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The Dynamics of a *Carabus auronitens* Population Subject to a Powerful Abiotic Key Factor

Robert Baumgartner
Malte Prigge
Udo Heimbach
Friedrich Weber

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Dr. Robert Baumgartner
Institut für Allgemeine Zoologie und Genetik
der Universität Münster
Schlossplatz 5
48149 Münster/Westfalen, Germany

Malte Prigge
Institut für Allgemeine Zoologie und Genetik
der Universität Münster
Schlossplatz 5
48149 Münster/Westfalen, Germany

Prof. Dr. Friedrich Weber
Institut für Allgemeine Zoologie und Genetik
der Universität Münster
Schlossplatz 5
48149 Münster/Westfalen, Germany
E-Mail: weber@nwz.uni-muenster.de

Dr. Udo Heimbach
Biologische Bundesanstalt für Land- und Forstwirtschaft
Institut für Pflanzenschutz in Ackerbau und Grünland
Messeweg 11-12
38104 Braunschweig, Germany
E-Mail: U.Heimbach@bba.de

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Contents

Abbreviations frequently used in text and legends

i - year of investigation

n - number of seasons

k - number of functions, and respectively variables, tested

p - significance level

pcorr - significance level corrected for the number of functions, and respectively, variables tested

pfunc - significance level of a non-linear regression

pmult - significance level of multiple regression analysis

b1 - regression coefficient of a linear function

b0 - constant of a linear regression function

r - coefficient of correlation

r^2 - coefficient of determination (%)

r_{part}^2 - coefficient of partial determination in multiple regression analysis

r_{mult}^2 - coefficient of multiple determination in multiple regression analysis

Ai - abundance of beetles in spring i (Ai refers to the density of females plus males or of females only); for an unequivocal discrimination from the following parameter the abbreviation $A_{i-1,with\ 1.5}$ is used instead of Ai.

$A_{i,without\ 1.5}$ - abundance of females younger and older than 1.5 years in spring i

$A_{i,\ 1.5}$ - abundance of 1.5 year old females in spring i

Aai - number of freshly emerged individuals (females plus males) in late summer / autumn i

Bi - net reproductive rate per female in year i; calculated as "number of beetles emerged in late summer / autumn i divided by the total abundance of parental females in spring i”; for an unequivocal discrimination from the following parameter the abbreviation $B_{i,with\ 1.5}$ is used instead of Bi

$B_{i,without\ 1.5}$ - net reproductive rate referred to the abundance of the females younger and older than 1.5 years in spring i ($A_{i-1,\ without\ 1.5}$)

$P_{i,1.5}$ - proportion of the abundance of 1.5 year old females in the abundance of the total female stock in spring i

CNL - cumulative number of individual last captures

PTi - "Prigge's temperature" in year i (the average of the mean daily meteorological temperature in the critical period of May)

TA2, TA3, TM1, TM2, TM3 - average of the mean daily meteorological temperature in the 2nd and 3rd decade of April and the 1st, 2nd and 3rd decade of May

BEVi - "Baumgartner's Expectation Value" for spring i, the value of the mean 4 year period of PTi corresponding to spring i

tau - the period length of a periodicity

A. Introduction

> "Logic and Mathematics are only of service, then, once you have found the right track ... "
> (G. E. Yule, 1920: cited after Dempster, 1983)

In a long-term field study we investigated the effect of temperature on reproduction in *Carabus auronitens* (Weber & Heimbach, 2001). Net reproductive rate (number of young divided by number of females in the parental generation) depends on temperature in a critical period in late spring (the mean daily temperature of the coldest of the seven seventeen day periods starting between May 9 and May 15 and ending between May 25 and May 31). In the present article the temperature in this period is shown to have a significant 4 year periodicity in the Westphalian Lowlands. The net reproductive rate of *Carabus auronitens* depends not only on the temperature in May in a given year i, but also on the corresponding value of the mean 4 year period in this temperature. Using field data a model is developed that explains this phenomenon. The outcome of our analyses is a model that combines two population processes, which both reduce the probability of extinction at the population level (see below): the new model is called "density-dependent reinforcement of risk spreading".

The fundamental problem of population ecology

Relative stability of populations of many organisms in space and time is the basic precondition for persistence and ongoing evolution of life on earth (Andrewartha & Birch, 1954, p. 665). What mechanisms, however, guarantee that in a stable population the number of animals that reach reproductive maturity each generation is, on an average, equal to the number of mature individuals that die? The population problem - the phenomenon of the relative stability of populations in unstable environmental conditions - has been discussed by many population biologists (Solomon, 1949; Murray 1999; Krebs, 2002; for a thorough survey of the early literature, from the qualitative description of the population problem by Malthus and Darwin to the quantitative models elaborated by Volterra and Lotka, and Gause's experimental approach, see Thompson, 1939). Two models are offered to explain ecological reality: density-independent and density-dependent population growth rates. In the first model the change in number of individuals is influenced by density only beyond an upper and lower critical limit; persistence is maintained by density-independent processes that minimize the probability of the density going beyond the critical limits; in the latter modal density of individuals influences the population growth rates also between these limits: consequently the change in number of individuals (or at least the direction of the change: positive, zero or negative) can be predicted from the present density. These two mechanisms are not mutually incompatible.

Safety range and critical limits of density

In both systems a population is not in danger of becoming extinct, if it remains within a certain range of density. This safety range is bounded by an upper and lower limit: "carrying capacity" (or "upper critical density") and "critical minimum density" ("lower critical density" or "minimum size of a viable population") (Solomon, 1949; Milne, 1957; Wilson & Bossert, 1971; Schwerdtfeger, 1979; Soulé, 1987; Murray, 1999). Beyond the carrying capacity populations are subjected to strong negative density-dependent effects, beyond the critical minimum by positive ("inverse") density-dependent effects on reproduction and survival. If the number of individuals exceeds the carrying capacity, environmental resources are overexploited, and the population declines: mean individual reproductive rate and perhaps also the mean individual survival decline. The forced return of a population from above the carrying capacity is called limitation or ceiling (Pollard, 1981). Limitation is a non-regulated density-dependent process and " ... a necessary feature of all populations because of the finite nature of resources ... ", Dempster, 1983, p. 462). It should be strictly distinguished from regulation (Pollard, 1981) as well as restriction (see below). In the extreme case, when populations outgrow and destroy their resources, they become extinct ("collective suicide": Milne, 1957; Schwerdtfeger, 1979, p. 373). Declining below the critical minimum density is even more dangerous: beyond this limit not only environmental, but also demographic uncertainties (genetic ones included) (Shaffer, 1987; Lande, 1993) and the so-called "Allee effect" endangers the persistence of populations. The term "Allee effect" refers to the consequences of a reduction in cooperative interactions when there are too few individuals: that is, of interactions that - in the right frequency at the right time - promote individual rates of reproduction and survival (Courchamp et al., 1999; Stephens & Sutherland, 1999).

Speaking of a "safety range" is somewhat ambiguous as within this range the number of individuals is nearly continuously irregularly varying, in both density-independent and density-dependent models, due to (density-independent) changes in environmental (biotic and abiotic) factors (mainly to short-term deviations in weather conditions) (Lande, 1993). Thus, the population density is nearly continuously in danger of being pushed to the upper or lower limits, or even beyond.

Relative stability and negative feedback loops

The question is, how can the population density be stabilized within the range of safety, and the probability of crossing the carrying capacity or the critical minimum density minimized. The density-dependent model of population growth suggests that within the safety range the mean individual birth and survival rates are regulated by the density of individuals via negative feedback loops (Nicholson, 1933, 1957; Smith, 1935; Solomon, 1949; Milne, 1962; MacArthur & Connell, 1970; Huffaker et al., 1971; Wilson & Bossert, 1971; May, 1980; Begon et al., 1986; Begon et al., 1997; Schwerdtfeger, 1979; Varley et al., 1980; Wilbert, 1970; Turchin, 1990, 1995, 1999; Sibly & Hone, 2002; Hixon et al., 2002). Nicholson (1933) characterized regulation ("balance" around a "steady state") with the words: " ... the action of the controlling factor must be governed by the density of the population controlled" (p. 135); and Smith (1935) wrote: " ... any tendency of the density to depart in either direction from the average modifies the environmental forces acting on the density in such a way as to restore it to the average" (p. 878; the average is the "equilibrium density"). That is, density influences other biotic factors, which act as a regulatory feedback. Regulatory factors may be predation, parasitism, infection by pathogenic organisms, heterospecific and conspecific competition for environmental resources; in well adapted regulatory mechanisms density influences mean individual birth rate, survival rate and/or emigration directly (autoregulation) by mutual interference between conspecifics, mediated by pheromones or other stimuli (Schwerdtfeger, 1979; Sibly & Hone, 2002). Several regulating factors may act jointly on a population (Hudson et al., 2002), or one or a few factors may dominate (Solomon, 1949). In any case, the lower the population density (within the range of safety) the more the population-specific individual reproductive capacity and life expectancy are realized (Schwerdtfeger, 1979); the intrinsic rates of reproduction and survival depend on habitat conditions, like temperature, moisture, food availability and degree of adaptation of the population to the habitat conditions. Negative feedback loops can stabilize density; however, time lags in the regulatory mechanism can induce oscillations around an equilibrium density (Smith, 1935; Solomon, 1949), and overcompensation induces bifurcations or even chaotic changes in density (May, 1980). In the case of perfect regulation the equilibrium density is below the carrying capacity (see Pollard, 1981, and Dempster, 1983; both authors, however, question the consistency of the equilibrium model; see also Huffaker et al., 1971), and even the peaks in abundance do not pass the upper limit of the safety range. Obviously, self-regulation by mutual interference can fulfil this best (Solomon, 1949: "The type of density-dependent effect in which capacity seems to play the least part is mutual interference", p. 16). Mutual interference is often not distinguished from intraspecific competition for requisites (Klomp, 1964), and in this sense Nicholson (1933) stated "... that any factor having the necessary property for the control of populations must be some form of competition" (p. 135). Obviously, the occurrence of regulation below the carrying capacity of the environment was appreciated by Darwin (1882): "The amount of food for each species of course gives the extreme limit to which each can increase; but frequently it is not the obtained food, but the serving as prey to other animals, which determines the average number of a species" (reprint 1958; pp. 71/72). - Unlike in the laboratory, constant equilibrium densities are unlikely to exist in nature, as the limits of the safety range as well as the effectiveness of regulating factors fluctuate in time and space, and thus the equilibrium density ("Folgeregelung": Schwerdtfeger, 1979; see, for example, also Smith, 1935); the equilibrium density of a population at one and the same site may even change within a year. The strength of compensating density-depending factors can differ at different population levels: for example, Jarosik & Dixon (1999) reported that a population of the tree-dwelling aphid, *Myzocallis* *boerneri*, was most regulated not at the peak but at the lowest densities. Furthermore, the density-dependent factors may not keep the density at a distinct equilibrium, but within certain bounds (Solomon, 1949; Begon et al., 1986, 1997; Hixon et al., 2002). Finally, it is possible that in spite of a regulating mechanism the density of a population can be pushed by (density-independent) environmental perturbations beyond the limits of the safety range; however, regulation will reduce the possibility of this happening (as long as such perturbations are not too strong; against dramatic changes in the environment or even catastrophes, of course, regulation is powerless).

Relative stability by spreading of risk

In the density-independent model it is assumed that feedback loops do not exist within the range of safety: density-dependent factors do not, or at best operate imperfectly. Fluctuations in density within the safety range are dominated by unpredictable changes in biotic and abiotic factors, especially weather (Solomon, 1949; Andrewartha & Birch, 1954; Milne, 1957; Den Boer & Reddingius, 1996); thus, density fluctuations are only predictable if population-intrinsic processes and/or environmental trends are regular: due to a seasonal rhythm of birth and death rates, associated with regular changes in weather during the course of a year. Effective density-dependent responses are not excluded completely, but are limited in the density-independent model to the limits of the safety range (Pollard, 1981; Dempster, 1983). There are two mechanisms in this model that give relative stability: "strategies of risk" (Den Boer, 1968), and "restriction" (Den Boer, 1981). Strategies of risk are especially significant when environmental conditions are adverse, and densities are around the lower limit, the critical minimum density. Strategies of risk depend on populations being multipartite, i. e. composed of distinct entities: of different subpopulations (call them interaction groups: Den Boer, 1979, 1981, 2002), generations, genotypes and alleles at gene loci (called spatial, temporal and genetic strategies of risk; Den Boer, 1968, 1973, 1981, 2002; Andrewartha & Birch, 1984). - The influence of stochastic fluctuations in environmental conditions is reduced (if they are not too strong and not too seldom) insofar as populations are able to adapt to such changes by the evolution of individual phenotypic tolerance and/or phenotypic (genetic and/or non-genetic) polymorphisms. In the case of genetic polymorphisms special balancing mechanisms prevent genetic homogeneity developing when environmental conditions remain constant for relatively long periods (Dobzhansky, 1970; Dobzhansky et al., 1977). - Tolerance and/or polymorphisms enable individuals of a population to occupy different sites in which environmental conditions and fluctuations differ so that - in an extreme case - subpopulations may flourish in one type of habitat, whilst in another type at the same time subpopulations may be near to extinction. In Solomon's (1949) words: " ... heterogeneity (of the environment) helps to ensure that whatever the general conditions, some part at least of the environment will be able to offer protection and refuge for some of the population". Effective spatial strategies of risk that operate over some distance require high individual powers of dispersal so that empty places can be recolonized and new populations founded when life conditions return to normal. Such spatial strategies of risk stake on the persistence of metapopulations (Hanski & Gilpin, 1997; Hanski & Kuussaari, 1995), but risk the existence of local subpopulations, whilst regulatory mechanisms and other mechanisms of risk spreading ensure the persistence of populations by stabilizing the subpopulations. - A temporal strategy of risk is effective when reproductive activity of the individuals, and thus the developmental stages are spread over a longer time span. Another important case of temporal risk spreading is realized when adults are long lived and able to reproduce several times; in this case, the population does not need to reproduce in every season: when reproduction fails in one season, the population survives by virtue of the longevity of its adults, and the survivors reproduce in a following season (Van Dijk, 1972, 1973, 1979 a, 1979 b; Luff, 1982; Sota, 1987; Davies, 1987). - Phenotypic (non-genetic) spreading of risk is realized when individuals of different ages do different things (Loreau & Ebenhöh, 1994), the same thing at different times, or in different ways. In particular, individuals of different ages could react differently to environmental stress (for example young individuals are irreversibly injured by hunger whilst older individuals can survive; or young and old adults reproduce at different times: when one generation reproduces environmental conditions may be better or worse than when the other generation reproduces; Van Dijk, 1972, 1973; Den Boer, 2002).

Relative stability achieved by restrictions

In the density-independent model the possibility of crossing the upper critical limit of the safety range is reduced by restrictions on population growth, especially by not too seldom and not too frequently occurring adverse weather events, which restricts the periods for which conditions are optimal for reproduction and population growth (Andrewartha & Birch, 1954; Andrewartha, 1957; Birch 1957, 1979; Den Boer & Reddingius, 1996). The effect of restrictions by climatic factors - called "balance of nature" - was also discussed by earlier authors (Bodenheimer, 1928; Uvarov, 1931; Thompson, 1939: " ... climate really is a controlling factor", p. 337). "Restriction" in this sense has to be distinguished from "limitation": restriction reduces the possibility that a population will approach the critical upper limit, limitation describes the reduction in density that results when carrying capacity is reached. A population is stabilized by restrictions only when the density is not reduced too drastically, but always remains within the safety range. Restrictions may occur more or less regularly (for example in the course of a year), or even randomly (for example by occasional extreme weather events that deviate from the norm). Den Boer (1981, p. 46) concluded from simulation experiments: "Hence, as could be expected, density restrictions at about the right size and occurring in about the right mean frequency will appreciably prolong the survival times of populations that otherwise would have shown an upward trend of numbers, but it is less expected, that it does not make much difference whether such restrictions occur about randomly or only at very high densities, though a rather low probability of occurrence at very low densities must generally be favourable of course".

What is right? Are there syntheses?

Faced with the multiple possibilities of stochastic risk spreading some population biologists are sceptical that selection pressure is high enough for the evolution of density regulating mechanisms under any environmental condition or in any ecological group of organisms. From his experiences with carabids Den Boer (2002, p. 358) concludes: "In short, I am sure that spreading of risk in nature is much more general and possibly also much more important for survival of populations than the sometimes (but not always and everywhere) also occurring density-dependent processes" (see also Den Boer, 1981, 1998; but cf. the controversy Baars & Van Dijk, 1984 a, b - Den Boer, 1986). Den Boer and his colleagues revealed several effective strategies of risk spreading in carabids (Den Boer, 1970, 1973, 1977, 1979, 1981, 1982, 1985, 2002; Den Boer et al., 1980; Den Boer et al., 1993; De Vries & Den Boer, 1990; De Vries et al., 1996; Van Dijk, 1972, 1973, 1979 a, 1979 b, 1982; Nelemans 1988, Nelemans et al., 1989; Rijnsdorp, 1980).

From a theoretical point of view, each of the processes discussed above - strategy of risk spreading, restriction, limitation, reduced critical minimum density as well as regulation within the safety range - can be important for the dynamics of a distinct population. This was admitted even by Den Boer (1981). Also the earlier scientists who stressed the significant role of climate did not deny the effect of biotic factors on the dynamics of populations. For example Thompson (1939) wrote: "The fact is that the fundamental cause of natural control is neither exclusively biotic nor exclusively abiotic" (p. 333); and Bodenheimer (1928) confessed: "We were wrong to underestimate, in the infancy of our discoveries, the actual part played by biotic factors, especially during the breaking down of gradations" (cited by Thompson, 1939, p. 324).

For advocates of density regulating mechanisms it is also acceptable that risk spreading could be important when a population is endangered to be pushed beyond the lower limit of the safety range. For example Nicholson (1933) wrote: "When interacting animals (host and parasite, both may be insects) are subject to increasing oscillation ... ... the densities of the interacting animals must sooner or later be reduced to very low values. ... ... the (host) animals must be scattered in the environment in more or less separated groups, for each female forms a centre from which its offspring diffuse. Some of these groups are found by parasites, and it is likely that these groups will be terminated during the next few generations. ... ... The other groups of hosts increase geometrically for a few generations, but are sooner or later found by parasites and are ultimately exterminated; in the meantime there has been a migration of hosts, some of which have established new groups" (pp. 161 - 163; words in brackets are added by us). Nowadays, such a mechanism that reduces the probability of extinction of a population is called (spatial) risk spreading in metapopulation dynamics.

A synthesis that results from studying a population of Carabus auronitens?

