

- Natoli, E. & De Vito, E. 1988. The mating system of feral cats living in a group. In: *The Domestic Cat: the Biology of its Behaviour* (Ed. by D. C. Turner & P. Bateson), pp. 99–108. Cambridge: Cambridge University Press.
- Packer, C. & Pusey, A. E. 1984. Infanticide in carnivores. In: *Infanticide* (Ed. by G. Hausfater & S. B. Hrdy), pp. 31–42. Chicago: Aldine.
- Schmidt, P. M., Chakraborty, P. K. & Wildt, D. E. 1983. Ovarian activity, circulating hormones and sexual behaviour in the cat. II. Relationships during pregnancy, parturition, lactation and postpartum oestrus. *Biol. Reprod.*, **28**, 657–671.
- Scott, P. P. 1970. Cats. In: *Reproduction and Breeding Techniques for Laboratory Animals* (Ed. by E. S. E. Hafez), pp. 192–208. Philadelphia: Lea & Febiger.
- Scott, P. P. & Lloyd-Jacob, M. A. 1955. Some interesting features in the reproductive cycle of the cat. *Stud. Fert.*, **7**, 123–129.
- van Aarde, R. J. 1978. Reproduction and population ecology in the feral house cats, *Felis catus*, at Marion Island. *Carnivore Genet. News.*, **3**, 288–316.

(Received 5 August 1989; initial acceptance  
12 September 1989; final acceptance 27 November 1989;  
MS. number: SC-510)

### Travel Costs and Ideal Free Distribution of Ovipositing Female Flour Beetles, *Tribolium confusum*

The theory of ideal free distributions (Fretwell & Lucas 1970) predicts that numbers of individuals in different patches of a resource should be linearly related to the profitabilities of these patches. Otherwise, individuals from relatively overcrowded patches would move to those with lower densities of competitors. However, empirical data do not always support this expectation. Some possible factors causing departures from the predictions of the theory have been discussed recently (Parker & Sutherland 1986; Houston & McNamara 1988; Milinski 1988; Korona 1989a). In this paper I consider how the costs of travelling between patches might diminish or even exceed the expected benefits of moving to another patch.

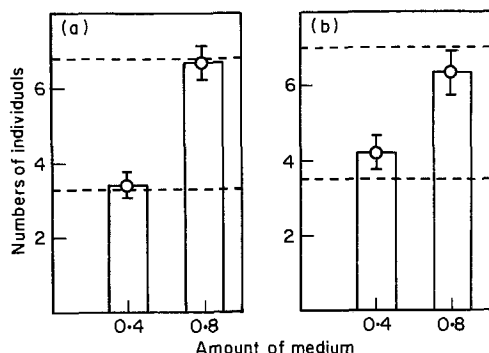
In the present experiments female flour beetles were allowed to choose between two patches containing different amounts of fresh flour and, after a defined period, individuals in the patches were counted. No new resources were added. The oviposition rate of the females was lowered by spatial limits and egg cannibalism. Travel times to the patches were high in one series of experiments and low in another. My aim was to detect whether average densities differed between patches, whether every individual could choose every patch freely,

and whether travel costs affected the distribution of individuals.

The beetles were kept in 95% wheat flour plus 5% baker's yeast at  $29 \pm 1^\circ\text{C}$  and a relative humidity of  $70 \pm 5\%$ . Individuals were taken at random from the stock. Each beetle was placed separately in a vial with a flour/yeast medium to find out whether each female could lay eggs. I used only those females that laid at least four normal eggs per 24 h. For patches of resource I used a pair of identical containers containing 0.8 g and 0.4 g of the medium, respectively. I ran two series of experiments. In one (the E-series) the resource was easily accessible; in the other series (the H-series) access was hard. For the E-series I used as the containers an open paper box ( $20 \times 20 \times 20$  mm) divided in half by a vertical wall. The bottom of the container with 0.4 g of flour was elevated in such a way that the upper surfaces of medium in both containers were on the same level. The box was placed in a glass vial (diameter 45 mm) the bottom of which was painted with an acrylic colour and covered with oak sawdust to roughen the surface thus allowing the beetles to walk easily. For the H-series I used as a container a small glass vial (diameter 15 mm, height 35 mm) with two strips of paper (width 3 mm) attached to its walls to enable beetles to walk inside and outside of the vial. Two such small vials were placed inside one bigger one (diameter 90 mm) with a rough bottom surface. In the H-series the distance between patches was longer and, presumably, they were harder to find.

In the first experiment I aimed to examine whether these two environments were perceived as different by flour beetles. In each series in 36 experimental sets single individuals were left for 24 h in vials without medium and then containers with medium were added for the next 24 h. After this period, in the E-series I found 31 females inside the bigger patches and five females in the smaller ones. This result does not support the hypothesis that females show no preferences (expected ratio 18:18,  $\chi^2 = 18.78$ ,  $df = 1$ ,  $P < 0.001$ ). Neither does it support the notion that the distribution of animals reflected the distribution of resources (expected ratio 24:12,  $\chi^2 = 6.13$ ,  $df = 1$ ,  $P < 0.02$ ). In the H-series the corresponding numbers were 16 and 20. Thus, the hypothesis that females show no preferences was corroborated in the H-series ( $\chi^2 = 0.44$ ,  $df = 1$ , NS). These findings suggest that only in the E-series was switching between patches sufficiently cheap to allow beetles to estimate the value of patches and choose the bigger one.

