

## Population Dynamics of Two Carabid Beetles at a Dutch Heathland. The Significance of Density-Related Egg Production\*

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Abstract: From our long-term investigations into the dynamics of two carabid beetles, Baars and Van Dijk calculated a negative correlation between mean density of adults and mean fecundity. They supposed this to be an important factor for the restriction of numbers in this heath area. To test this hypothesis in the present paper it is shown that:

- (1) at all densities so far recorded mean density of eggs is higher with higher mean densities of adults,
- (2) the variation in mean egg density is much lower than that in mean density of recruits and of adults that survived from preceding years,
- (3) in peak years the possible reduction of fecundity is too small to reverse the course of density.

Therefore, it is concluded that our present data do not support the above hypothesis.

The method used to compare the variation of mean egg density with that of the mean density of recruits and of old adults can be considered an extension of the key-factor analysis of Varley and Gradwell to cases in which adults from different generations participate in reproduction.

### Introduction

From the long-term investigations of the Biological Station Wijster into the dynamics of carabid populations Baars and Van Dijk (1984b) deduced an interesting relationship between mean density of adults and mean fecundity. Mean density was estimated as the number of adults caught in a standard set of pitfalls during a year. It had already been shown by

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Baars (1979), that such year-catches constitute reliable relative estimates of mean density of adults around these pitfalls, at least at this heathland and for the species concerned: Calathus melanocephalus L. and Pterostichus versicolor Sturm. Mean fecundity was estimated as the weekly averages of the numbers of eggs in the ovaries of ♀♀ collected in pitfalls and summed over the reproductive season, i. e. this measure is expected to approximate the total number of eggs that might have ripened in the ovaries of an average female during that year. In the case of C. melanocephalus this measure indeed gives a reliable relative estimate of mean egg production (Van Dijk, 1983), but in the case of P. versicolor it is not yet clear how this measure can be applied to approximate mean egg production in the field (Van Dijk, 1979b). The relationships found were significant and negative correlations between the year-catches of adults in two standard sets of pitfalls, (the grassy field and the mosaic field: Baars and Van Dijk, 1984a) and the relevant measures for total number of eggs in the ovaries of an average female (eggs in ovaries/female): C. melanocephalus, 1963-1979 (n= 25) :  $r = -0.646$  ( $p < 0.01$ ),  $r$  (Spearman) =  $-0.698$  ( $p \approx 0.0006$ ); P. versicolor, 1969-1979 (n= 18) :  $r = -0.727$  ( $p < 0.01$ ),  $P = -0.567$  ( $p = 0.018$ ). Baars and Van Dijk (1984b; their Fig. 1) formalized these relations as least squares lines (Sokal and Rohlf, 1969). They put these together with such lines for the highly variable relations between eggs in ovaries/female in year t and recruits/female in year t+1 (their Fig. 3) and between eggs in ovaries/female in year t and survival of the breeding animals from year t to t+1 (their Fig. 4) into a deterministic model. This they used to study the numerical consequences of this density-related egg production for the restriction of population size. From this model they concluded that at high densities a reduced fecundity forms "a powerful factor for potential restriction of the numbers". As they did not try to incorporate variation I wondered whether our field data in fact give any indication of the occurrence of an actual restriction of numbers.

To shed more light on this question, in the following I will first consider egg production more closely, and next compare variation in egg production with variation in recruitment and survival.

### Egg production

Baars and Van Dijk (1984b: Fig. 1) computed for C. melanocephalus the negative relationship between mean density of adults (x) and eggs in ovaries/female (y) as:  $y = -0.03232x + 128.061$  (n= 25), the slope of which is significantly different from zero ( $p < 0.001$ ). This means, that to reduce eggs in ovaries/female by 50%, e. g. from 100 to 50, mean density of adults would have to increase by a factor of 2.8, e.g. from 868 to 2415. Hence, at the higher density of adults (2415) total eggs in ovaries of all females (mean egg density), viz. 60,375, is much higher (28%) than at the lower density (868), viz. 43,400. For P. versicolor the equation is  $y = -0.09972x + 132.916$  (n= 18) (slope significantly dif-

ferent from zero with  $p \approx 0.001$ ), by which a reduction of eggs in ovaries/female from 100 to 50 corresponds with an increase of mean density of adults from 330 to 831, i. e. an increase by a factor of 2.5. Also in this case total eggs in ovaries of all females (mean egg density) is higher (21%), viz. 41,550, at the higher density (831) than at the lower (330), viz. 33,000. This does not seem to fit a "powerful factor" for restriction of numbers. The least squares lines were calculated according to a Model I regression (Sokal and Rohlf, 1969), but a Model II regression, which would have given slightly different lines, would not have altered the above results.