In the Westphalian Lowlands a distinct bad weather event (low temperature at a critical period in May, called "Prigge's critical period") occurs regularly every few years and dramatically influences the reproductive success of *C. auronitens* there. This bad weather event especially adversely affects early development. Between two adverse weather events the population grows more or less continuously because of successful reproduction. Thus, it is likely the population will be abundant when the next bad weather event occurs. Such a relationship is advantageous as the population survives each bad weather event because the adults are long lived. In our 2001 paper we mentioned a puzzling phenomenon: "We were surprised to find that the minimum mean weight of females that was observed in early spring ... depended on the temperature in Prigge's critical interval, which started at the earliest on May 9" (Weber & Heimbach, 2001, p. 151). We thought the anticipatory influence of the critical temperature was mediated by high density: " ..., not only can temperature mimic density-dependences, but inversely density-dependent factors, if they are effective, would mimic a temperature influence" (Weber & Heimbach, 2001, p. 151). In the present paper the connection between density and bad weather events is strengthened. Now, we have evidence that by density the variability in several population parameters is influenced, and that this enables the population to survive bad weather events that occur with a certain periodicity. This is a case categorically excluded by Den Boer (2002): " ... in my opinion, it will never be possible to predict local weather conditions ... ... a year ahead, which would be necessary to predict density in the following year" (p. 359); however, there is the well-known counter-evidence of the El Nino-Southern Oscillation (ENSO) occurring in and around the tropical part of the Pacific ocean every few years (Grant & Grant, 1989; after Tudhope & Collins, 2004, El Nino effects are felt worldwide). Moreover, the ten-eleven year sunspot / climate cycles affect the boreal forest ecosystem in North America (Sinclair et al., 1993) and possibly also other terrestrial ecosystems in the Northern Hemisphere (Elton, 1924/1925; Myers & Rothman, 1995) as well as the marine ecosystem in the English Channel and other areas of the North Atlantic (Southward et al., 1975; Colebrook, 1976; Southward, 1980).

The *Carabus auronitens* population is "informed" by the female population density and probably the generation structure of the female stock whether bad weather is likely to occur during the early development of the larvae of the beetle in late spring; in the case of a pessimistic prognosis the females reduce their investment in reproduction (vitellogenesis) already in early spring (males may also reduce reproductive investment: mate searching activity). There are indications that in years in which reproductive investment is reduced the beetles are "rewarded" by an increased probability of survival. We conclude from several observations that the carrying capacity of the habitat is much higher than the densities, that trigger the reduction in reproductive investment. Thus, this density-dependent reaction may be caused by pheromone-mediated interference. This is a precondition that in the same year reproductive success is reduced and survival is increased. At the carrying capacity, when intraspecific competition for food is intense, not only reproductive success but also adult longevity would be adversely affected.

Individual survival after reproductive failure is essential for population survival: it is a strategy of temporal risk spreading (see above). If, by responding to "information factors", unprofitable costly investments in reproduction are avoided, and individual survival is increased, the strategy of temporal risk spreading is selected for; therefore we call this co-effectiveness of density dependence and risk spreading "density-dependent reinforcement of risk spreading". This model is described in the present paper for the first time. In describing the model we use some metaphorical terms, but this new phenomenon is a completely mechanistic process based on known biological processes. Although this new model is based on empirical data (on "natural experiments", Brandmayr & Weber, 1981), "experiments in nature" to test the model have still to be done.

B. Material and Methods

B. I. Methods of investigation, computation, statistics and documentation of data

Material and Methods relevant to this article are described in Weber & Heimbach (2001), chapters 2.1 - 2.16. Only some additional notes need to be given here (the number of the respective sub-chapter in the 2001 paper is given in brackets).

B. I. 1. (2.4) Individual parameters

Mean values are calculated when at least 5 individual values are available for a distinct season and, respectively, a distinct interval within a season. Concerning the relative mean weight of the females in the total spring stock (mean weight of females divided by mean weight of males) the minimal numbers are five females and five males per time interval; in the case of the relative mean weight of females of a distinct generation the minimal numbers are three females and three males per decade (chapter I. 2.).

The degree of individual mandible wear (chapter D. I.) is attributed to one of 5 classes (class 0 = no wear, class 5 = loss of a mandible). Right and left mandible of an individual are separately judged; the more worn mandible is weighted by a factor of 5, the less worn by a factor of 1: for example, a beetle with a lost mandible and non-worn mandible is given a wear value of (5 x 5 + 0 x 1) / 6 = 4.17; a beetle with one mandible assigned to class 4 and the other to class 1 a value of (4 x 5 + 1 x 1) / 6 = 3.5.

B. I. 2. (2.6; 2.7) Calculation of net reproductive rate and estimate of abundance

Mean net reproductive rate, Bi, is defined as "number of beetles that emerge in autumn i divided by number of reproductive females in spring i" (**Table 1**; cf. Weber & Heimbach, 2001).

Table 1 Abundance and net reproductive rate of the population at the 0.2 ha area of investigation. - Ai - number of individuals in the plateau-phase in spring i. – Aai - number of freshly emerged individuals in autumn i. - Bi - net reproductive rate (number of beetles that emerge in autumn i divided by number of females in the plateau-phase of spring i). For the period 1982 - 1992 the number of females in spring and net reproductive rate Bi were calculated assuming a temperature dependent sex ratio in spring (cf. chapter C. IV. 8.). - Aai for 1982 - 1992, 1996 and 2001 not in brackets were calculated using the formula $y = 1.1649 x + 3.5365$, Aai in brackets were calculated using the formula $y = 1.1482 x + 8.6234$ (cf. text). y = total number of freshly emerged individuals; x = Jolly-Seber estimate of the number of freshly emerged individuals trapped in autumn i ; the corresponding Bi is not in brackets, and respectively, in brackets.

year i	Ai		Aai	Bi
	females + males	females	females + males	
1982	421	221	340 (340)	1.54 (1.54)
1983	375	196	101 (105)	0.51 (0.54)
1984	252	138	197 (199)	1.43 (1.44)
1985	256	152	315 (315)	2.07 (2.07)
1986	315	188	353 (353)	1.88 (1.88)
1987	403	233	27 (32)	0.12 (0.14)
1988	271	164	275 (276)	1.68 (1.68)
1989	316	191	434 (433)	2.27 (2.27)
1990	532	319	382 (382)	1.20 (1.20)
1991	452	257	51 (56)	0.20 (0.22)
1992	307	190	305 (306)	1.60 (1.61)

Tab. 1 (continuation)

year i	Ai		Aai	Bi
	females + males	females	females + males	
1993	290	168	522	3.11
1994	503	284	373	1.31
1995	586	324	90	0.28
1996	382	234	3 (9)	0.01 (0.04)
1997	211	132	168	1.27
1998	209	139	116	0.83
1999	210	119	138	1.16
2000	105	52	53	1.02
2001	102	51	155 (158)	3.04 (3.10)

The number of females that are potentially reproductively active (**Table 1**) is the Jolly-Seber estimate in the so-called plateau-phase in spring (Weber & Heimbach, 2001). For the investigation in 1993 - 2001, when the study area was enclosed with a beetle-proof fence, the number of retrapped animals was high enough to estimate both the number of females and males in the plateau-phase; the sex ratio varied between 49.52 % and 66.51 % females (**Table 1**; mean: 57.36 %; SD = 5.6 %; n = 9). In the beetle-proof enclosure the number of individuals present in spring i (**Table 2**) and the number estimated by the Jolly-Seber method for the plateau-phase of spring i (**Table 1**) are highly correlated (r^2 = 98.6 %; cf. chapter D. I.).

Table 2 a, b Number of the individuals trapped between autumn 1992 and 2001 in the area enclosed by a beetle-proof fence which was erected in summer 1992. A, late summer / autumn; S, spring. **Table 2a:** number of individuals trapped in seasons A' 92 - A'97; **Table 2b:** in seasons S'98 - A'01. Rows give the number of individuals belonging to the indicated generation, the columns the number of individuals present in the indicated season. The rows begin with the season of first catch. For each generation the number of individuals present in successive seasons is given (including those individuals that were not trapped in spring i, but re-trapped in a following spring). For spring the percentages of surviving individuals are indicated (autumn of emergence -> 1st spring; spring i -> spring i+1, etc.). Note that only a few old beetles were active in autumn. In autumn season 1996 no newly emerged beetles were caught.

[1] Amongst these beetles there may be some immigrants that arrived at the end of spring 1992; for calculating the net reproductive rate in 1992 it is assumed that 50 % of these beetles emerged in autumn 1992; 2probably emerged in autumn i but not trapped until spring i+1.

Table 2a			season										
			A '92	S '93	A '93	S '94	A '94	S '95	A '95	S '96	A'96	S '97	A'97
generation	before A '92	females		56		24		10		3		0	
		males		37		12		3		2		0	
	A '92	females	147	113 (76.9)	0	66 (58.4)	0	29 (43.9)	0	18 (62.1)	1	7 (38.9)	0
		males	112	85 (75.9)	1	50 (58.8)	0	22 (44.0)	0	5 (22.7)	0	3 (60.0)	0
		females		$(13)^1$	0	(7) (53.8)	1	(3) (42.9)	0	(1) (33.3)	0	0 (0)	
		males		$(15)^1$	0	(10) (66.7)	0	(4) (40.0)	0	(2) (50.0)	0	0 (0)	
	A '93	females			201	157 (78.1)	1	105 (66.9)	1	66 (62.9)	1	45 (68.2)	5
		males			163	124 (76.1)	2	90 (72.6)	2	45 (50.0)	0	23 (51.1)	0
		females				62^2	1	36 (58.1)	0	26 (72.2)	0	17 (65.4)	4
		males				60^2	2	39 (65.0)	0	20 (51.3)	0	11 (55.0)	0
	A '94	females					182	140 (76.9)	1	96 (68.6)	1	70 (72.9)	1
		males					135	102 (75.6)	0	71 (69.6)	2	47 (66.2)	0
		females						21^2	0	14 (66.7)	0	11 (78.6)	1
		males						22^2	0	15 (68.2)	0	8 (53.3)	0
	A '95	females							46	14 (30.4)	0	11 (78.6)	0
		males							40	7 (17.5)	0	4 (57.1)	0
		females								1^2	0	1 (100.0)	0
		males								0			
	A'96	females									0		
		males									0		
		females										1^2	0
		males										2^2	0
	A'97	females											73
		males											62
		females											
		males											

For the investigation 1982 - 1992, when the enclosure fence was not beetle-proof, the total number of beetles (females plus males) in spring i is estimated by the Jolly-Seber method for the respective plateau-phase; the number of females (**Table 1**) is estimated using the temperature dependent sex ratio: for the 1993 - 2001 data the sex ratio of the Jolly-Seber estimates in spring i regresses on the sum of the temperature in the second decade of May of the previous years i-1, i-2 and i-3: sex ratio = -0.9953 x temperature sum + 98.9678; $p_{b1} = 0.001$, $p_{b0} < 0.001$, $r^2 = 78.5$ % (as the sex ratio varied relatively little it is not arcsine transformed; Sachs 1992, p. 354; cf. chapter C. IV.8).

For the years 1993 - 1995 and 1997 - 2000 the abundance of young females and males emerged in late summer/autumn (abbreviated as "autumn") is the number of unmarked beetles trapped in autumn i and spring i+1 plus the estimated number of young beetles that were not trapped in autumn and did not survive the winter. The latter is calculated by means of the survival probability: this is the proportion of retrapped beetles in spring i+1 of those marked in autumn i. For the years 1982 - 1992, 1996 and 2001 the number of freshly emerged beetles are Jolly-Seber estimates for the plateau-phase in autumn corrected by the formula:

$$y = 1.1649\,x + 3.5365$$

y = calculated total number of young individuals,

x = number of freshly emerged individuals trapped in autumn i (Jolly-Seber estimate)

y - x = the number of young individuals not trapped in autumn, which includes the beetles that did not

The beetle-proof fence was erected in summer 1992; nevertheless, the number of beetles freshly emerged in autumn 1992 is calculated by this formula, as amongst the unmarked beetles trapped in spring 1993 there may be specimens which immigrated at the end of spring 1992.

Table 2b			season								
			A'97	S'98	A'98	S'99	A'99	S'00	A'00	S'01	A'01
generation	A'92	females	0	1 (14.3)	0	0 (0)					
		males	0	0 (0)							
		females									
		males									
	A '93	females	5	23 (51.1)	5	4 (17.4)	0	0 (0)			
		males	0	4 (17.4)	2	1 (25.0)	0	0 (0)			
		females	4	5 (29.4)	0	1 (20,0)	0	0 (0)			
		males	0	1 (9.1)	0	1 (100.0)	0	0 (0)			
	A'94	females	1	42 (60.0)	5	16 (38.1)	0	1 (6.2)	0	0 (0)	
		males	0	12 (25.5)	2	2 (16.7)	0	0 (0)			
		females	1	8 (72.7)	0	2 (25.0)	0	0 (0)			
		males	0	2 (25.0)	1	1 (50.0)	0	0 (0)			
	A '95	females	0	7 (63.6)	1	5 (71.4)	0	0 (0)			
		males	0	1 (25.0)	0	1 (100.0)	0	0 (0)			
		females	0	1 (100.0)	0	1 (100.0)	0	0 (0)			
		males									
	A'96	females									
		males									
		females	0	1 (100)	0	0 (0)					
		males	0	1 (50.0)	0	0 (0)					
	A'97	females	73	62 (84.9)	2	43 (69.3)	1	18 (41.9)	0	5 (27.8)	1
		males	62	51 (82.3)	2	35 (68.6)	0	22 (62.9)	0	9 (42.9)	0
		females		16^2	0	11 (68.7)	0	6 (54.5)	1	2 (33.3)	0
		males		12^2	2	7 (58.3)	1	3 (42.9)	1	1 (33.3)	0
	A'98	females			43	35 (81.4)	0	13 (37.1)	0	3 (23.1)	0
		males			44	39 (88.6)	2	23 (59.0)	0	10 (43.5)	0
		females				12^2	0	5 (41.7)	0	3 (60.0)	0
		males				13^2	1	7 (53.8)	0	2 (28.6)	0
	A'99	females					61	29 (47.5)	0	12 (41.4)	0
		males					61	32 (52.5)	0	14 (43.7)	2
		females						5^2	0	4 (80.0)	0
		males						3^2	0	1 (33.3)	1
	A'00	females							21	19 (90.5)	1
		males							19	17 (89.5)	1
		females								9^2	1
		males								3^2	0
	A'01	females									77
		males									53
		females									
		males									

The parameters $b_1 = 1.1649$ and $b_0 = 3.5365$ in the above equation are calculated from the number of freshly emerged individuals trapped in autumn/spring 1994/1995, 1995/1996, 1997/1998, 1998/1999, 1999/2000 and 2000/2001 (statistics of the above equation: $p_{b1} < 0.001$, $p_{b0} = 0.665$; $r^2 = 99.3$ %). Data for 1993/1994 are not included because of the unusually large number of unmarked individuals in spring 1994. This was probably due to gaps in the trapping program in autumn 1993 and marking with less durable colour spots in autumn 1993 (**Table 2**). Data for 1996/1997 are not included because no young individuals were found in autumn 1996 (**Table 2**). Data for 1995/1996 are included although both the number of young that emerged in autumn 1995 and their survival rate were relatively small (**Table 2**). In our 2001 article we assumed that the small survival rate of this generation is due to an inappropriate marking procedure; now, however, we can show that the low survival rate of this generation fits rather well with the dependence of the survival of the young females and males on an abiotic factor (cf. chapter C. VII. 2.). Nevertheless the data for 1995/1996 could be more or less incorrect; when the data are not included the parameters in the above equation are $y = 1.1482\ x + 8.6234$ (number of emerged animals in autumn calculated using this formula and the accordingly changed Bi values are given in brackets in **Table 1**). The two series of Aai, and respectively, Bi values given in **Table 1** are highly correlated (r^2 = 99.98, and 99.96 %, respectively). - The statistical parameters reported in this article are based on the Bi values not in brackets (if the other Bi values are used the significance levels remain unchanged).

B. I. 3. (2.14) Statistics

All significance levels (p) given in this article are based on two-tailed tests. We consider the following significance levels: weakly significant: $p < 0.10$; significant: $p < 0.05$; highly significant: $p < 0.01$. For regression and correlation analyses the SPSS Version 6.1 for Power Macintosh computers is used. - In two cases (1, 2) the indicated significance levels need to be corrected. (1) Usually we assume a linear regression a priori (if not stated analyses refer to linear regressions). A posteriori we also checked for logarithmic, inverse, quadratic, cubic, power, compound, S, logistic, growth and exponential dependences (according to the possibilities offered by SPSS). In the case of a non-linear regression the indicated significance level is corrected using the formula $p_{corr} = 1 - (1 - p)^k$ (Sachs, 1992, p. 183) with $k = 11$ functions tested. If the linear and (after correction) the most significant non-linear regression display the same significance level, a linear relationship is assumed. In a few cases a distinct non-linear regression is assumed a priori (in these cases the indicated significance level is not corrected). - (2) When we test for a linear regression of a distinct dependent variable on several potential independent variables, and respectively, for the influence of a distinct independent variable on several dependent variables, the significance levels are corrected according to the above formula with k = number of potentially independent, and respectively, dependent variables tested. After a distinct working hypothesis is developed significance levels of statistical tests are no longer corrected. - When the same variable of females and males is separately tested a correction is not applied (however, an iso-directional dependence of a female and male trait is interpreted as a corroboration of the relevance of the dependence). For the application of this rule 3 examples are given (1-3). (1) As an indicator of the end of the activity season in spring the 75 % mark of the cumulative number of individual last captures, CNL, is used (chapter C. II.); if the 75 % mark for females and males is included in a series of regressions k is increased by only 1. (2) As a further parameter of post-reproductive "recreation" (chapter C. II.) the relative weight - the mean of the quotient "individual weight divided by the individual length" - measured in June is used for females and the relative weight measured in the 3rd decade of May for males; also in this case k is only increased by 1 if the parameter of post-reproductive "recreation" of females and males is tested; (3) as a measure of reproductive investment in females the relative mean weight of females - the quotient "mean weight of females divided by mean weight of males" - in the 1st decade of May is used (chapter C. I. 2.); in males the measure of reproductive investment is the probability of individuals being trapped in the plateau-phase in spring (chapter C. I. 3.); if the measures of reproductive investment of females and males are included in a series of regressions, k is increased by 2 (!). - It has to be stressed that corrections of the significance levels are performed only in the analysis of data relevant to particular questions, for example: what abiotic and biotic factors in spring i influence the survival of young from autumn i until spring i+1 (cf. chapter C. VI.)? When corrections are performed on the result of all tests, the uncorrected significance level of a linear regression must be $p \leq 0.001$ in order to remain at least weakly significantly ($p \leq 0.10$) after correction (these cases are not explicitly referred to; however, the uncorrected significance levels are given in the tables).

Multiple regression analyses are performed assuming that the functions of all independent variables are linear. In the case of a significant non-linear function in multiple regression, the dependent variable is fitted by this function; the fitted value is tested for a significant linear influence on the dependent variable; when this is the case the fitted value is used in the multiple linear regression (the significance levels of T- and F-test are corrected depending on the increased number of estimated parameters). - For stepwise regression by SPSS Version 6.1 in the field "Stepping Method Criteria - Use probability of F" 0.099 is set into the field "Entry" (field "Removal": 0.10).

