperse more intensively (Ziegler 1976). The genetical variation in dispersal activity was also found in *Tribolium* (Ogden 1970, Ritte 1977). However, in the present

experiment, the populations of large and small individuals had the same genetical composition, because both groups were taken at random from the same pool when still in larval stage. Contrary to all explanations mentioned above, the experiment with single females (C1) showed that both the bigger females and the smaller ones had a similar tendency to occupy oviposition sites.

Even if one accepted the hypothesis that smaller females emigrated more frequently due to lower oviposition efficiency, this would not necessarily mean that they could estimate opponent's size. One could imagine that smaller individuals are always more migratory when they meet other competitors. This behavior might be adaptive when an individual has a proper estimate of its own relative size, but it does not (or cannot) evaluate sizes of other competitors in every contest. However, contrary to the main experiment, in the control with similar-sized pairs (C2), small individuals were less migratory than large ones. This finding makes the results of the main experiment even more meaningful. It might suggest, also, that the females were able to estimate, to some extent, the absolute opponent's size and not only the relative one.

Finally, if smaller females cannibalized opponents' eggs more effectively, it would diminish or even reverse the asymmetry resulting from the difference in oviposition efficiency. But, experiment C4 (egg-cannibalism) revealed that females of *T. confusum*, at least under these conditions, could not recognize their own eggs and that both phenotypes cannibalized eggs at the same rate. Egg can-

nibalism considerably lowered patch value because pairs from the main experiment left about three times fewer eggs than single individuals, no matter whether individuals were large or small (C1). Perhaps this high rate of egg destruction makes the oviposition efficiency especially important, because eggs have to be continuously replaced. Interestingly, in the experiment with similar-sized pairs (C2), large individuals left more eggs. However, during single oviposition, both phenotypes left similar numbers of eggs (C1), and they cannibalized eggs at the similar rate (C4). It may be that bigger females protected their eggs from cannibalism more effectively. This mechanism might reinforce the effect of the difference in the oviposition rates.

Acknowledgements. I thank Jan Kozłowski, Adam Lomnicki, Danuta Padley and Roman Tertl for comments and criticism. This study was supported by a grant of the Polish Academy of Sciences CPBP 04.03-I/1.

References

- Korona R (1989) Evolutionarily stable strategies in competition for resource intake rate maximization. I. The model. *Behav Ecol Sociobiol* 25:193–199
- Ogden JC (1970) Artificial selection for dispersal in flour beetles (Tenebrionidae: *Tribolium*). *Ecology* 51:130–133
- Ritte U, Lavie B (1977) The genetic basis of dispersal behaviour in the flour beetle *Tribolium castaneum*. *Can J Genet Cytol* 19:717–722
- Sokoloff A (1974) *The Biology of Tribolium*. Vol. 2. Oxford University Press, Oxford
- Ziegler JR (1976) Evolution of the migration response: emigration by *Tribolium* and the influence of age. *Evolution* 30:579–592