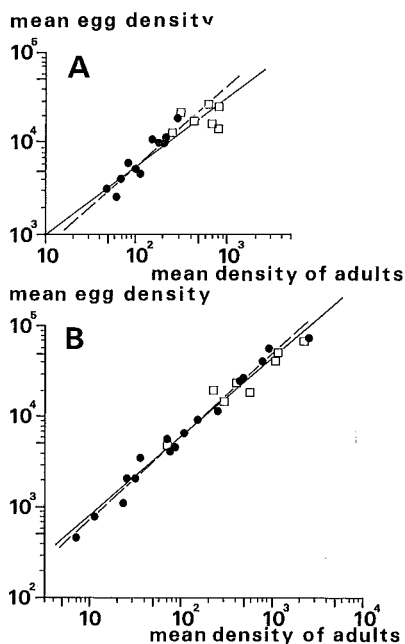


Fig. 1: Relationship between  $\log_{10}$  mean density (year-catch) and  $\log_{10}$  of the total number of eggs in ovaries of all females (half of year-catch times eggs in ovaries/female (egg number)); data from Appendix to Baars and Van Dijk, 1984b) at the grassy field ( $\bullet$ ) and the mosaic field ( $\square$ ). A. *P. versicolor*: grassy field ( $n=11$ )  $r=0.939$  ( $P=0.927$ ), least squares line (- - -)  $y=1.9742+0.8971x$ ; all data ( $n=18$ )  $r=0.912$  ( $P=0.920$ ), least squares line (—)  $y=2.2529+0.7555x$ . B. *C. melanocephalus*: grassy field ( $n=17$ )  $r=0.990$  ( $P=0.990$ ), least squares line (- - -)  $y=1.9664+0.8989x$ ; all data ( $n=25$ )  $r=0.987$  ( $P=0.978$ ), least squares line (—)  $y=2.0289+0.8677x$

If one wants to know why density of adults has changed from one year to another, the above will have shown, that it is useful not only to look at the changes of mean fecundity but also at the changes of mean egg density: Fig. 1.

Fig. 1 shows that our field data do not support the idea that at high densities of adults egg production would be reduced sufficiently to prevent a further growth of numbers. Even the suggestion that in P. versicolor at the mosaic field mean egg density reaches a ceiling would be based on only two points in Fig. 1A, and in any case the assumption that in this species eggs in the ovaries of ♀♀ collected in pitfalls are reliable estimates of eggs deposited in the field has not been supported so far.

#### Variation in mean egg density as compared with that in mean density of recruits and of old adults

To compare the respective contributions of variation in the numbers of different stages in the life cycle to the changes in numbers from year to year I could not make use of key-factor analysis (Varley and Gradwell, 1960), because carabid numbers result from an addition of young adults (recruits) to a stock of surviving old adults. We have thus to use a mixed multiplicative and additive model. Therefore, I compared the actual changes of mean density of adults (year-catch) from each year  $t$  to year  $t+1$  ( $N_t$  to  $N_{t+1}$ ) with the changes that would have occurred if one or two of the three variables, viz. (1) eggs in ovaries/female in year  $t$  (eggs/♀), (2) recruitment rate from eggs, i. e. mean density of young adults in year  $t+1$  divided by mean density of eggs in year  $t$  (recr. rate) (+) and (3) survival rate, i. e. fraction of adults that survived from year  $t$  to year  $t+1$  (surv. rate), had been fixed at their expected (= mean) values ( $\hat{E}$ ). As we are concerned here with the possible significance of the density-related egg production (eggs/♀) as found by Baars and Van Dijk (1984b), we will only compare the actual changes of each  $N_t$  to its  $N_{t+1}$  with those obtained when fixing both (2) and (3) at their expected values or when only fixing (1) at its expected value. Following Baars and Van Dijk (1984b) we assume that in all years mean density of females =  $1/2N_t$ . Hence, we will compare:

$$\begin{aligned} N_{t+1} &= 1/2 N_t * \text{eggs}/\varphi * \text{recr. rate} + \text{surv. rate} * N_t = R * N_t & \text{(I)} \\ \text{with: } N_{e_{t+1}} &= 1/2 N_t * \text{eggs}/\varphi * \hat{E} (\text{recr. rate}) + \hat{E} (\text{surv. rate}) * N_t & \\ &= R_e * N_t & \text{(II)} \\ \text{and with: } N_{s_{t+1}} &= 1/2 N_t * \hat{E} (\text{eggs}/\varphi) * \text{recr. rate} + \text{surv. rate} * N_t & \\ &= R_s * N_t & \text{(III)} \end{aligned}$$

Note, that all values used can be derived from the Appendix to Baars and Van Dijk (1984b). In Figs. 2 and 3 both the quantitative influence of variation in eggs/♀ on the changes of numbers from year to year (equation II:  $N_{e_{t+1}}$ , above) and that of variation in recr. rate and surv. rate (equation III:  $N_{s_{t+1}}$ , below) are compared with the actual changes in numbers (equation I:  $N_{t+1}$ ).

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(+) Note that my recruitment rate is different from that used by Baars and Van Dijk (1984b).

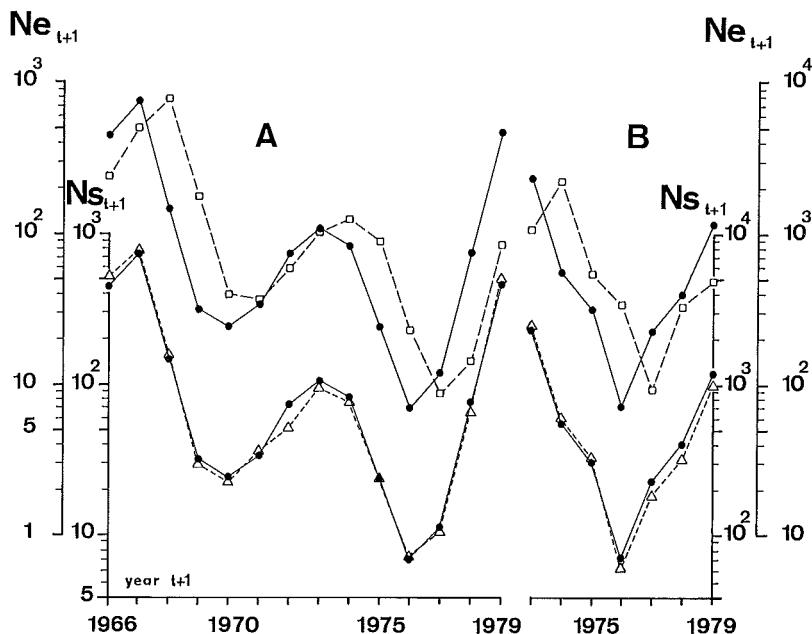


Fig. 2: Log<sub>10</sub>-values of mean density of adults of *C. melanocephalus* in year  $t+1$ : actual values of  $N_{t+1}$  (●—●) as compared with values computed from the actual  $N_t$ -values by either fixing recr. rate and surv. rate ( $Ne_{t+1}$ , □---□, above) or eggs/♀ ( $Ns_{t+1}$ , Δ---Δ, below) at the expected values ( $\bar{E}$ ); see further Table 1 and text; A, grassy field, B, mosaic field.

It will be evident from the Figs. 2 and 3 that in both species at both sites and in most years variation in eggs/♀ hardly contributes to the changes in numbers from year  $t$  to year  $t+1$ : most open squares ( $Ne_{t+1}$ ; II) are more at the level of the closed circles of the year before ( $N_t$ ) than at that of the closed circles of that year ( $N_{t+1}$ ; I). This effect was already foreshadowed by Fig. 1. On the other hand, in most years the combined variation in recruitment rate and survival rate nearly completely covers the changes in numbers from that year  $t$  to that year  $t+1$ : most open triangles ( $Ns_{t+1}$ ; III) are very close to the closed circles of that year ( $N_{t+1}$ ; I). The few exceptions, though interesting in themselves in order to "understand" the change of numbers in specified years, do not suggest an actual restriction of numbers by a reduced fecundity at high densities. This means that in a peak year it is not the possibly reduced fecundity that reverses the course of density (compare  $N_t$ ,  $Ne_{t+1}$  and  $Ns_{t+1}$  in Table 1); the reduction is too small for that. This surprisingly small effect of the negative relationship between mean density of adults and mean fecundity results from the variation of mean fecundity between years being much lower than the variation in both