To test for periodicity in a series of data the periodogram analysis of Lamprecht & Weber (1970) combined with the statistics of Sokolove & Bushell (1978) is used; moreover, the probably phase-identical values are regressed on the phases of the indicated period assuming a cubic function a priori.

B. I. 4. Simulation of the fluctuation in net reproductive rate and parameters of the female stock

The fluctuations in net reproductive rate and abundance of the female generations in spring are simulated on the basis of the empirical parameters of a temperature and density-dependent reproduction function (assuming 55 % of the young beetles of autumn are females), a temperature dependent probability of the young females surviving from autumn i until spring i+1, density-dependent probabilities for 0.5 and 1.5 year old females and constant probabilities of the females of the older generations of surviving from spring i until spring i+1. For computing survival functions the measured survival probabilities are not arcsine transformed; however, simulated survival probabilities higher (lower) than the observed maximum (minimum) probability are replaced by the maximum (minimum) observed.

B. I. 5. (2.16) Documentation

Original data are in the theses of F. W.'s students. A list of these theses, since 1999, is given in our 2001 publication (Weber & Heimbach). This list is completed by the following titles. Theses that were "in preparation" in 2001 are also cited here; in some cases the final title is different.

Reding. G., 2001: Stabilität durch räumliche Risikoverteilung innerhalb einer Subpopulation? Untersuchungen an *Carabus auronitens* im Forst Tinnen (Münster).

Köhl, I., 2001: Die Körpergröße adulter *Carabus auronitens* als Parameter der präimaginalen Entwicklungsbedingungen.

Köhl, S., 2001: Untersuchungen zur Dichteabhängigkeit des Aktivitätsverhaltens bei einer Gehegepopulation von *Carabus auronitens*.

Dörr, N., 2001: Experimentelle Untersuchungen zur intra- und interspezifischen Attraktion bei *Carabus auronitens* und *C. nemoralis*.

Wibbeler, E., 2001: Untersuchungen zur Wirkung lokaler Unterschiede innerhalb eines Waldes auf die Entwicklung des Laufkäfers *Carabus auronitens* (Coleoptera, Carabidae).

Koch, B., 2001: Zur Eignung des Ausmaßes der altersbedingten Exoskelett-Abnutzung als populationsdynamischer Parameter bei Carabiden (empirische Untersuchungen an *Carabus auronitens*).

Baumgartner, R., 2002: Die Abhängigkeit der individuellen Überlebensfitness von der Ausprägung phänotypischer Merkmale in einer lokalen Population von *Carabus auronitens* F. (Coleoptera, Carabidae) (mit einer Abschätzung des Adaptationspotentials der Population).

Zeidler, M., 2002: Die langjährige Natalitäts-Mortalitätsbilanz zweier eingehegter *Carabus auronitens*-Populationen (mit eigenen Untersuchungen im Jahr 2001).

Drees, C., 2003: Ausbreitung flugunfähiger Arthropoden über Heckenkorridore: Untersuchungen an einer Metapopulation von *Carabus auronitens* im Münsterland.

All theses are in the Library of the Zoological Institutes of the University of Muenster (Westphalia).

B. II. Corrections

While preparing this article we detected mistakes in our 2001 publication (Weber & Heimbach) that we want to correct:

- p. 106, last paragraph, 1st sentence: "females" and "males" were interchanged.
- p. 125, legend of Fig. 4.2-1: read: "p = 0.0934".

B. III. Life history of *Carabus auronitens* in the population studied

In the Westphalian Lowlands *Carabus auronitens* is an univoltine spring breeder with summer larvae (Larsson, 1939; Thiele, 1977). Depending on ambient temperature, activity season in spring starts in March or the 1st half of April. Spring season ends in the 2nd half of June or the 1st half of July. Surviving old beetles remain in rotten wood until March / April of the following year. During this long-term dormancy they appear to remain in the same resting place. Weight loss during dormancy is surprisingly low (Weber & Heimbach, 2001). Adult females live for up to 5.5 years and have then six reproductive seasons (**Table 2**). Survival of males is somewhat lower than that of females.

In the late summer/autumn season almost exclusively freshly emerged beetles are active (**Table 2**). This season starts in August and continues until October or the beginning of November. During post-ecdysial ripening young beetles are obligatorily active for food uptake (Klenner, 1989; Weber & Heimbach, 2001), before searching for a hibernating place. During post-ecdysial ripening the exocuticle is sclerotized, endocuticle deposited and fat body developed. During the ripening process the individual weight increases by about 30 % to 75 % in females and by 25 % to 65 % in males. The duration of the post-ecdysial ripening process differed between years of investigation: it lasted for three to six or more weeks (Weber & Heimbach, 2001).

The young beetles that emerge in late summer/autumn are the descendants of the beetles that reproduced in the spring of the same year. Thus, preimaginal development takes 2 - 3 months and occurs in late spring/early summer. In high mountain regions *Carabus auronitens* is also a spring breeder, but there are indications that the larvae hibernate and young beetles emerge in spring of the following year (Weber & Heimbach, 2001).

B. IV. Advantages and disadvantages of studying population dynamics in C*arabus auronitens*

Population studies in *Carabus auronitens* have several advantages (1 - 4).

(1) The species is abundant at many sites.

(2) The adults live on the ground and are readily caught in pitfall traps. Indeed, adults of *Carabus auronitens* climb trees; but as they do not fall when climbing they are unlikely to escape from enclosures via trees (Weber & Heimbach, 2001).

(3) The adults are large and easy to handle. It is simple to encode them individually and durably by polishing marks on their elytra while they are narcotized with CO_2. Only very freshly emerged individuals are difficult to mark by polishing; branding, however, should be avoided (Weber & Heimbach, 2001). Adults are rather tolerant of submergence in rain water that collects in the pitfall traps (Weber & Heimbach, 2001); nevertheless traps should be covered with a roof.

(4) An important advantage is the possibility of estimating the net reproductive rate of groups living in open areas: in late summer/autumn almost exclusively young adult (freshly emerged) beetles are active (cf. B. III.). Net reproduction is defined as the quotient "number of freshly emerged beetles divided by number of females active in the plateau-phase in spring of the same year" (Weber & Heimbach, 2001). For estimating net reproduction in an open area, of course, one needs to use many pitfall traps on a relatively small area which are frequently left open; however, they should not be left continuously open. We opened the traps twice a week for one night (Weber & Heimbach, 2001). If capture and recapture rates are high the Jolly-Seber method (Southwood, 1978) can be used to estimate the abundance of beetles present at the trapping area on the particular night. The trapping area, however, is larger than the area with traps. If it is not possible to estimate the size of the trapping area, the area with traps should be surrounded by a beetle-proof fence (Weber & Heimbach, 2001).

A disadvantage of using *Carabus auronitens* for population studies is one it shares with most carabid species: the larval stages are only occasionally captured in pitfall traps. Thus, the developmental rates of the larval stages remain unknown: the net reproductive rate as defined above is a "black box": it is made up of egg laying rate, developmental rates of the preimaginal stages and partially also the early mortality of the freshly emerged adults.

C. Results

C. I. Reproductive investment

C. I. 1. Net reproductive rate

The generation table of the enclosed population shows remarkably high variability in the number of young beetles that emerged in late summer/autumn (**Table 2**). In the 0.2 ha enclosure the estimated number of freshly emerged beetles varied between 3 (1996) and 522 (1993): obviously, mean net reproductive rate per female, Bi, varied greatly. Taking a temperature-dependent sex ratio in the spring stocks of 1982 - 1992 as a basis (chapter B. I. 2.), Bi varied between 3.11 and 0.01 over the 20-year study (**Table 1**). A consequence of the varying reproductive rate is an unstable generation structure of the population (**Table 2**, cf. chapter C. VIII. 1. & C. VIII.4.).

Bi is the result of the reproductive investment of both females and males active in the spring of year i. The specific reproductive investment of females is in oogenesis, that of males is in mate searching (Baumgartner, 2000). In the following two chapters (chapter C. I. 2. & C. I. 3.) the dependence of Bi on these gender-specific reproductive investments is analysed.

C. I. 2. Weight increase of females in spring (intensity of oogenesis)

Egg production could not be measured directly. However, we estimate the intensity of oogenesis by the changes that occur in the relative mean weight of females. The quotient "mean weight of the females divided by the mean weight of the males trapped over the same period in spring" serves as an operational measure of egg production: the larger the number of chorionized eggs in the ovaries of a female the larger is its relative weight; thus, an increase in a females' relative weight predominantly reflects egg growth by vitellogenin incorporation (Weber & Heimbach, 2001). The advantage of using the quotient "mean weight of females divided by mean weight of males" is that differences in body size between different age cohorts are largely eliminated (appendix 1). The weight quotient is based on the weight of all females and males trapped in a distinct interval (decade or month) in spring; each individual is considered as often as it was trapped. The weight of trapped beetles was regularly determined from 1985 until 2001.

If the relative mean weight of females reflects intensity of oogenesis, the average of this parameter should increase during the course of spring and decrease at the end of spring. Indeed, the average of the relative mean weight almost continuously increases from the end of winter until the 3rd decade of May, and thereafter decreases (**Table 3a**). - If the variability in Bi is (at least in part) due to variability in egg production, the coefficient of variation (CV) of the relative mean weight of females should be largest when the eggs are developing, that is, in the intervals in which the relative mean weight is high. This assumption seems to be fulfilled (**Table 3a**). The a priori assumptions that the development of both the relative mean weight and the CV of the relative mean weight during spring can be described by a quadratic function are fulfilled (**Fig. 1a - c**). - The assumption that the development of the females' relative mean weight reflects oogenesis is also supported by the following finding. In some years females were dissected on several days in spring, and the number of eggs with a chorion in each female determined (Weber & Heimbach, 2001: Table 3.7.-1 & 3.7.-2). The mean number of chorionized eggs per female follows a quadratic function with a (relatively flat) maximum in mid May ($p_{func} = 0.010$, $r^2 = 14.3$ %).

Table 3 a Average and standard deviation (S.D.) of the relative mean weight of females at intervals during the course of spring. n = 17. Relative mean weight: mean absolute weight of females divided by mean absolute weight of males trapped in the same period in spring.

time interval	**average**	**S.D.**	**n**
end of winter*	1.274	0.048	16
3rd decade of March	1.332	0.086	9
1st decade of April	1.348	0.078	16
2nd decade of April	1.371	0.086	17
3rd decade of April	1.394	0.099	17
1st decade of May	1.394	0.115	17
2nd decade of May	1.382	0.100	17
3rd decade of May	1.404	0.101	17
June (1st - 3rd decade)	1.375	0.059	17

* sampled in resting places outside the enclosure

Table 3 b Linear regression of net reproductive rate B_i **(Table 1)** on the relative mean weight of females in the 2nd and 3rd decade of April, 1st, 2nd and 3rd decade of May and June (p_{corr}: corrected for the number of independent variables tested {k = 6}). n = 17.

time interval	**sign**	**p**	**coefficient of determination (%)**	p_{corr} **(k = 6)**
2nd decade of April	+	0.202	10.6	
3rd decade of April	+	**0.004**	**43.5**	**0.024**
1st decade of May	+	**0.001**	**53.8**	**0.005**
2nd decade of May	+	**0.002**	**49.1**	**0.010**
3rd decade of May	+	0.408	4.6	
June	+	0.216	10.0	

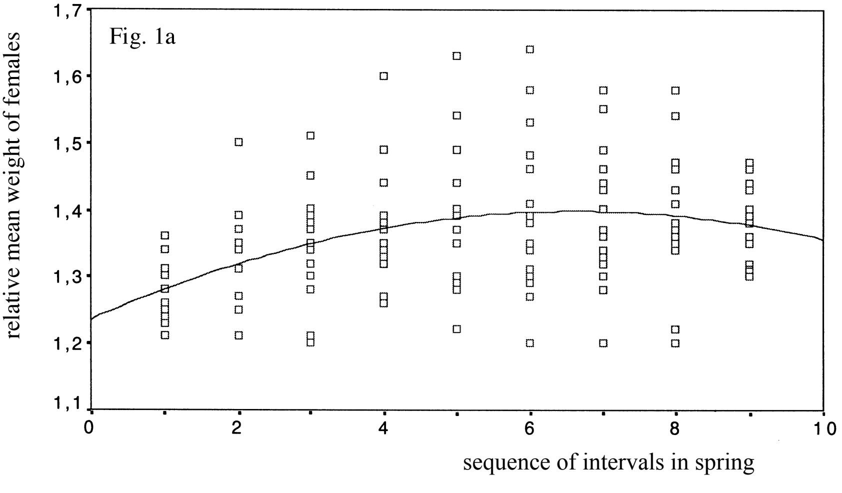


Fig. 1 a Regression of relative mean weight of females ("mean weight of females divided by mean weight of males") developed during spring on the sequence of intervals in spring (cf. **Fig. 1c**). Quadratic function: $y = 0.0491\ x - 0.0037\ x^2 + 1.2348$; $p_{b1} < 0.001$, $p_{b2} = 0.003$, $p_{b0} < 0.001$, $p_{func} < 0.001$, $r^2 = 15.6\ \%$.

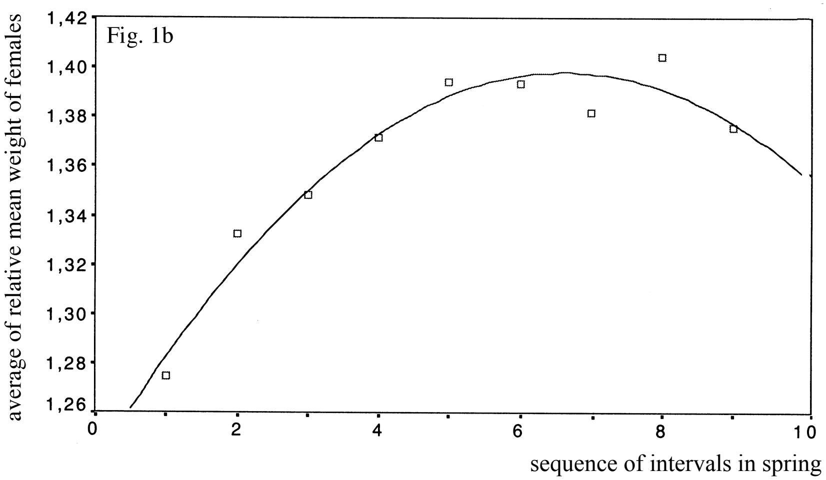


Fig. 1 b Regression of averaged relative mean weight of females on the sequence of intervals in spring (cf. **Fig. 1c**). Quadratic function: $y = 0.04483\ x - 0.0036\ x^2 + 1.2378$; $p_{b1} < 0.001$, $p_{b2} = 0.001$, $p_{b0} < 0.001$, $p_{func} < 0.001$, $r^2 = 94.8\ \%$.

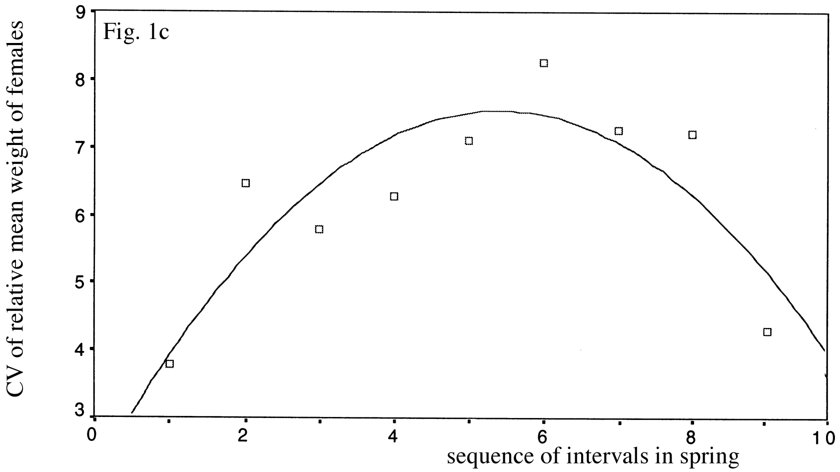


Fig. 1 c Regression of the CV of the relative mean weight of females on the sequence of intervals in spring. Quadratic function: $y = 2.0147\ x - 0.1861\ x^2 + 2.0829$; $p_{b1} = 0.008$, $p_{b2} = 0.011$, $p_{b0} = 0.116$, $p_{func} = 0.0228$, $r^2 = 71.6\ \%$. Abscissa: 1: end of winter, 2: 3rd decade of March, 3: 1st decade of April, 4: 2nd decade of April, 5: 3rd decade of April, 6: 1st decade of May, 7: 2nd decade of May, 8: 3rd decade of May, 9: June.

From **Table 3a** we conclude that the relative mean weight in the 2nd and 3rd decade of April, in the 1st - 3rd decade of May and in June could influence net reproductive rate Bi. Indeed, Bi regresses positively on females relative mean weight in the 3rd decade of April and 1st and 2nd decade of May (also when the significance levels are corrected for the number of independent variables tested: k = 6; **Table 3b**;

Fig. 2). Regressions on the relative mean weight developed in the other intervals, are not significant (even the uncorrected significance levels are > 0.10).

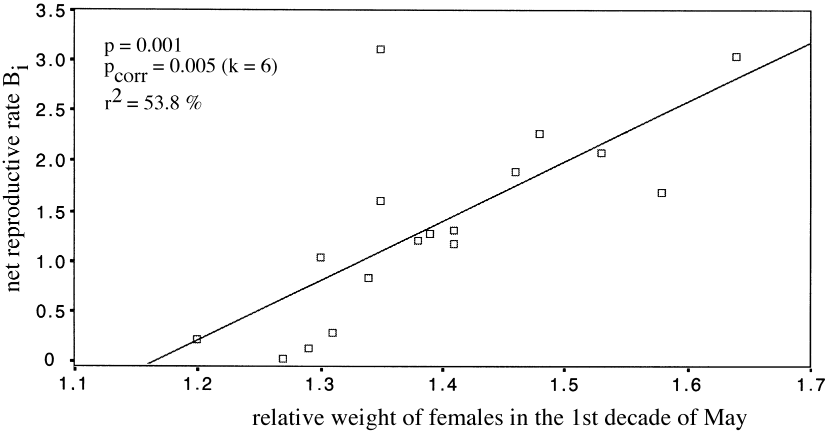


Fig. 2 Linear regression of net reproductive rate, Bi (**Table 1**), on the relative mean weight of females in the 1st decade of May. The significance level is corrected for the number of weight parameters tested: the relative mean weight in the 2nd decade and 3rd decade of April, in the 1st, 2nd and 3rd decade of May and in June (k = 6) (cf. **Table 3**).