In the second experiment, for both series, I used eight groups of 12 randomly chosen and individually marked beetles. I followed the same procedure as in the previous experiment but I repeated it



**Figure 1.** Results of competition in groups of 12 females: (a) for the E-series (low travel costs) and (b) for the H-series (high travel costs). Bars show the average numbers of individuals with 95% confidence limits. Broken lines indicate the expected values for smaller and bigger patches (in E-series: 6.750 and 3.375; and in H-series: 7.000 and 3.500, correspondingly).

four times for the same individuals. The average numbers of individuals in both patches were not equal either in the E-series ( $F=126.60$ ,  $df=1,56$ ,  $P<0.001$ ) or in the H-series ( $F=33.04$ ,  $df=1,56$ ,  $P<0.001$ ). There were no differences between runs and no interactions, so results from all runs were pooled. The numbers of individuals in the E-series reflected the distribution of resources ( $t=0.359$  and  $-0.287$  for small and large patches, respectively,  $N=32$ , ns; Fig. 1a). In the H-series (Fig. 1b) the differences between the observed and expected numbers were significant both for small ( $t=3.040$ ,  $N=32$ ,  $P<0.01$ ) and large patches ( $t=-2.238$ ,  $N=32$ ,  $P<0.05$ ).

In total, in the E-series of the second experiment in 214 out of 384 occurrences ( $8 \times 12 \times 4$ ) females were found in bigger patches. This proportion was taken as the average probability of choosing this patch. Then, from the binomial distribution the numbers of individuals expected to be in the bigger patch zero, one, two, three and four times were calculated. The empirical distribution does not differ from the theoretical one ( $\chi^2=2.665$ ,  $df=3$ , ns). Similar results were obtained for the H-series ( $\chi^2=4.803$ ,  $df=3$ , ns). These findings are consistent with the hypothesis that every individual has equal chances of choosing every patch.

Females that were never found outside patches in four runs and those that were found there at least once weighed the same in the E-series ( $58$  and  $38$  females,  $\bar{X} \pm SE = 2.82 \pm 0.31$  and  $2.80 \pm 0.28$  mg, respectively,  $F=0.159$ ,  $df=1,94$ , ns) and in the H-series ( $74$  and  $22$  females,  $2.78 \pm 0.27$  and  $2.81 \pm 0.27$  mg,  $F=0.170$ ,  $df=1,94$ , ns). The coefficient of variation of body weight ( $V$ ) was  $0.10$ .

To summarize, in the absence of competition by exploitation (the single-females experiment) individuals chose bigger patches unless high travel costs prevented it. In groups, on the contrary, in both series animals tended to distribute themselves in a way reflecting the distribution of the resource. However, only in the series with easy access to resource patches was such a distribution reached. Thus, my results can be treated as evidence that the free distribution of flour beetles depends on travel costs. An ideal free distribution was favoured here by the lack of any despotism, so that every individual had free access to both patches. No apparent aggression among mature flour beetles has been observed (Sokoloff 1974). Moreover, the differences in body weight were relatively small. Alternatively, smaller females could be more migratory in order to escape from joint exploitation with bigger and more effective neighbours (Korona 1989b).

Jan Kozłowski, Adam Lomnicki and Roman Tertli provided many valuable suggestions during preparation of this paper. The study was supported by a grant of the Polish Academy of Sciences CPBP 04.03-1/1.

RYSZARD KORONA

*Institute of Environmental Biology,  
Jagiellonian University,  
M. Karasia 6, 30-060 Krakow, Poland*

## References

- Fretwell, S. D. & Lucas, H. L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta biotheor.*, **19**, 16–36.
- Houston, A. I. & McNamara, J. M. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. *Anim. Behav.*, **36**, 166–174.
- Korona, R. 1989a. Ideal free distribution of unequal competitors can be determined by the form of competition. *J. theor. Biol.*, **138**, 347–352.
- Korona, R. 1989b. Evolutionarily stable strategies in competition for resource intake rate maximization. II. Oviposition behaviour in *Tribolium confusum*. *Behav. Ecol. Sociobiol.*, **25**, 201–205.
- Milinski, M. 1988. Games fish play: making decisions as a social forager. *Trends Ecol. Evol.*, **3**, 325–330.
- Parker, G. A. & Sutherland, W. J. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype limited ideal free models. *Anim. Behav.*, **34**, 1222–1242.
- Sokoloff, A. 1974. *The Biology of Tribolium*. Vol. 2. Oxford: Oxford University Press.

(Received 17 January 1989; initial acceptance  
15 June 1989; final acceptance 18 November 1989;  
MS. number: sc-529)