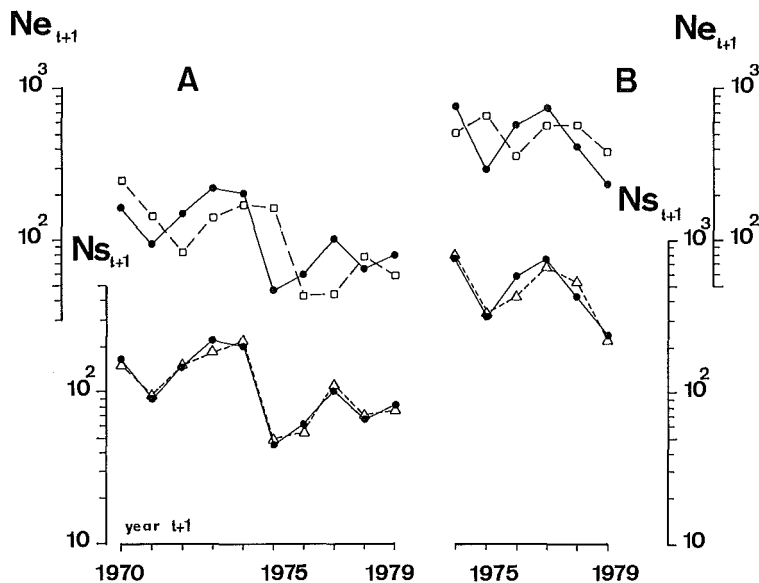


Fig. 3:  $\log_{10}$ -values of mean density of adults of *P. versicolor* in year  $t+1$ : actual values of  $N_{t+1}$  (●—●) as compared with values computed from the actual  $N_t$ -values by either fixing recr. rate and surv. rate ( $Ne_{t+1}$ , □---□, above) or eggs/♀ ( $Ns_{t+1}$ , △---△, below) at the expected values ( $\hat{E}$ ); compare Table 1 and see text; A. grassy field, B. mosaic field.

mean density of recruits and mean density of old adults between years. This becomes especially evident if we compare the variance of the values of net reproduction as based on equation II ( $\text{Var } R_e$ ), which is only determined by variation in eggs/♀, with that of the values of net reproduction as based on equation III ( $\text{Var } R_s$ ), in which the influence of variation in eggs/♀ is excluded: Table 2. In all cases  $\text{Var } R_s$  is many times greater than  $\text{Var } R_e$ , whereas  $\text{Var } R_s$  is of the same magnitude as  $\text{Var } R$  (eq. I), and thus probably leaves an only small margin for variation in mean fecundity. That this margin is indeed very small is also shown by the mean square of the differences between  $R$  and  $R_s$ , which is very small as compared with the mean square of the differences between  $R$  and  $R_e$ : Table 2.

Table 1: Contribution of egg production and recruitment rate + survival rate to the decrease of population numbers after a peak year (compare Figs. 2 and 3).

peak year	$N_t$	eggs/♀	recr. rate	surv. rate	$N_{t+1}$ (II)	$N_{t+1}$ (III)	$N_{t+1}$ (I)	Variance in egg-prod. may give reduction of $N_{t+1}$ of:
<u>Calathus melanocephalus</u> at the "grassy field" (1965 - 1979)								
1967	760.3	103.5	0.0020	0.0927	807.62	153.41	148.7	3%
1973	105.3	119.6	0.0019	0.6772	123.66	82.22	83.3	none ( $N_{t+1}$ greater)
<u>Calathus melanocephalus</u> at the "mosaic field" (1972 - 1979)								
1973	2336.0	59.8	0.0016	0.1882	1731.08	318.70	553.0	none ( $N_{t+1}$ greater)
<u>Pterostichus versicolor</u> at the "grassy field" (1969 - 1979)								
1973	223.7	98.2	0.0073	0.5646	179.18	219.63	206.7	6%
1977	105.0	88.4	0.0024	0.5304	80.21	69.88	66.7	4.5%
<u>Pterostichus versicolor</u> at the "mosaic field" (1973 - 1979)								
1974	790.3	62.6	0.0019	0.3303	675.00	311.25	307.0	1%
1977	764.0	38.6	0.0091	0.3695	575.98	521.19	417.0	20%