The relative mean weights developed in the 3rd decade of April and in the 1st and 2nd decade of May are highly correlated with each other (the coefficient of determination is between 64.6 and 81.6 %, p is < 0.001 in each pairwise comparison). Correspondingly, in the stepwise regression of Bi on female relative mean weight developed in these decades, the relative mean weight in the 1st decade of May is influential, whereas that for the 3rd decade of April and 2nd decade of May are not, and eliminated:

stepwise regression of B_i on:

rel. mean weight in 1st decade of May: +, $p = 0.001$, $r^2 = 53.8$ %

rel. mean weight in 3rd decade of April: -, $p = 0.965$

rel. mean weight in 2nd decade of May: +, $p = 0.559$

In further analyses we use female relative mean weight in the 1st decade of May as a measure of their reproductive investment (egg production).

Bi is the reproductive performance of the population in year i and dependent on the total number of females present in the plateau-phase in spring i. It should be possible to estimate the contribution of the different age cohorts to reproduction by using the relative mean weight of their females (referred to the mean weight of the males of the respective age cohort). A tentative analysis of our data shows that there is a weakly significant regression of Bi on the relative mean weight of 0.5 year old females in the 1st decade of May (+, $p = 0.056$, $r^2 = 55.2$ %). Also the relative mean weight of 2.5 year old females in the 1st decade of May has a significant influence (+, $p = 0.017$, $r^2 = 79.4$ %), whereas, remarkably, the relative mean weight of 1.5 year old females does not (+, $p = 0.214$, $r^2 = 24.3$ %; significance levels uncorrected). However, the relative mean weights of 1.5 year old females in the spring intervals averaged as in **Fig. 1b** for the total stock are not smaller than those of the other female age cohorts (data not shown). Obviously our data sets are too small in order to critically estimate the reproductive contribution of the various age cohorts of females by means of relative mean weight: data are available since 1993 for the 0.5 year old females, and since 1994 for the 1.5 year old females etc.; because of the extremely low reproductive rate in 1996 (**Table 1 & Table 2**) a further value is missing. However, the adaptation of the population studied to an abiotic key factor (temperature in a critical period of May) can only be explained by assuming that the age cohorts contribute differently to egg production (chapter C. VIII. 1.).

C. I. 3. Level of activity of males in spring (mate searching activity)

Possibly, the reproductive investment of males is in mate searching activity. As a measure of this we use the mean number of catches per individual and trapping day during the plateau-phase in spring. The number of values (= number of seasons with data) is 9 (1993 - 2001).

Bi regresses highly significantly on the arcsine transformed mean trapping probability of males (linear, +, $p < 0.001$, $r^2 = 89.5$ %; **Fig. 3**). Thus, the result supports the hypothesis that the specific reproductive effort of males is mate searching activity. As females do not engage in mate searching (Baumgartner, 2000) Bi does not regress on the arcsine transformed mean trapping probability of females (+, p = 0.485). This observation lessens the possibility that the regression of Bi on the male activity level merely reflects the dependence of both Bi and the catching probability on temperature (for multiple regressions see chapter C. IV.4. & C. IV.5.).

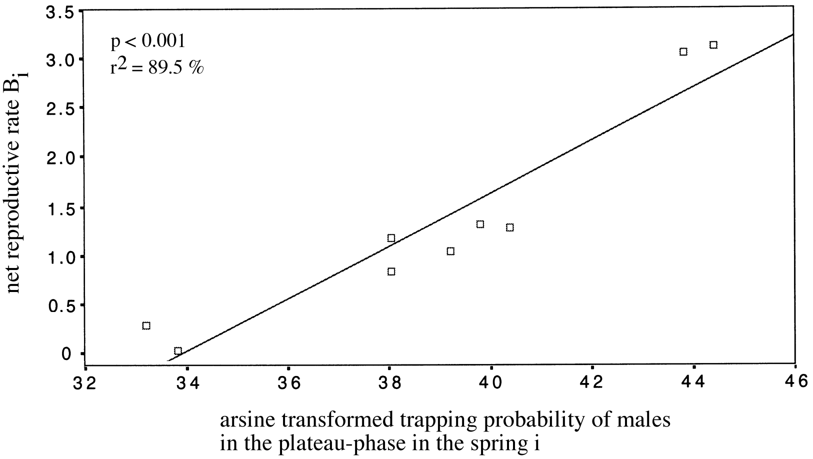


Fig. 3 Linear regression of net reproductive rate, Bi, on the probability of trapping males in the plateau-phase of spring i.

As can be expected from these results the specific investments of females and males are positively correlated:

relative mean weight of females in the 1st decade of May vs activity level of males in the plateau-phase:

r = +, 0.627, p = 0.070 (uncorrected).

C. I. 4. Multiple regression of net reproductive rate on biotic key factors of reproduction

To what extent is the variability in net reproductive rate, Bi, explained by the biotic key factors oogenesis (chapter C. I. 2.) and male activity level (chapter C. I. 3.)?

regression of Bi on:

female relative mean weight in the 1st decade of May: +, $p = 0.362$

male activity level: +, $p = 0.002$

constant: $p = 0.001$

$p_{mult} = 0.005$, $r^2 = 90.9$ %

Remarkably, the coefficient of determination is only marginally smaller when Bi is monofactorially regressed on the male activity level (see above).

C. II. Post-reproductive "recreation" in late spring

After the reproductive activities ceased, females and males prepare for a long period of dormancy by developing their fat body in late spring (Weber & Heimbach, 2001). We assume that fat consumption and reproductive investment are positively correlated: (1) the relative body weight (mean of individual weight divided by individual length) of females and males should be the smaller after reproduction, and (2) the duration of post-reproductive activity should be longer the higher the reproductive investment; we use the 75 % mark of the cumulative number of individual last captures (CNL) as a measure of the end of the spring season (i.e. the number of the day in the year when the cumulative number of individual last captures passes 75 %). - The parameter "weight divided by length" in late spring and the 75 % mark of CNL are used as parameters of post-reproductive "recreation".

(1) We regress the relative weight (individual weight divided by length) of females and males in the 3rd decade of May and in June on net reproductive rate, Bi, (chapter C. I. 1.) and the gender-specific parameters of reproductive investment (chapter C. I. 2. & C. I. 3.). In females and males the parameters "weight divided by length" in the 3rd decade of May and in June are positively correlated, but only significantly in males (females: $r^2 = 3.8$ %, $p = 0.613$; males: $r^2 = 60.5$ %, $p = 0.013$). As expected all regressions are negative: the higher Bi, and the higher the reproductive investment of females and males, the lower is the body-size related weight in the 3rd decade of May and in June (**Table 4 a, b**). In females, the regression of "weight divided by length" in the 3rd decade of May and in June on Bi is not significant; the regression of this parameter in June on the relative mean weight in the 1st decade of May is significant (also after correction using $k = 2$), whereas the regression of this parameter in the 3rd decade of May on the females' investment is not significant. In further analyses we use "weight divided by length" in June as the parameter of post-reproductive "recreation" in females. - In males, both regressions on Bi are significant, as is the regression of "weight divided by length" in the 3rd decade of May on the activity level. Thus, in males, "weight divided by length" in the 3rd decade of May seems to be an adequate measure of post-reproductive "recreation".

Table 4 a Linear regression of female relative weight (mean of "individual weight divided by individual length") in the 3rd decade of May and in June on net reproductive rate Bi, and the parameter of reproductive investment of females. Values for "weight divided by length" are available from 1993 (n = 9).

regression of "weight divided by length" in the 3rd decade of May on:			
	sign	**p**	**r^2**
net reproductive rate Bi	-	0.581	4.6 %
relative mean weight in 1st decade of May	-	0.243	18.8 %

regression of "weight divided by length" in June on:				
	sign	**p**	**r^2**	**p_{corr} (k = 2)**
net reproductive rate Bi	-	0.298	15.3 %	
relative mean weight in 1st decade of May	**-**	**0.013**	**60.6 %**	**0.027**

Table 4 b Linear regression of male relative weight (mean of "individual weight divided by individual length") in the 3rd decade of May and in June on net reproductive rate Bi, and reproductive investment of males (activity during plateau-phase). n = 9.

regression of "weight divided by length" in the 3rd decade of May on:				
	sign	**p**	**r^2**	**p_{corr} (k = 2)**
net reproductive rate Bi	**-**	**0.030**	**51.1 %**	**0.060**
activity level in plateau-phase	**-**	**0.020**	**56.5 %**	**0.039**

regression of "weight divided by length" in June on:				
	sign	**p**	**r^2**	**P_{corr} (k = 2)**
net reproductive rate Bi	**-**	**0.035**	**49.2 %**	**0.069**
activity level in plateau-phase	**-**	**0.075**	**38.3 %**	**0.145**

(2) We assume that the duration of the spring season (75 % mark of CNL) positively depends on net reproductive rate, Bi, and the degree of reproductive investment (chapter C. I. 2. & C. I. 3.): the higher Bi and the reproductive investment in early spring, the later the 75 % mark of CNL is passed. Moreover, we assume that the 75 % mark of CNL for males regresses negatively on "weight divided by length" in the 3rd decade of May, and the 75 % mark of CNL of females on "weight divided by length" in June: the lower the weight parameter, the longer the spring season continues. CNL values are available from 1993 (n = 9), they vary greatly: in females they were recorded between May 24 and June 29, in males between May 17 and June 26. - In females the 75 % mark of CNL is positively correlated with the end of the plateau-phase (r^2 = 47.8 %, p = 0.039), in males there is no such correlation.

Indeed, 75 % marks of CNL for females and males regress on net reproductive rate and gender-specific reproductive investment as expected positively (**Table 5 a, b**). However, neither for females or males, is the regression on Bi significant. - On the other hand, for females, the regression is significant with respect to the relative mean weight in the 1st decade of May (**Table 5a**; however, the significance disappears when the largest CNL value is deleted; **Fig. 4**); it seems that it takes longer to develop a weight sufficient for long term dormancy the higher the reproductive investment. - The regression on male reproductive investment (activity level) is not significant (**Table 5b**).

Table 5 a Linear regression of 75 % mark of CNL of females on net reproduction rate Bi, the operational measure of reproductive investment of females (mean weight of females divided by mean weight of males in 1st decade of May) and that of post-reproductive "recreation" of the females (mean of "individual weight divided by individual length" in June). Values for the 75 % mark of CNL are available from 1993 (n = 9).

	sign	**p**	**r^2**	**p_{corr} (k = 3)**
net reproductive rate Bi	+	0.413	9.8 %	
reproductive investment				
relative mean weight in 1st decade of May	+	**0.021**	55.8 %	**0.060**
post-reproductive "recreation" parameter				
weight divided by length in June	-	**0.002**	75.2 %	**0.007**

Table 5 b Linear regression of 75 % mark of CNL for males on net reproductive rate Bi, the operational measure of reproductive investment (activity level) in males and that of post-reproductive "recreation" of males ("mean of individual weight divided by individual length" in the 3rd decade of May). n = 9.

	sign	**p**	**r^2**
net reproductive rate Bi	+	0.331	13.5 %
reproductive investment			
trapping rate in plateau-phase	+	0.380	11.1 %
post-reproductive "recreation" parameter			
weight divided by length in the 3rd decade of May	-	0.152	26.9 %

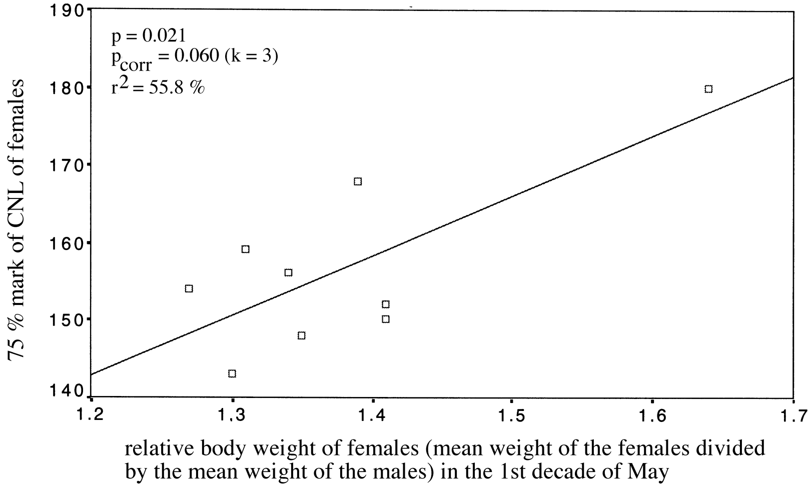


Fig. 4 a Linear regression of 75 % mark of female CNL (number of the day in the year) on the relative mean weight of females ("mean weight of females divided by mean weight of males") in the 1st decade of May. The significance disappears when the largest CNL value is omitted: p = 0.655 (uncorrected), r^2 = 3.5 %. Cf. **Table 5a**.

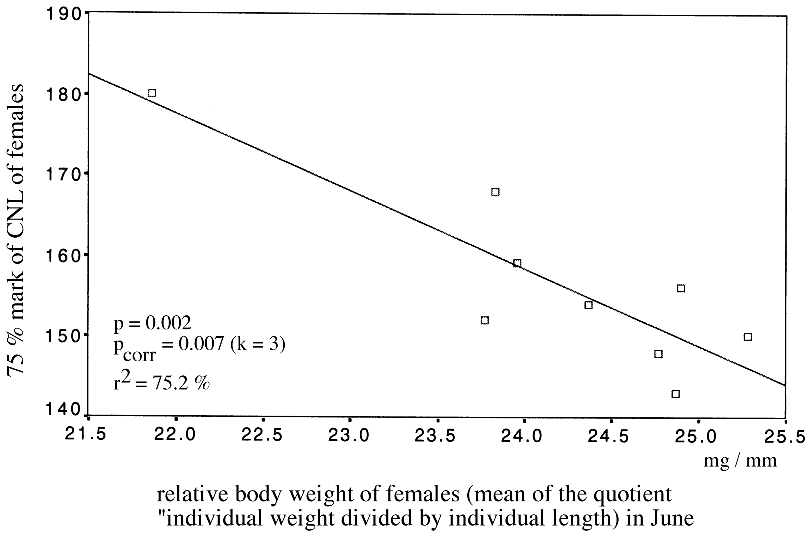


Fig. 4 b Linear regression of 75 % mark of female CNL on the relative body weight of females (mean of the quotient "individual weight divided by individual length") in June. The regression is still weakly significant when the largest CNL value is omitted: $p = 0.099$ (uncorrected), $r^2 = 38.7$ %. Cf. **Table 5a**.

Also as expected, the regression of the 75 % mark of CNL on "weight divided by length" in the 3rd decade of May, and respectively in June is negative; for females the regression is highly significant, even after correcting the significance level (**Table 5a**, **Fig. 4**). For males, also this regression is not significant (**Table 5b**).

In summary, the assumptions concerning the factors affecting the female post-reproductive "recreation" are largely confirmed; in males the assumptions are statistically not fulfilled.

C. III. Probability of survival in spring

C. III. 1. Survival of females

In this chapter the relationship between reproductive investment in spring i and the probability of surviving until spring i+1 is analysed. - Survival rates could be measured since the enclosure was beetle-proof; thus, for the total female stock the number of values is 8; for the distinct generations the number of values is smaller; also for the 0.5 year generation it is smaller, as in spring 1997 only a few young beetles were active (**Table 2**). The probability of survival of females and males from the 1st to the 2nd, the 2nd to the 3rd and the 3rd to the 4th spring is on average around 60 %; thereafter the probability of survival is smaller, decreasing more quickly in males than females (**Table 2; Table 6**).

The arcsine transformed probability of survival of all females (irrespective of age) as well as of distinct female generations regress negatively on Bi; however, in no case is the regression significant (uncorrected significance level > 0.10). - Also, the probability of survival of females of the total stock does not significantly depend on the females' reproductive investment (relative mean weight in the 1st decade of May; chapter C. I. 2.; uncorrected significance level > 0.10); however, it is noteworthy that also this regression, as expected, is negative.

Table 6 Mean, minimum and maximum survival of females and males measured from 1993 in the beetle-proof enclosure (cf. **Table 2**). The (not arcsine transformed) percentage of surviving beetles (rounded) is given.

females	**mean (%)**	**minimum (%)**	**maximum (%)**
1st spring - 2nd spring	61	38	80
2nd spring - 3rd spring	54	44	74
3rd spring - 4th spring	58	29	75
4th spring - 5th spring	29	0	45
5th spring - 6th spring	13	5	18
males			
1st spring - 2nd spring	60	43	69
2nd spring - 3rd spring	47	25	64
3rd spring - 4th spring	38	25	52
4th spring - 5th spring	18	0	43
5th spring - 6th spring	18	0	33

Also, the probability of survival of the total female stock does not significantly depend on the females' post-reproductive "recreation" parameters ("weight divided by length" in June and the 75 % mark of CNL; chapter C. II.; uncorrected significance level > 0.10): however, as expected, the regressions are positive.

These poor results do not support a trade-off between reproductive investment and probability of survival in females. However, in chapter C. V. 5. & C. IX. 2. good reasons are presented for assuming such a trade-off.

C. III. 2. Survival of males

The probable male investment in reproduction is in mate searching activity (chapter C. I. 3.). The arcsine transformed survival rate of the males of the total stock (irrespective of age) does not regress on this parameter or on Bi (uncorrected significance level > 0.10); however, as expected, the regressions are negative. - Also, the probability of survival of all males regresses positively, but not significantly on the males' post-reproductive "recreation" parameter, "weight divided by length" in the 3rd decade of May (uncorrected significance level > 0.10). - On the other hand, the probability of survival of the males highly significantly regresses on the 75 % mark of CNL, but by a rather questionable quadratic function (convex viewed from above; $p_{func/corr} = 0.001$ {corrected using k = 11; cf. chapter B. I. 3.}, $r^2 = 97.8\%$): 6 of the 8 values are clustered around the maximum of the curve.

C. IV. Temperature in spring - a key factor in the dynamics of the *Carabus auronitens* population studied

C. IV. 1. The influence of temperature on net reproductive rate

Soon after the start of this study (Althoff et al., 1994) we realized that Bi is small when temperature in May of spring i is low. Malte Prigge determined the period in May, when the average mean daily temperature most strongly influences Bi: this is the coldest of the seven seventeen day periods starting between May 9 and May 15, and ending between May 25 and May 31. The regression of Bi on this temperature is highly significant: +, $p < 0.001$; $r^2 = 59.3$ % (**Fig. 5**). This critical 17 days period is called

"Prigge's interval" and the average temperature for this period "Prigge's temperature", abbreviated as PTi. Malte Prigge determined the critical period using Bi values estimated between 1982 and 1998. Remarkably, the overwhelming influence of PTi on reproduction is confirmed for the entire 20 year study.

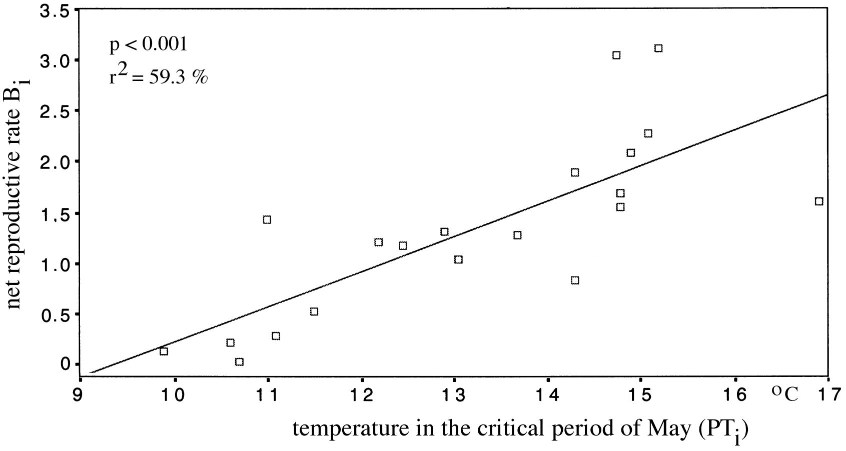


Fig. 5 Linear regression of net reproductive rate, Bi, (**Table 1**) on the temperature in the critical period of May (Prigge's temperature, PTi).

PTi is positively correlated with the average mean daily temperature in the 2nd and 3rd decade of May:

PTi vs temperature 2nd decade of May: +, $p < 0.001$, $r^2 = 76.9$ %

PTi vs temperature 3rd decade of May: +, $p = 0.001$, $r^2 = 46.2$ %

In some years, Prigge's interval includes one or two days in the 1st decade of May (May 10, or May 9 and 10). However, PTi is not correlated with the temperature in the 1st decade of May (+, $r^2 = 5.1$%, $p = 0.339$), and also it is not correlated with decadal temperatures in April and June.

Correspondingly, Bi regresses significantly on the temperatures in the 2nd and 3rd decade of May:

monofactorial regression of Bi on:

2nd decade of May: linear: +, $p = 0.002$, $r^2 = 41.5$ %

3rd decade of May: linear: +, $p = 0.055$, $r^2 = 18.9$ %

(significance levels not corrected)

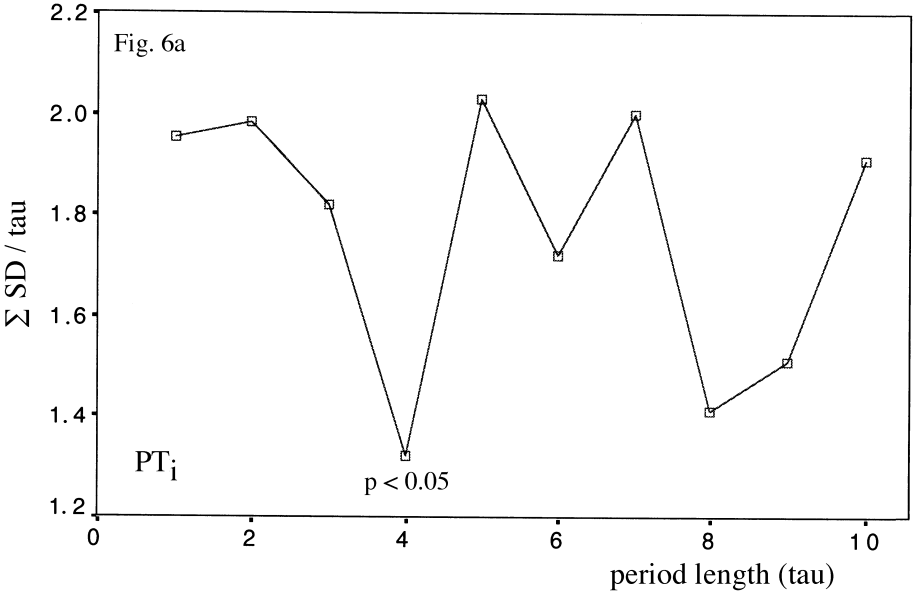
On the other hand, Bi does not regress on the temperature in any other decade in spring, even not on the temperature in the 1st decade of May (+, $p = 0.261$ {uncorrected}, $r^2 = 6.9$ %).

When Bi is bifactorially regressed on PTi and the temperature in the 2nd or 3rd decade of May, the influence of PTi is highly significant (+, $p_{part} = 0.013$ and, respectively, +, $p_{part} = 0.001$), whereas that of the decadal temperatures is not (-, $p_{part} = 0.677$, $p_{mult} < 0.001$; $r_{mult}^2 = 59.8$ %, and respectively, -, $p_{part} = 0.435$, $p_{mult} < 0.001$, $r_{mult}^2 = 60.8$ %). When Bi is trifactorially regressed on PTi and the temperatures in the 2nd and 3rd decade of May, the influence of PTi is highly significant (+, $p = 0.007$), whereas that of the temperature in the 3rd decade of May is weakly significant, and that of the temperature in the 2nd decade of May not significant (remarkably the influence of both is negative): $p = 0.081$ and, respectively, $p = 0.103$; $p_{mult} < 0.001$, $r_{mult}^2 = 67.0$ %. When Bi is bifactorially regressed on the average of both decadal temperatures and PTi, the influence of the decadal average temperature is weakly significant (-, $p = 0.071$), and that of PTi is highly significant again (+, $p = 0.004$) ($p_{mult} < 0.001$, $r_{mult}^2 = 66.6$ %). Thus, PTi influences Bi more strongly than the temperature in the 2nd and 3rd decade of May. - The negative influence of the temperature in the 2nd and 3rd decade of May in the multiple regressions with PTi is puzzling (their influence is positive in the monofactorial regressions; see above).

We assume that egg ripening, incorporation of vitellogenin into the oocytes, starts in April, and when conditions are favourable increases in late April and early May; egg laying is assumed to start in late April or in early May. PTi could also influence egg ripening (vitellogenesis), however, we assume that the strong influence of PTi on Bi is predominantly due to its effect on the development of embryos and young larvae: egg growth in the 1st decade of May most strongly influences Bi (chapter C. I. 2., **Table 3b**), but temperature in later May (PTi, and temperature in the 2nd and 3rd decade of May) also influences Bi (see above).

C. IV. 2. Periodogram analysis of the fluctuations in critical temperature, PTi, and net reproductive rate, Bi

The periodogram analysis of the fluctuations in Prigge's temperature, PTi, and net reproductive rate, B_i, indicates that they both display a periodicity of 4 years (**Fig. 6**). **Fig. 7** shows the regression of PTi and Bi on the phases 1, 2, 3 and 4 of the 4 year period. As expected the regressions are cubic; in both cases this a priori assumption is significant. Remarkably, the coefficient of determination for the Bi values is clearly larger than that for PTi values, i.e. Bi shows a considerably stronger 4 year periodicity than PTi (cf. also the significance of the respective minimum in **Fig. 6**). This may be due to the concerted action of PTi and certain periodically fluctuating biotic factors on the determination of Bi (cf. chapter C. VII. 6. & chapter D. III. 2.).



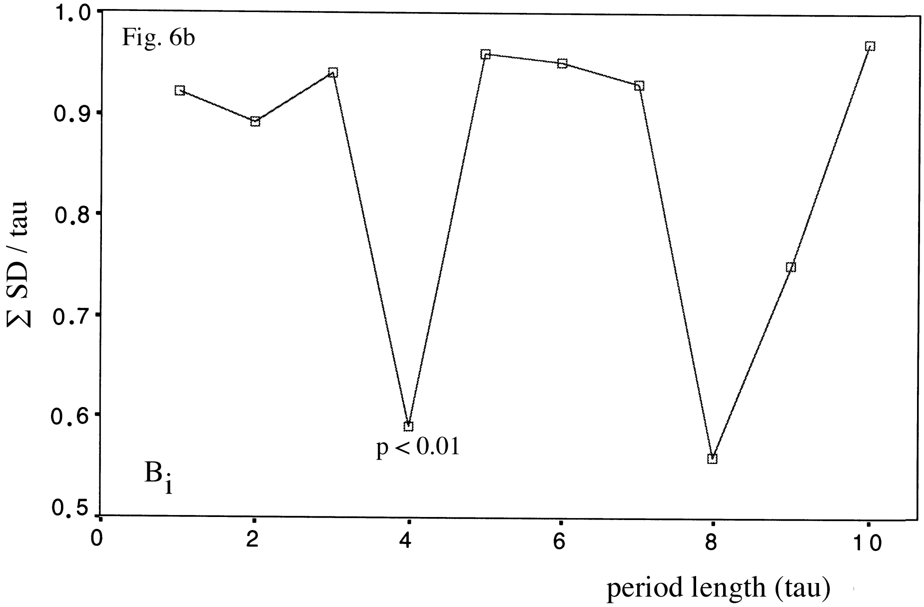
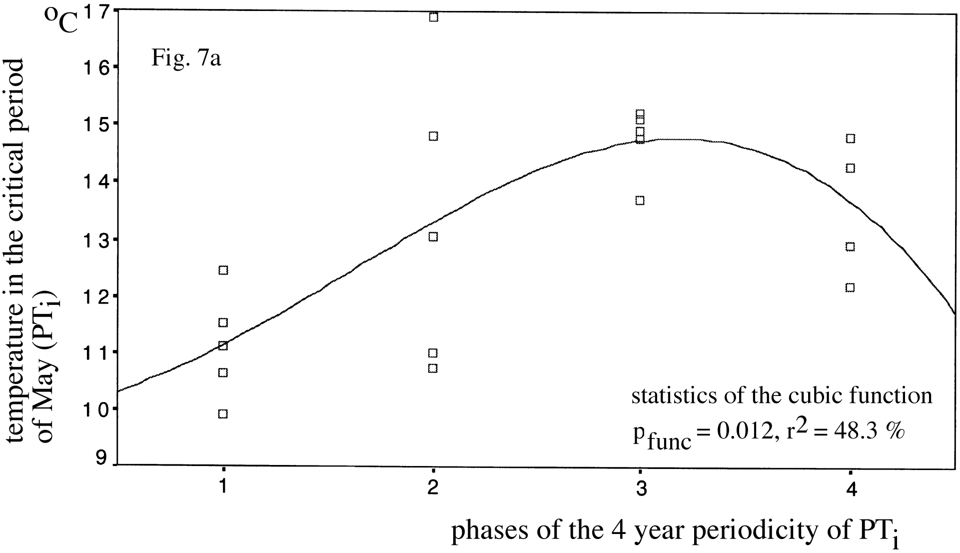


Fig. 6 Periodogram analysis of Prigge's temperature, PTi, for 1982 - 2001 (**Fig. 6a**) and net reproductive rate, Bi, for 1982 - 2001 (**Fig. 6b**, **Table 1**). Periodogram analysis after Lamprecht & Weber (1970), statistics after Sokolove & Bushell (1978).



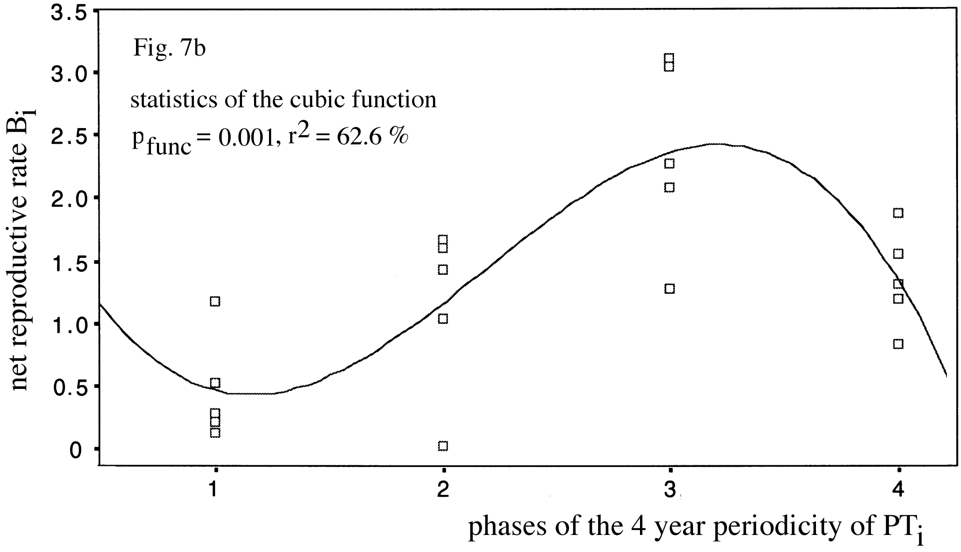


Fig. 7 Cubic regression of Prigge's temperature, PTi, for 1982 - 2001 **(Fig. 7a)** and net reproductive rate, Bi, for 1982-2001 **(Fig. 7b**, **Table 1)** on the phases of the 4 year periodicity . The plots are phase identical. An adverse weather event is likely to occur in year 1.

In addition, reproductive investments (the relative mean weight of females in the 1st decade of May, and the arcsine transformed probability of trapping of males in the plateau-phase in spring) on which Bi regresses highly significantly (chapter C. I. 2. & C. I. 3.) show a minimum at tau = 4 years in the periodogram analysis, however, the periodicity is not significant (not shown).

Malte Prigge calculated the critical May interval and the temperature in this interval since 1891 (since 1891 mean daily temperatures are known for the region of the city of Münster, Westphalia). The resulting 111 values of PTi display a 4 year and furthermore a 7 year periodicity, which seems to differ from a period of 8 years (multiple of the 4 year periodicity; **Fig. 8**). The regression of the 111 PTi values on the period phases 1, 2, 3 and 4 is cubic and significant (p = 0.0354). The coefficient of determination, however, is rather small (**Fig. 8**) (appendix 2).

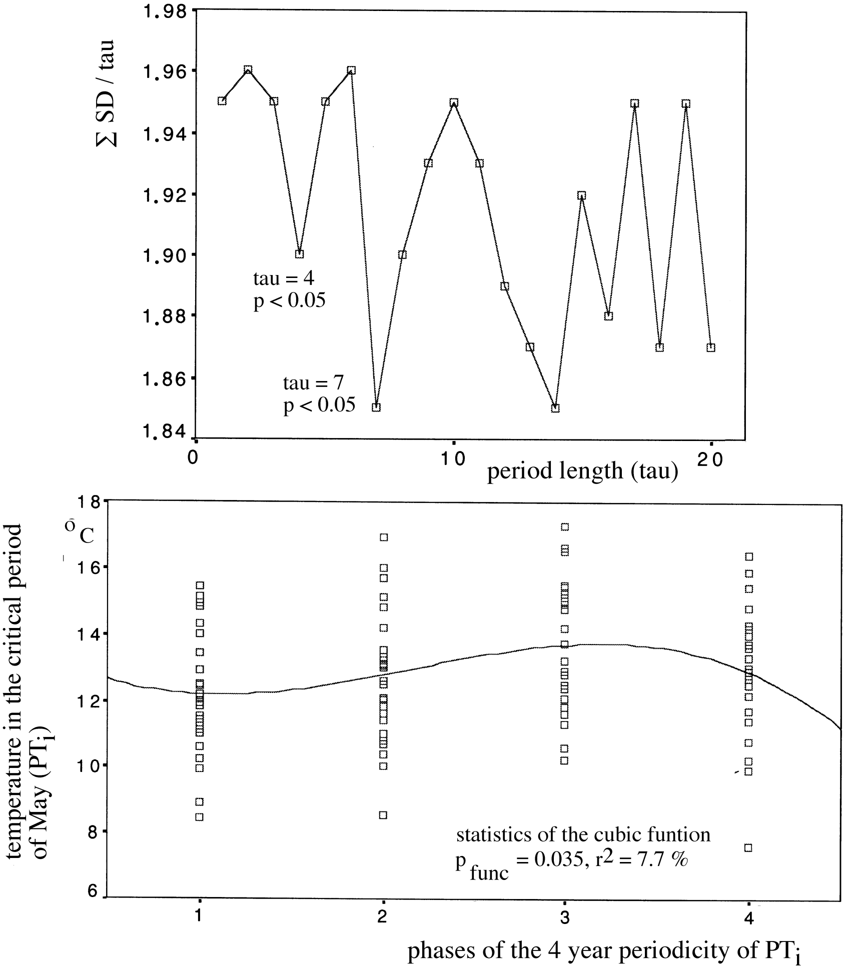


Fig. 8 Periodogram analysis of Prigge's temperature, PTi, for 1891 - 2001 (after Lamprecht & Weber, 1970, statistics after Sokolove & Bushell, 1978) (above) and cubic regression of PTi 1891-2001 on the phases of the 4 year periodicity (below). An adverse weather event is likely to occur in year 1.

C. IV. 3. The effect of temperature on the weight increase of females (oogenesis)

To what extent is the relative mean weight of females in the 1st decade of May (a measure of the females' reproductive investment; chapter C. I. 2.) influenced by temperature? We test the influence of the mean daily temperature of this decade, the previous decades and Prigge's critical interval on this parameter (**Table 7**). The relative mean weight of females in the 1st decade of May regresses with a quadratic function on the temperature in the 2nd decade of April; the significance level, however, is > 0.10 after second correction. As the physiological basis of such influence is obscure this phenomenon is not likely to control the dynamics of the population (chapters D. III. 1. & D. III. 6.; however, the questionable influence of the temperature in the 2nd decade of April on the weight development of females will be considered in some critical tests in this chapter and in chapters C. IV. 5. & C. V. 3.).

Table 7 Regression of the relative mean weight of females (mean weight of females divided by that of males) in the 1st decade of May, which is a measure of female reproductive investment (oogenesis, **Table 3b**), on the average of mean daily temperature at intervals in spring. For p_{corr} cf. chapter B. I. 3. n = 17. "Form of function" gives the sign of the linear regression, and respectively, the form of the quadratic regression (viewed from above).

mean daily temperature in	**function**	**form of function**	**p**	**r^2**	**p_{corr} (k = 11)**	**p_{corr} (k = 5)**
1st decade of April	linear	+	0.779	0.5		
2nd decade of April	linear	-	0.344	6.0		
	quadratic	**concave**	**0.006**	**51.6**	**0.066**	0.2896
3rd decade of April	linear	-	0.119	15.4		
1st decade of May	linear	+	0.282	7.7		
Prigge's interval	linear	+	**0.010**	**36.4**		**0.050**

The relative mean weight of females in the 1st decade of May regresses significantly on Prigge's critical temperature, PTi (**Table 7**; for PTi cf. chapter C. IV. 1.). This is surprising as Prigge's critical interval in some years only includes only one or two days (May 10, or May 9 and 10) of the 1st decade of May. Obviously, there is an anticipatory influence of PTi on the weight development of females. We described an example of this strange phenomenon, called "Prigge's paradox", in our paper (Weber & Heimbach, 2001; appendix 3). The anticipatory effectiveness of PTi could simply be due to a correlation between the temperatures in Prigge's interval and those in previous decades. This however is not the case:

correlations

PTi vs temperature in the 1st decade of April: +, $p = 0.665$, $r^2 = 1.1$ %

PTi vs temperature in the 2nd decade of April: -, $p = 0.385$, $r^2 = 4.2$ %

PTi vs temperature in the 3rd decade of April: -, $p = 0.284$, $r^2 = 6.3$ %

PTi vs temperature in the 1st decade of May: +, $p = 0.339$, $r^2 = 5.1$ %

PTi and the temperature in the 2nd decade of April (see above) do not mutually abolish their influence on the relative weight of females in the 1st decade of May (as the relative mean weight regresses with a quadratic function on the temperature in the 2nd decade of April it is fitted by this function; the fitted value is used as an independent variable; the significance level of the influence of the fitted value and p_{mult} are corrected as outlined in chapter B. I. 3.):

regression of the relative mean weight of females in the 1st decade of May on:

PTi: +, $p = 0.012$

$fit_{weight\ in\ 1st\ decade\ of\ May}$: +, $p < 0.02$

$p_{mult} < 0.05$, $r_{mult}^2 = 69.8$ %

Also the mean daily temperature in the 3rd decade of April and 1st decade of May do not abolish the significance of the influence of PTi on the relative mean weight of females in the 1st decade of May:

regression of the females' relative mean weight in the 1st decade of May on:
PTi: +, $p = 0.018$
temperature in 3rd decade of April: +, $p = 0.193$
$p_{mult} = 0.017$, $r_{mult}^2 = 43.9$ %
regression of the females' relative mean weight in the 1st decade of May on:
PTi: +, $p = 0.019$
temperature in 1st decade of May: +, $p = 0.508$
p_{mult} 0.033, $r_{mult}^2 = 38.5$ %

When the relative mean weight of females in the 1st decade of May is regressed on PTi, the value fitted by the quadratic function of the temperature in the 2nd decade of April, the temperature in the 3rd decade of April and 1st decade of May (cf. **Table 7**), the influence of PTi is still significant (data not shown).