Note: the expectation-values ( $\hat{E}$ ) are computed as weighed averages over the relevant years, e. g.

$$\hat{E}(\text{eggs}/\varphi) = \sum (1/2N_t * \text{eggs}/\varphi) / \sum (1/2N_t), \text{ etc.}$$

Table 2: Comparison of net reproductive rates (see text) of the two species at two sites

	<u>C. melanocephalus</u>		<u>P. versicolor</u>	
	grassy field	mosaic field	grassy field	mosaic field
Var R (I)	4.097	1.604	0.253	0.349
Var Re (II)	0.044	0.032	0.006	0.025
Var Rs (III)	3.620	1.235	0.258	0.175
$\Sigma(R-Re)^2/n$	4.1215	1.3876	0.2476	0.2007
$\Sigma(R-Rs)^2/n$	0.0973	0.0813	0.0100	0.0436

Because of the mixed model I had to use I could not apply a simple analysis of variance to these data. This is already indicated by Var Rs in P. versicolor at the grassy field which is slightly greater than Var R. In a mixed model this is indeed possible, and results from the sequence in which the values of the relevant variables are realized in the multiplicative and the additive part of the model respectively. Though I am still involved in a further analysis along the above lines I can already state that in all cases variation in the mean density of young adults as well as variation in the survival of old adults, also when treated separately, are much greater than variation in mean fecundity between years. Hence, a further analysis does not alter the conclusions of the present paper.

## Discussion

With this paper I hope to have demonstrated that it is risky to draw conclusions from a deterministic model about the impact of variables, the variation of which has not been studied thoroughly. This is especially critical, of course, if these variables are also interrelated and/or if the magnitude of variation of the separate variables is quite different, as in the present case. The variable with the greatest variation in effect will also greatly determine the fluctuation pattern of density, on which was based the key-factor analysis of Varley and Gradwell (1960). This also applies to variables that are inversely related to density itself. Therefore, if the reduction of fecundity with an increase of density is generally smaller than the effect of other variables on density the first cannot have an important influence on subsequent numbers. This has already been distinctly expressed by Lack (1954: ch. 7) concerning the generally small variation in reproductive rate of birds under the influence of density. Such a variable bobs up and down, so to speak, on the density "waves" that result from other variables with greater effects on density (see also: Den Boer, 1981). In the present case these density "waves" are pictured by the dashed lines between the open triangles in the lower parts of the Figs. 2 and 3. We can imagine now the closed circles bobbing up and down with these waves, but as we see in



these pictures the height of the waves is hardly influenced by it. This does not mean that I consider the whole treatment of our data by Baars and Van Dijk (1984b) to be nugatory, but only that our data do not give an indication of the occurrence of an actual restriction of numbers. Therefore, I reject the deterministic model, because it cannot tell us what happened in the field. This does not exclude the possibility that at densities still higher than so far observed some kind of restriction of numbers would occur. But at the moment such a potential restriction is only speculation. The backbone of their paper, however, the inverse relationship between mean density and mean fecundity is interesting in itself. Moreover, their preoccupation with this relationship has stimulated us to plan experiments to investigate whether egg production is directly density-dependent, or is only indirectly correlated with density. This is especially necessary because in our beetles - unlike in e. g. birds (Lack, 1954, 1966) - egg production is highly variable, both between individual females of the same population (even under constant conditions) and in the same females under different conditions, e. g. different temperatures (Van Dijk, 1979a). Because of this, mean fecundity is an only very rough estimate of the outcome of a number of different processes which may combine in many different ways, and we should like to know where - and how - density comes in.

Apart from this we will continue, of course, our investigations into the contribution of different mortality factors to the variation from year to year in the mean densities of young adults and surviving old adults respectively. In this connection the most significant fact at present, is that the pattern of fluctuations of both densities over periods of 7 years can be simulated rather accurately by multiple regressions with some relevant weather factors (Baars and Van Dijk, 1984a). In spite of the fact that this may point to an important influence of weather factors on the changes of density, I agree with Baars and Van Dijk (1984a) that this does not exclude the possibility that some density restricting processes can still be hidden in these fluctuations.

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