The main challenge of this study is to develop a theory to account for the population dynamics of this *Carabus auronitens* population which explains the apparent anticipatory influence of PTi on the weight development of females in early spring. This phenomenon can easily be interpreted as an adaptation: investment is reduced when conditions will be adverse during the early development of the offspring. The question however is: What (biotic) factor(s) in early spring could "inform" the females of the conditions which are likely to occur during early development of their offspring in later spring (see chapters C. VII. 6., C. IX. 1. & D. III. 2.)?

C. IV. 4. The effect of temperature on the activity of males

The arcsine transformed trapping probability of males in the plateau-phase in spring i (see chapter C. I. 3.) regresses highly significantly on PTi (+, $p < 0.001$, corrected with $k = 8$, the number of temperature parameters tested: $p_{corr} = 0.004$; $r^2 = 84.2$ %; data are available since the enclosure is beetle-proof: from 1993 till 2001, $n = 9$; **Fig. 9**). Although the plateau-phase regularly started in mid April male activity is not dependent on the temperature in April and May decades, and June. There is a dependence on the temperature in the 2nd decade of May which disappears when PTi is included in the regression (data not shown). Thus, the question arises, whether the dependence of male reproductive investment on PTi reflects a temperature influence, or - like the apparent influence of PTi on female reproductive investment - an adaptation mediated by an unknown biotic factor (see chapter C. VII. 4.).

In chapter C. I. 3. it is assumed that the dependence of Bi on male activity level is not because they both depend on temperature. Indeed, when Bi is regressed on the male activity and PTi the influence of the male activity is highly significant ($n = 9$):

regression of Bi on:
male activity: +, $p = 0.018$
PTi: +, $p = 0.714$
$p_{mult} = 0.001$, $r_{mult}^2 = 89.7$ %

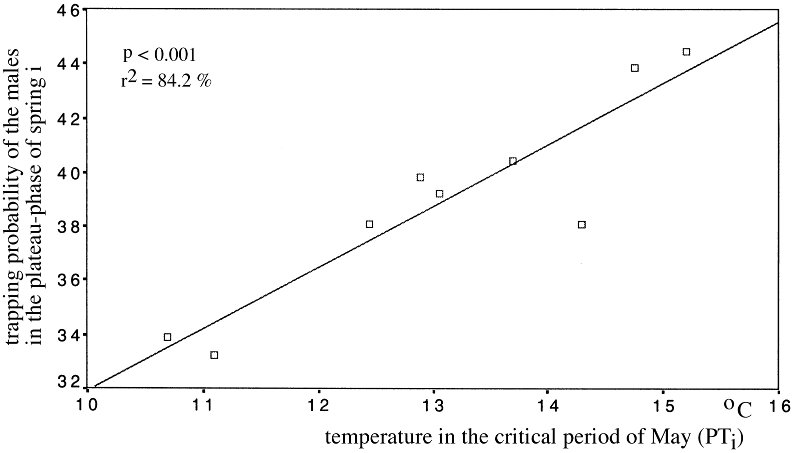


Fig. 9 Linear regression of the arcsine transformed probability of trapping males in the plateau-phase of spring i on PTi.

C. IV. 5. Multiple regression of net reproductive rate on temperature

At least two temperature parameters influence the net reproductive rate, Bi, and the reproductive investments of females and males: (1) PTi influences Bi (chapter C. IV.1.), female reproductive investment (chapter C. IV. 3.), and male activity (chapter C. IV.4.); (2) temperature in the 3rd decade of May may influence Bi (chapter C. IV. 1.); {(3) there is a questionable influence of temperature in the 2nd decade of April on female reproductive investment, see chapter C. IV. 3}.

Bi is regressed on these temperature parameters (for the temperature in the 2nd decade of April the fitted value of female relative mean weight in the 1st decade of May is used; cf. chapter C. IV. 3.):

PTi: +, $p = 0.002$

$\mathrm{fit}_{\mathrm{weight}}$ in 1st decade of May: +, $p < 0.10$

TM3: -, $p = 0.526$

$p_{\mathrm{mult}} < 0.05$, $r^2 = 65.3$ %

The multiple regression confirms the overwhelming influence of PTi on the variability of net reproductive rate, Bi: only the influence of PTi is significant.

C. IV. 6. The effect of temperature on post-reproductive "recreation"

The 75 % mark of CNL and the relative weight (weight divided by length) in late spring are used as indicators of post-reproductive "recreation" (cf. chapter C. II.). The 75 % mark of CNL for females regresses significantly on temperature in the 2nd and 3rd decade of April (temperature in the decades in April and May, PTi and temperature in June are tested: $k = 8$). The higher TA2 and TA3 the shorter the spring season (-, $p = 0.006$, $r^2 = 67.9$ %, corrected with $k = 8$: $p_{\mathrm{corr}} = 0.049$, and respectively, $p = 0.008$, $r^2 = 65.3$ %, $p_{\mathrm{corr}} = 0.065$; cf. **Fig. 10**). Although TA2 and TA3 are not correlated ($r = +0.185$, $p = 0.435$), in bifactorial regression TA2 and TA3 are not significant, in stepwise regression TA2 is influential. - No other temperature parameter influences female 75 % mark of CNL, neither PTi nor the temperature in June (even uncorrected significance levels are >0.10).

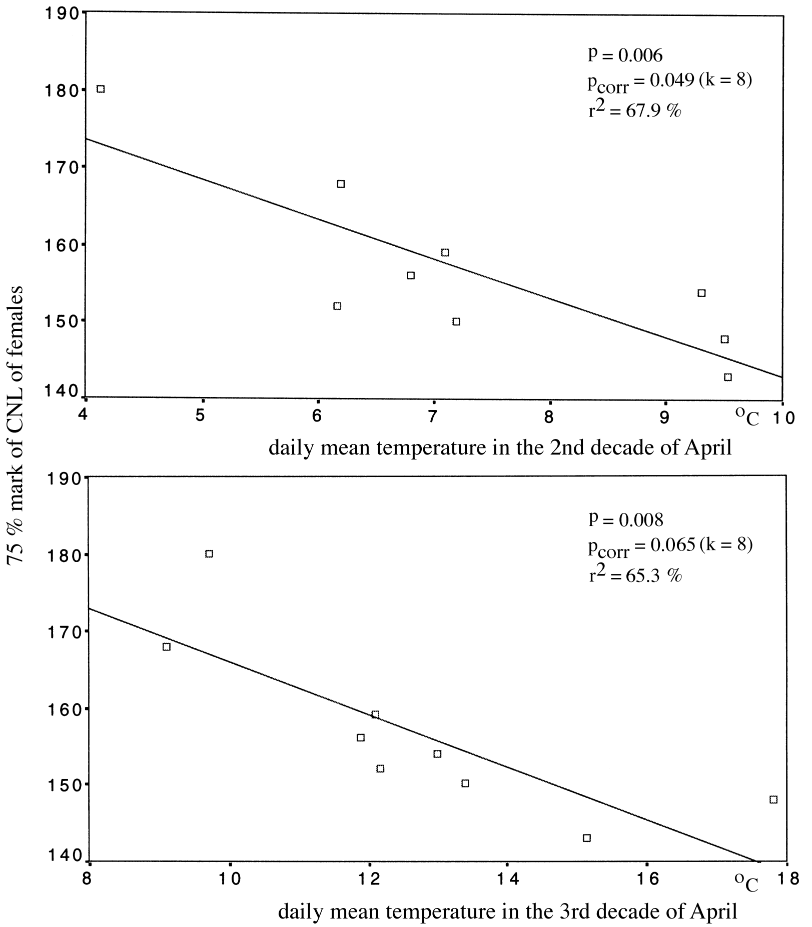


Fig. 10 Linear regression of 75 % mark of female CNL (number of the day in the year) on the mean daily temperature in the 2nd decade of April (above) and the 3rd decade of April (below). Both regressions remain significant when the largest CNL value is omitted ($p = 0.074$, $r^2 = 43.7$ %, and respectively, $p = 0.009$, $r^2 = 70.2$ %, significance levels uncorrected). Cf. chapter C. IV. 6.

The 75 % mark of CNL for females is also influenced (positively) by female relative mean weight (mean weight of the females divided by the mean weight of the males) in the 1st decade of May (**Table 5a**, chapter C. II.), which regresses on TA2 (**Table 7**, chapter C. IV. 3.). Is the influence of temperature in early spring on the duration of the female spring season mediated by its influence on female reproductive investment?

When female 75 % mark of CNL is regressed on TA2 and female relative mean weight in the 1st decade of May the influence of both independent variables is no longer significant; however, p_{mult} amounts to 0.028 and r_{mult}^2 to 69.5 % (r_{part}^2 of TA2 = 31 %, r_{part}^2 of relative mean weight = 5.2 %); in stepwise regression TA2 is influential (-, $p = 0.006$, $r^2 = 67.9$ %). Thus, the influence of temperature in the 2nd decade of April on the female 75 % mark of CNL seems to be partly mediated via its obscure influence on oogenesis (cf. chapter C. IV. 3.).

Also in males the temperature in the 2nd and 3rd decade of April negatively influences the duration of the spring season (TA2: -, $p = 0.048$, $r^2 = 45.0$ %, TA3: -, $p = 0.036$, $r^2 = 48.9$ %). Although the significances disappear when corrected for the number of temperature parameters tested (k = 8; see above) the regressions could be relevant, as the relationship is negative as in females. Like in females only TA2 is influential in bifactorial stepwise regression. The 75 % mark of CNL for males is not influenced by male reproductive investment (**Table 5b**, chapter C. II.).

The influence of TA2 on 75 % mark of CNL for females and possibly also males gives rise to test the relationship of the other parameter of post-reproductive "recreation" (a weight parameter in late spring; chapter C. II.) with this temperature. Indeed, there are hints that temperature influences female and male relative weight (weight divided by length) in the 3rd decade of May, and respectively in June. The regressions are positive: the higher the temperature in mid April the higher the post-reproductive relative weight (significance levels are corrected using k = 2).

female "weight divided by length" in June

TA2: +, $p = 0.023$, $r^2 = 54.6$ %, $p_{corr} = 0.045$

male "weight divided by length" in the 3rd decade of May

TA2: +, $p = 0.066$, $r^2 = 40.4$ %, $p_{corr} = 0.127$

When the female "weight divided by length " in June is regressed on TA2 and female relative mean weight in 1st decade of May, the measure of the female reproductive investment, no parameter is significant, in stepwise regression, however, the mean weight in the 1st decade of May has a significant effect (-, $p = 0.013$, $r^2 = 60.6$ %). The negative influence of female reproductive investment on "recreation" weight of females has been shown in chapter C. II. Also in this case the influence of TA2 might be mediated by the degree of oogenesis, which could be under the influence of TA2. - On the other hand, the possible influence of TA2 on male post-reproductive weight can not be interpreted analogously, as the male reproductive investment (level of activity in the plateau-phase) does not depend on this temperature parameter (cf. chapter C. IV. 4.).

C. IV. 7. Weak influences of temperature on survival in spring

The survival of young females and males that emerge in autumn i depends on the mean temperature they are exposed to during early development: the survival probability from autumn i until spring i+1 is higher the higher the temperature in the 2nd decade of May in spring i (see chapter C. VII. 2.). Does the (arcsine transformed) survival probability of older females and males depend on the average of the mean daily temperature in the 2nd decade of May in the year they have developed? With one exception the regressions are not significant. The exception concerns the 3.5 year old females whose survival probability positively regresses on the temperature in the 2nd decade of May of the year they developed (i-4) (+, $p = 0.021$, $r^2 = 95.8$ %, n = 4). - A further test using the temperature dependence of the survival of the young is performed in chapter C. IV. 8.

With two exceptions, the probability of females and males of the total stock (irrespective of age) and distinct age cohorts to survive spring i is not dependent on temperature in spring i. One exception is the survival of 1.5 year old males, which depends negatively on PTi (-, $p = 0.048$, $r^2 = 66.3$ %, n = 6); the other is the survival of 0.5 year old males, which regresses negatively on the average of the mean daily temperature in June: (-, $p = 0.028$, $r^2 = 65.2$ %, n = 7). In both cases the significance disappears when the significance level is corrected for the number of tests performed (k = 8).

C. IV. 8. Dependence of the sex ratio in spring i on temperature in previous springs

The abundances of females and males in the plateau-phase in spring (**Table 1**) are highly correlated (1993 - 2001: +, $p < 0.001$, $r^2 = 93.3$ %). However, the sex ratio of the total stock varies between 49.5 % and 66.5 % females in the plateau-phase of the springs in 1993 - 2001 (**Table 1**). This variability could be due to a larger effect of environmental factors on the male longevity. Our working hypothesis is based on the following observation: the survival of both young females and males from autumn i to spring i+1 depends on the average of the mean daily temperature in the 2nd decade of May (TM2) in spring i; but the dependence of male survival on $TM2_i$ seems to be stronger than that of female survival (chapter C. VII. 2.). To test the hypothesis that the variability in the sex ratio observed in the spring stock depends on a temperature-induced difference in fitness of freshly emerged females and males we regress the sex ratio of the 0.5 year old generation in spring i on TM2 in spring i-1, the sex ratio of the 1.5 year old generation in spring i on TM2 in spring i-2 etc; and the sex ratio of the total spring stock is regressed on the sum of the temperature in the previous 2nd decades in May (**Table 8**).

Table 8 Linear regression of the sex ratio of the 0.5 year old generation in spring i on the temperature in the 2nd decade of May (TM2) in spring i-1, the sex ratio of the 1.5 year old generation in spring i on TM2 in spring i-2 etc. The sex ratio of the total stock is regressed on the sum of the temperature in 2nd decade of May of previous years (sum = $TM2_{i-1} + TM2_{i-2} + TM2_{i-3}$). The sex ratio is based on the sum of all females and males recorded. As the sex ratio varies relatively little it is not arcsine transformed (Sachs 1992, p. 354). The significance levels are not corrected as the regressions are based on a well founded working hypothesis: the dependence of the survival of young from autumn i until spring i+1 on TM2i (chapter C. VI. 3.).

sex ratio'	**independent variable (temperature parameter)**	**sign of regression**	**significance level**	**coefficient of determination (%)**	**number of values[4] (enclosed area: 1993 - 2001)**
0.5y old[1]	$TM2_{i-1}$	**-**	**0.059**	**47.5**	8
1.5 y old[1]	$TM2_{i-2}$	**-**	**0.014**	**73.1**	7
2.5 y old[1]	$TM2_{i-3}$	**-**	**0.004**	**89.5**	6
3.5 y old[1]	$TM2_{i-4}$	-	0.265	5.0	5
total stock in the spring[1]	sum[3]	**-**	**0.003**	**74.1**	9
total stock in the plateau-phase[2]	sum[3]	**-**	**0.001**	**80.3**	9

[1] number of individuals present in spring (**Table 2**); [2] Jolly-Seber estimates for the plateau-phase of spring i (**Table 1**); [3] $TM2_{i-1} + TM2_{i-2} + TM2_{1-3}$. [4] generation 1996 is lacking (nearly no reproduction in 1996).

Indeed, the sex ratio of the 0.5, 1.5 and 2.5 year old beetles regresses negatively on the temperature in the 2nd decade of May of the year in which the beetles developed; the sex ratio of the total stock regresses negatively and highly significantly on the temperature sum $TM2_{i-1} + TM2_{i-2} + TM2_{i-3}$ (**Table 8**; for the formula of the regression cf. chapter B. I. 2.). This means that the lower the sum of the temperature in the previous 2nd decades in May the higher the proportion of females in spring i (**Fig. 11**). In multiple regression $TM2_{i-3}$ has the highest influence on the sex ratio of the total stock (-, p_{part} = 0.015, r_{part}^2 = 72.5 %), the partial regression coefficient of the influence of TM_{i-2} is 50.9 % (-, p_{part} = 0.072) and that of TM_{i-1} is 61.7 % (-, p_{part} = 0.036) (the temperature in spring i-4 has no influence, either when added to the sum or included in a multiple regression).

Is the deviation in the sex ratio of the young stock in autumn i due to an influence of $TM2_i$ on the survival of the preimaginal stages? To test this possibility we regress the sex ratio of the young trapped in the beetle-proof enclosure in the autumn i (1992 - 2001) on $TM2_i$: the regression is not significant (+, p = 0.985; r^2 = 0.0 %). Thus, the deviation from 0.50 in the sex ratio of the young in autumn and the variability in this ratio (1992 - 2001: 49.4 % - 59.2 %; **Table 2**) could be due to measuring errors or unknown factors.

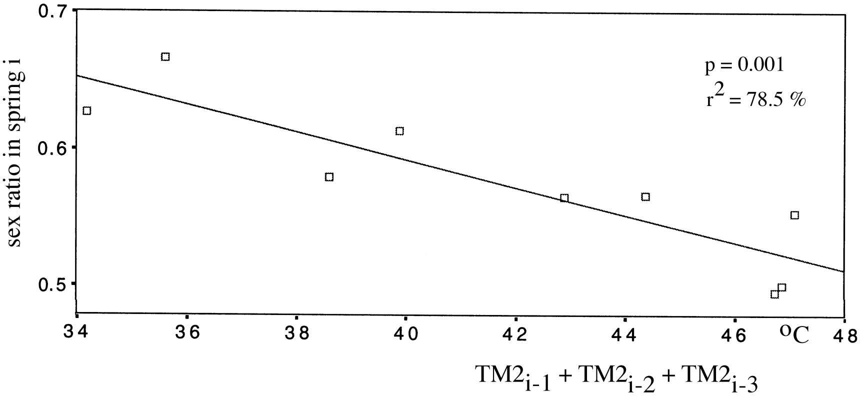


Fig. 11 Linear regression of the (not arcsine transformed) sex ratio in the plateau-phase of spring i on the sum of the temperature in the 2nd decade of May in previous years (cf. chapter C. IV. 8.). - The result is similar when the sex ratio is arcsine transformed ($p = 0.001$, $r^2 = 80.2$ %).

C. V. The influence of abundance on beetles in spring

C. V. 1. Abundance and food availability

We concluded in our 2001 paper (Weber & Heimbach) that a density-dependent food availability does not affect the *Carabus auronitens* population over the range of the abundances measured during this long-term investigation (**Table 1**). In order to re-examine this the relative mean body weight (weight divided by body length, mg / mm) measured during the spring season i is regressed on the abundance in spring i. As any limitation in food availability could be restricted to rather short periods the mean relative weight measured in April, May and June are tested for density dependence (the significance level is corrected using $k = 7$). As a measure of abundance the number of females plus males present in spring i is used (**Table 2**). Neither in females nor males is a dependence of body weight on abundance observed (**Table 9a**).

Table 9 a, b Regression of the relative weight (mean of "individual weight divided by individual length", mg / mm) of females and males in April, May and June on the number of females and males present in spring i and i-1 **(Table 2)**. An influence of abundance in spring i is the a priori assumption, thus significance levels of the regressions on abundance in spring i-1 have to be corrected with $k = 2$; moreover, the significance levels are corrected with the number of dependent variables tested ($k = 7$). Data measured from 1993 are used ($n = 9$); the critical number of beetles for calculating a mean (= 5) is not reached in early spring in some years ($n < 9$).

Table 9 a

independent variable: number of females and males present in spring i

females

month / decade	**n**	**sign**	**p**	**r^2 (%)**
April, 1st decade	6	-	0.172	40.9
April, 2nd decade	8	-	0.277	19.2
April, 3rd decade	9	-	0.184	23.7
May, 1st decade	9	-	0.342	12.9
May, 2nd decade	9	-	0.372	11.5
May, 3rd decade	9	+	0.485	7.2
June	9	+	0.227	20.0

males

month / decade	**n**	**sign**	**p**	**p_{corr} (k = 7)**	**r^2 (%)**
April, 1st decade	7	**-**	**0.082**	0.451	**48.5**
April, 2nd decade	8	-	0.311		16.9
April, 3rd decade	9	-	0.519		6.2
May, 1st decade	9	-	0.572		4.8
May, 2nd decade	9	-	0.705		2.2
May, 3rd decade	9	+	**0.096**	0.506	**34.6**
June	9	+	**0.090**	0.484	**35.6**

Table 9 b

independent variable: number of females and males present in spring i-1

females

month / decade	**n**	**sign**	**p**	**p_{corr} (k = 2)**	**p_{corr} (k =7)**	**r^2 (%)**
April, 1st decade	5	-	0.156			54.3
April, 2nd decade	7	**-**	**0.076**	0.147		**49.8**
April, 3rd decade	8	**-**	**0.030**	**0.059**	0.345	**57.2**
May, 1st decade	8	**-**	**0.024**	**0.048**	0.289	**59.9**
May, 2nd decade	8	**-**	**0.003**	**0.005**	0.037	**80.0**
May, 3rd decade	8	+	0.118			35.7
June	8	+	0.496			8.0

males

month / decade	**n**	**sign**	**p**	**p_{corr} (k =2)**	**p_{corr} (k=7)**	**r^2 (%)**
April, 1st decade	6	**-**	**0.047**	**0.092**	0.490	**66.8**
April, 2nd decade	7	**-**	**0.018**	**0.036**	0.227	**70.4**
April, 3rd decade	8	**-**	0.066	0.129		45.5
May, 1st decade	8	-	0.325			16.1
May, 2nd decade	8	-	0.658			3.5
May, 3rd decade	8	+	**0.040**	**0.078**	0.434	**53.3**
June	8	+	0.145			31.8

Although it is unlikely that a density-dependent over-exploitation of food in spring i-1 leads to a limitation of food availability in spring i, the mean relative weights measured in spring i are regressed on the abundance observed in spring i-1. Because of this a posteriori assumption, a further correction of the significance levels using k = 2 is applied. Surprisingly, some of the regressions are significant: in one case for females it is significant even after the two corrections (the sign is negative, **Tab. 9b).** This case concerns the weight in the 2nd decade of May. We assume that there is no density-dependent limitation of food, but a direct inhibiting influence of the density in spring i-1 on the physiological (and behavioural) conditions of the beetles ("mutual interference", chapter D. III. 4.): the level of mutual interference experienced in spring i-1 affects the reproductive investment of the surviving beetles in spring i and - if also the reproductive investment of the 0.5 year old beetles depends on the density in spring i-1 - the development of the gonads of the young generation (F1) in spring i. These assumptions are confirmed by the analyses presented in the chapters C. V. 2., C. V. 3., C. V. 4., C. V. 5. and C. VI. 5.

C. V. 2. Abundance and net reproductive rate

To test the above assumption that mutual interference in spring i-1 is effective, reproductive success (Bi; in this sub-chapter), reproductive investment (sub-chapters C. V. 3. & C. V. 4), and post-reproductive "recreation" and survival (sub-chapter C. V. 5) in spring i are regressed on density in spring i-1. The female abundance in the plateau-phase in spring is used as independent variable (**Table 1**).

To critically assess the influence of abundance in spring i-1 on net reproductive rate, Bi, in spring i we assume an influence of Ai a priori. Bi regresses negatively on female abundance (**Table 10**); although Ai and Ai-1 are highly correlated (+, p = 0.007, r2 = 36.0 %) Ai-1 has a much more marked effect: even after two corrections of the significance level it is still weakly significant.

Table 10 Linear monofactorial regression of net reproductive rate, Bi, and other parameters of the population dynamics in spring i on parameters of abundance (Ai and Ai-1: Jolly-Seber estimates for female density in the plateau-phase in spring, **Table 1**). The following dependent variables are tested (see also text in chapter C. IV.): (1) net reproductive rate, Bi; (2) the gender-specific measure of reproductive investment: female relative mean weight (mean weight of females divided by that of males) in the 1st decade of May, and male activity in the plateau-phase of the spring season; (3) the probability of surviving from spring i until spring i+1 (irrespective of age) of females and males; (4) the post-reproductive "recreation" parameter; females: mean of "individual weight divided by individual length in June"; males: mean of "individual weight divided by individual length in the 3rd decade of May"; (5) 75 % mark of CNL of females and males. - p: concerning Bi an influence of Ai is assumed a priori; the level of significance of the influence of Ai-1 on Bi is corrected using k = 2; concerning the other dependent variables an influence of Ai-1 is assumed a priori , and the significance level of the influence of Ai is corrected using k = 2 (cf. text in chapter C. V. 2.). - Moreover, a correction is applied using k = 6 (= number of dependent variables tested; cf. chapter B. I. 3.). In the case of the regression of Bi on Ai-1, the correction using k = 6 is a 2nd correction.

regression of net reproductive rate Bi; n = 20 (Ai) and 19 (Ai-1)

parameter of abundance	sign	p	p_{corr} (k = 2)	p_{corr} (k = 6)	r^2 (%)
Ai	**-**	**0.041**		0.221	21.2
Ai-1	**-**	**0.008**	**0.015**	**0.087**	**35.1**

regression of female relative mean weight in the 1st decade of May. n = 17

parameter of abundance	sign	p	p_{corr} (k = 2)	p_{corr} (k= 6)	r^2 (%)
Ai	**-**	**0.090**	0.171		18.0
Ai-1	**-**	**0.011**		**0.064**	**53.8**

regression of activity of males (arcsine-transformed probability of being trapped in the plateau-phase in spring). n = 9

parameter of abundance	sign	p	p_{corr} (k = 2)	p_{corr} (k = 6)	r^2 (%)
Ai	**-**	**0.099**	0.188		**34.1**
Ai-1	**-**	**0.046**		0.244	**45.7**

regression of arcsine-transformed probability of females surviving from spring i until spring i+1. n = 8

parameter of abundance	sign	p	p_{corr} (k= 2)	p_{corr} (k = 6)	r^2 (%)
Ai	+	**0.015**	**0.030**	0.169	**65.2**
Ai-1	+	**0.008**		**0.049**	**71.3**

regression of the arcsine-transformed probability of males surviving from spring i until spring i+1. n = 8

parameter of abundance	sign	p	r^2 (%)
Ai	+	0.195	26.1
Ai-1	-	0.979	0.0

regression of "weight divided by length" for females in June, n = 9

parameter of abundance	sign	p	r^2 (%)
Ai	+	0.292	15.6
Ai-1	+	0.419	9.5

regression of "weight divided by length" for males in the 3rd decade of May, n = 9

parameter of abundance	sign	p	p_{corr} (k = 2)	p_{corr} (k = 6)	r^2 (%)
Ai	+	**0.094**	0.179		**34.9**
Ai-1	+	**0.057**		0.297	**42.6**

regression of 75 % mark of female CNL, n = 9

parameter of abundance	sign	p	r^2 (%)
Ai	-	0.572	4.8
Ai-1	-	0.625	3.6

regression of 75 % mark of male CNL, n = 9

parameter of abundance	sign	p	r^2 (%)
Ai	-	0.729	1.8
Ai-1	-	0.989	0.0

When Bi is regressed on Ai and Ai-1 the influence of Ai-1 is weakly and Ai is not significant. In stepwise regression Ai-1 is influential, and Ai eliminated:

enter regression of Bi on:

Ai: -, $p = 0.508$

Ai-1: -, $p = 0.071$

$p_{mult} = 0.025$, $r_{mult}^2 = 36.9$ %

stepwise regression of Bi on:

Ai-1: -, $p = 0.008$, $r^2 = 35.1$ %.

Ai: - , $p = 0.508$

As Bi is the biotic key factor in the dynamics of the population under study, we assume a priori an influence of Ai-1 on other traits of the spring stock (**Table 10**) (significance levels are corrected for a possible influence of Ai).

The negative regression of Bi on abundance supports the hypothesis of population regulation by a negative density-dependent effect on reproduction (cf. chapter A.). However, in our 2001 paper (Weber & Heimbach, 2001) we have assumed that such a density-dependent effect could be mimicked by a negative correlation between abundance and temperature. It is an essential aim of the present paper to test this assumption using the total data available.

Indeed, abundance (Jolly-Seber estimates for female density in the plateau-phase in spring, **Table 1**) and PTi are weakly negatively correlated (PTi vs Ai: -, $p = 0.087$, $r^2 = 15.4$ %; PTi vs. Ai-1: -, $p = 0.090$, $r^2 = 16.0$ %), and also the periodogram of abundance shows a minimum at 4 years, which however is not significant (**Fig. 12**). The cause of this biologically absurd correlation is the following. PTi and thus also Bi display a periodicity of 4 years (chapter C. IV. 2.; **Fig. 6**). In a year with an adverse weather event (year 1 of the 4 year cycle) net reproductive rate is small (**Fig. 7**). In the extreme case the population survives because the adults are long lived. Because of high net reproductive rates in years with optimal temperature conditions the beetle becomes abundant again by year 4 of the cycle and in the following year (in year 3 of the cycle, however, beetle abundance is still relatively low, **Fig. 12**; a probable cause of this is given in chapter D. III. 2.). Consequently, when the next adverse weather event is likely to occur, beetles are abundant again: an adverse weather event in year i and a relatively high abundance in year i-1 and year i coincide with high degree of probability (cf. the cubic regression of PTi and Ai on the phases of the 4 year periodicity of PTi in **Fig. 7** & **Fig. 12**). - This explanation was presented in our 2001 article.

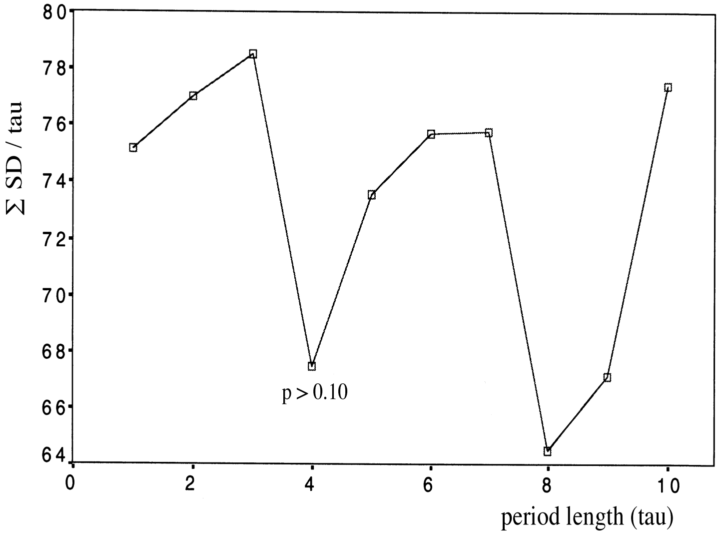
When Bi is regressed on PTi and Ai-1, both factors are significant (see chapter C. VIII. 1. for the parameters of the reproductive function):

bifactorial regression of Bi on:

PTi: +, $p = 0.001$

Ai-1: -, $p = 0.040$

$p_{mult} < 0.001$, $r_{mult}^2 = 69.6$ %



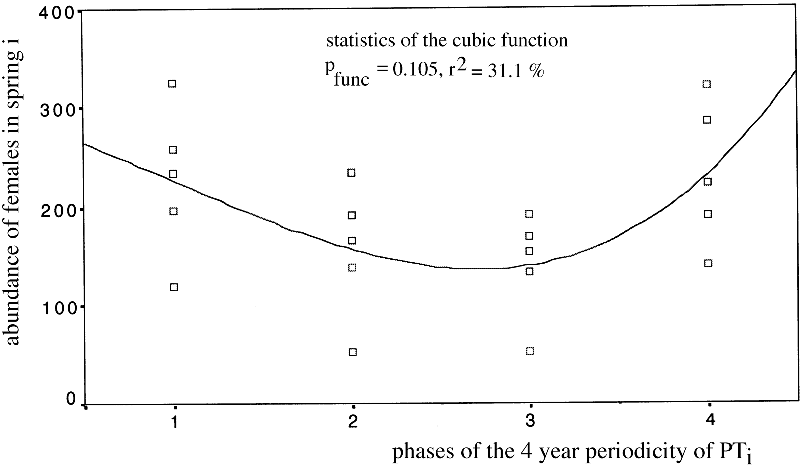


Fig. 12 Periodogram analysis of female abundance in spring (above) and cubic regression of female abundance in spring on the phases of the 4 year periodicity in PTi (below, the phases are identical to those in **Fig. 7**: in year 1 low temperature is likely to occur in Prigge's interval). - Periodogram analysis after Lamprecht & Weber (1970); statistics after Sokolove & Bushell (1978).

Also when Bi is regressed on the influential temperature parameters (PTi , TM2 and TM3, cf. chapter C. IV. 1.) and Ai-1 we get the same result:

multiple regression of Bi on:

PTi: +, $p = 0.005$

TM2: -, $p = 0.041$

TM3: -, $p = 0.107$

Ai-1: -, $p = 0.022$

$p_{mult} < 0.001$, $r_{mult}^2 = 77.6$ %

Thus, it seems that the abundance parameter Ai-1 has a significant distinct effect on the variability in Bi (an effect that is independent of the correlation between PTi and abundance).

C. V. 3. Abundance and the reproductive investment of females

Does abundance affect the reproductive investment of females? The measure of oogenesis is the relative mean weight ("mean weight of the females divided by the mean weight of the males", chapter C. I. 2.) in the 1st decade of May. Does such an effect explain "Prigge's paradox", i. e. the anticipatory effect of PTi on the female relative mean weight in the 1st decade of May (chapter C. IV. 3.)?

Table 10 gives the statistical parameters of the influence of Ai-1 on female relative mean weight in the 1st decade of May (in this and the following analyses the independent variable is the abundance of the total female stock in the plateau-phase in spring; **Table 1**). The influence is negative and significant, when the significance level is not corrected for the number of dependent variables tested; after correction it is still weakly significant.

Whether the negative effect of abundance on the measure of oogenesis explains "Prigge's paradox" is checked by regressing the relative mean weight in the 1st decade of May (1) on PTi, the temperature in the 2nd decade of April (cf. chapter C. IV. 3., **Table 7**) and Ai-1, (2) on PTi, the temperature in the 3rd decade of April and Ai-1, and (3) on PTi, the temperature in the 1st decade of May and Ai-1.

(1) enter regression on PTi, the temperature in the 2nd decade of April and Ai-1:

PTi: +, $p = 0.034$

Ai-1: -, $p = 0.194$

fit_{weight} in 1st decade of May: -, $p < 0.01$

$p_{mult} < 0.05$, $r_{mult}^2 = 73.6$ %

(2) enter regression on PTi, the temperature in the 3rd decade of April (TA3) and Ai-1:

PTi: +, $p = 0.109$, $r^2 = 36.4$ %

Ai-1: -, $p = 0.0180$

TA3: -, $p = 0.052$

$p_{mult} = 0.003$, $r_{mult}^2 = 64.1$ %

stepwise regression on PTi, the temperature in the 3rd decade of April (TA3) and Ai-1:

Ai-1: -, $p = 0.003$

TA3: -, $p = 0.024$

$p_{mult} = 0.003$, $r_{mult}^2 = 56.0$ %

PTi: +, $p = 0.109$

(3) enter regression on PTi, the temperature in the 1st decade of May (TM1) and Ai-1

PTi: +, $p = 0.061$

Ai-1: -, $p = 0.082$

TM1: -, $p = 0.890$

$p_{mult} = 0.021$, $r_{mult}^2 = 51.6$ %

stepwise regression on PTi, the temperature in the 1st decade of May (TM1) and Ai-1

PTi: +, $p = 0.052$

Ai-1: -, $p = 0.055$

$p_{mult} = 0.006$, $r_{mult}^2 = 51.6$ %

TM1: +, $p = 0.890$

Obviously, the abundance parameter does not abolish the anticipatory effect of PTi on female relative mean weight in the 1st decade of May, but it weakens the effect of PTi (compare the above regressions with those without the parameter of abundance in chapter C. IV. 3.).

Instead of the parameter of abundance the quotient "Ai-1 / PTi" is used in the following analysis. If the quotient has a consistent effect it would support the idea that both PTi and abundance affect the female reproductive investment.

(1) enter regression on PTi, the temperature in the 2nd decade of April and the quotient "Ai-1 / PTi":

PTi: +, $p = 0.184$

$fi_{tweight}$ in 1st decade of May: +, $p < 0.01$

Ai-1 / PTi: -, $p = 0.198$

$p_{mult} < 0.05$, $r_{mult}^2 = 73.5$ %

stepwise regression on PTi, the temperature in the 1st decade of May and the quotient "Ai-1 / PTi":

PTi: +, $p = 0.012$

fit_{weight} in 1st decade of May: +, $p < 0.01$

$p_{mult} < 0.05$, $r_{mult}^2 = 69.8$ %

Ai-1 / PTi: -, $p = 0.198$

(2) enter regression on PTi, the temperature in the 3rd decade of April (TA3) and the quotient "Ai-1 / PTi":

PTi: +, $p = 0.687$

TA3: -, $p = 0.044$

Ai-1 / PTi: -, $p = 0.018$

$p_{mult} = 0.003$, $r_{mult}^2 = 64.0$ %

(3) enter regression on PTi, the temperature in the 1st decade of May (TM1) and the quotient "Ai-1 / PTi":

PTi: +, $p = 0.370$

TM1: -, $p = 0.831$

Ai-1 / PTi: -, $p = 0.099$

$p_{mult} = 0.024$, $r_{mult}^2 = 50.5$ %

stepwise regression on PTi, the temperature in the 1st decade of May (TM1) and the quotient "Ai-1 / PTi":

Ai-1 / PTi: -, $p = 0.002$, $r^2 = 46.6$ %

PTi: +, $p = 0.327$

TM1: -, $p = 0.705$

Similar results are obtained in (1), (2) and (3) when the inverse quotient "PTi / Ai-1" is used. In cases (2) and (3) the quotient "Ai-1 / PTi" has an effect. Thus abundance probably has a distinct direct effect on the variability in female relative mean weight in the 1st decade of May. However, the negative density-dependence does not seem to completely explain "Prigge's paradox", the anticipatory effect of PTi on female reproductive investment.

C. V. 4. Abundance and the reproductive investment of males

The reproductive investment of males is in mate searching measured as (arcsine transformed) trapping probability in the plateau-phase in spring (chapter C. I. 3.). The parameter Ai-1 (female abundance in the plateauphase, **Table 1**) influences male activity negatively; the uncorrected significance level is < 0.05, after correction, however, it is > 0.10 (**Table 10**).

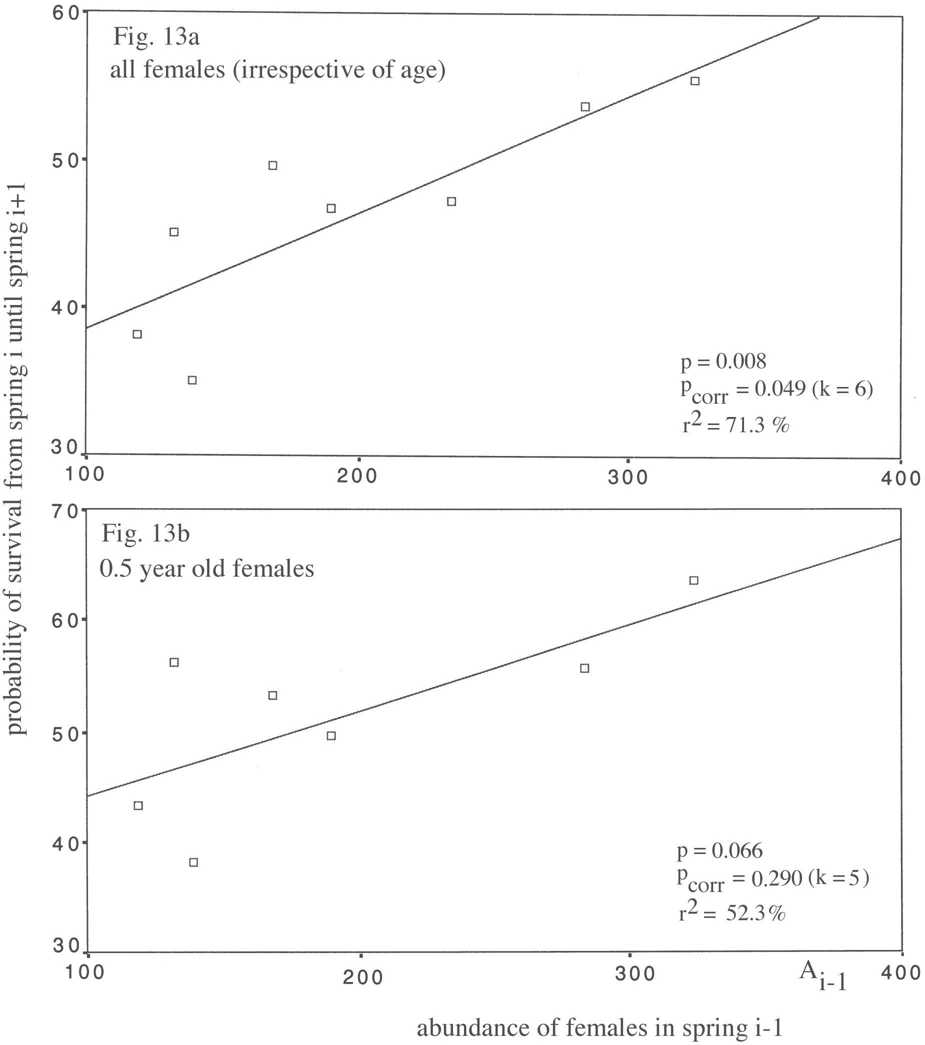
The arcsine transformed trapping probability of the males regresses highly significantly on PTi (chapter C. IV. 4.). Bifactorially regressed the effect of temperature remains highly significant, whereas that of abundance is not significant; the statistical outcome is similar when the trapping probability is regressed on PTi and the quotient "Ai-1 / PTi" or the inverse quotient (data not shown).

Also, the (arcsine transformed) trapping probability for females negatively regresses on abundance (Ai-1); but the regression is not significant: -, $p = 0.107$ (uncorrected), $r^2 = 32.8$ %.

C. V. 5. Tests for influence of abundance on survival and post-reproductive "recreation"

Does abundance influence the survival (chapter C. III.) and post-reproductive "recreation" of both females and males, measured by "weight divided by length" in June and the 3rd decade of May, and the duration of spring activity (75 % mark of CNL; chapter C. II.)? Survival probabilities are calculated from **Table 2**; female abundance from **Table 1** is used as independent variable.

The arcsine transformed survival probability of females (irrespective of age) from spring i to spring i+1 depends highly significantly on Ai-1; the significance level remains below 0.05 after correction using the number of independent variables tested ($k = 6$; **Table 10**, **Fig. 13**). Unexpectedly, the sign of the regression is positive: survival is higher the higher the abundance (Ai-1). Also the survival of 0.5, 1.5, 2.5 and 3.5 year old females and all females older than 1.5 years is regressed on Ai-1. As the hypothesis of a dependence of survival on Ai-1 is well founded, the significance levels are corrected with $k = 5$ (= number of age classes tested) (cf. chapter B. I. 3.). The survival of 0.5 and 1.5 year old females increases with increasing abundance in spring i-1: uncorrected the significance level is < 0.10, and respectively, < 0.01; after correction the regression is still significant in case of the 1.5 year old females (**Fig. 13 b, c**). The regression of the survival of 2.5 and 3.5 year old females on Ai-1 is not significant, however, also positive (2.5 year old females: +, $p = 0.529$, $r^2 = 14.4$ %, $n = 5$; 3.5 year old females: +, $p = 0.487$, $r^2 = 26.3$ %, $n = 4$; uncorrected significance levels are given) (in these four analyses the females found unmarked in spring 1993 are considered; when they are omitted the results are not different; cf. **Table 2**). When the number of all females older than 1.5 years is pooled, the uncorrected significance level is < 0.05 (+, $p = 0.047$, $p_{corr} = 0.215$, $r^2 = 57.8$ %, $n = 7$; **Fig. 13d**); when the extremely deviating value (survival from 1999 to 2000, when the abundance of this age class was rather low; **Table 2**) is omitted, even the corrected significance level is < 0.01 ($p = 0.002$; $p_{corr} = 0.009$, $r^2 = 93.2$ %).



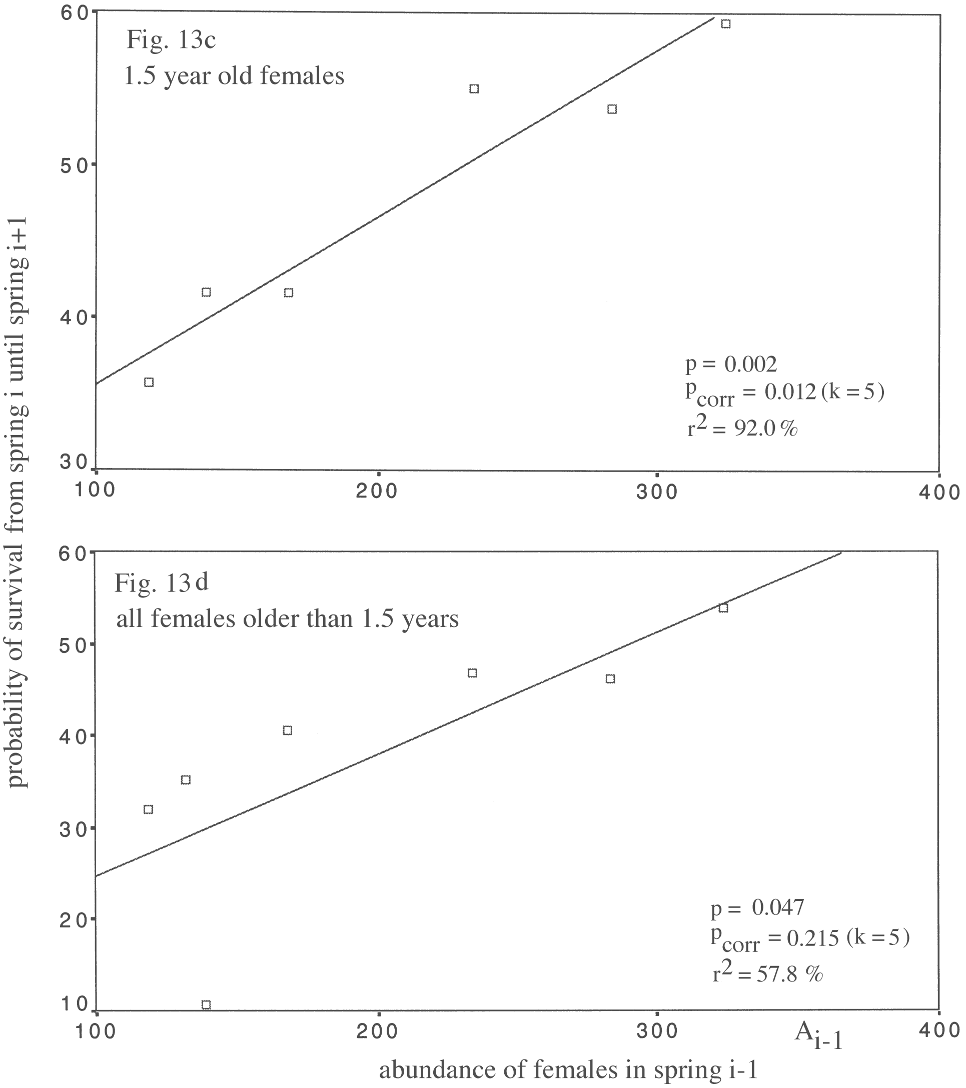


Fig. 13 a-d Regression of the arcsine transformed probability of females surviving from spring i until spring i+1 on the female abundance parameter Ai-1. Survival probabilities are calculated from **Table 2**; female abundance from **Table 1** is used as independent variable. - **Fig. 13a.** The survival probability of females irrespective of age is corrected with k = 6 (= number of dependent variables tested; cf. **Table 10**). - **Fig. 13 b - d.** The survival probability of females of a distinct age is corrected with k = 5 (= number of age classes tested; cf. text).

Neither PTi nor other temperature parameters significantly affect the survival of females; only temperature in the 2nd decade of May in the year i-4 ($TM2_{i-4}$) affect the survival of 3.5 year old females (chapter C. IV. 7.). - When the survival of females (irrespective of age) is regressed on the abundance parameter Ai-1, the temperature in the 2nd decade of May of year i-4 and PTi, abundance emerges as important in stepwise regression whereas PTi and $TM2_{i-4}$ are eliminated:

stepwise regression of the survival of females (irrespective of age):

Ai-1: +, $p = 0.008$, $r^2 = 71.3$ %

PTi: +, $p = 0.507$

$TM2_{i-4}$: +, $p = 0.474$

The same result is obtained when either the temperature in the 2nd decade of May of another previous year or a decade temperature in spring i is used instead of $TM2_{i-4}$. Thus, abundance has a distinct effect on the survival of females. Importantly, the influence is positive: the higher abundance the higher the survival (**Fig. 13**), which is contrary to expected (chapter A).

The abundance parameter Ai-1 has no influence on the survival of males (irrespective of age; **Table 10**) or of the males of a particular age.

The female post-reproductive "recreation" parameter "weight divided by length" in June does not regress on Ai-1 (**Table 10**). Male relative weight in the 3rd decade of May regresses weakly significantly; however, the significance disappears after correcting; unexpectedly, the sign is positive both in females and males (**Table 10**). - Also the regressions of the 75 % marks of CNL on parameters of abundance are not significant (again unexpectedly, the sign is negative both in females and males; **Table 10**). - The density-independence of the "recreation" parameters, and the unexpected sign of the regression functions indicate that there is no density-dependent food shortage in spring.

C. V. 6. Summary of the effects of abundance on the population dynamics of *Carabus auronitens* in spring

Net reproductive rate, Bi, and female and male reproductive investments regress negatively on a parameter of abundance (Ai-1, **Table 10**). With regard to Bi the abundance parameter seems to have a significantly distinct effect: tested multifactorially together with PTi, TM2 and TM3 the negative effect of abundance remains. Moreover, there seems to be a distinct negative effect of abundance on female reproductive investment, the relative mean weight in the 1st decade of May. However, the anticipatory effect of PTi on female reproductive investment cannot simply be explained by the effect of abundance as the influence of PTi on the female relative mean weight in the 1st decade of May seems to be weakened but not abolished by abundance (chapter C. V. 3.).

Unexpectedly, there is a strong positive effect of abundance parameter Ai-1 on the survival of females (irrespective of age); the effect remains significant when the significance level is corrected (**Table 10**). Also, this effect is stable in multifactorial regressions that include parameters of temperature.

The opposite sign of density-dependent effects on Bi and survival of females confirms the conclusion drawn in chapter C. V. 2. that density-dependent food shortage is not the cause of the abundance-dependences observed, as a density-dependent limitation of food availability would reduce reproductive success and probably also imaginal survival. We assume a direct effect via mutual interference in spring i-1 on the physiology and behaviour of the surviving females in spring i, and an inhibiting effect of the female abundance on the development of the gonads of their offspring (chapter C. VI. 5.).

The reverse sign of the density effect on net reproductive rate and survival suggests a trade-off: survival is high when reproductive investment was small. However, the survival of females and males does not regress on Bi or the parameters of reproductive investment, however, the sign of regression is negative in all cases (chapter C. III. 1. and 2.). Thus, the indications on a trade-off are weak (but see chapter C. IX. 2.).

Features of post-reproductive "recreation" in females and males do not regress significantly on abundance, however, the sign (positive in case of the parameter "weight divided by length" in June, and the 3rd decade of May; negative for the 75 % mark of CNL) of these relationships is such that like in the female survival adverse effects of intraspecific competition are improbable. - Furthermore, there are no indications that larvae or the freshly emerged beetles in autumn compete for food (chapter C. VI. 1. & C. VI. 2.).

C. VI. Survival and other traits of the young individuals

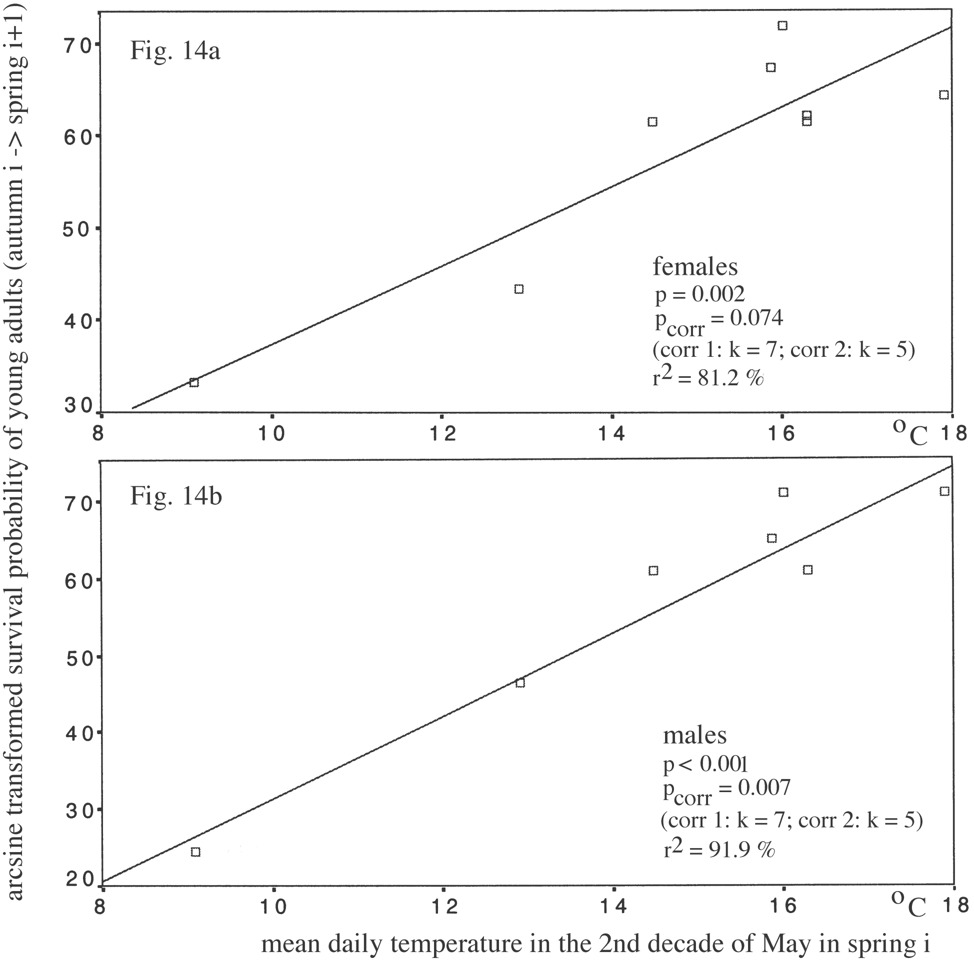
C. VI. 1. Dependence of survival of young on traits expressed after emerging

Does the (arcsine transformed) survival probability of the young depend on their abundance and traits expressed after emerging? The following parameters are considered: (1) abundance of young (as in contrast to spring, females and males do not behave differently in autumn, Weber & Heimbach, 2001, numbers of females and males are pooled; **Table. 1**); (2) the relative mean weight after emerging (so long as the integument is still "very soft", Weber & Heimbach, 2001; the relative weight is the mean of the absolute weight of very soft females {males} divided by the mean length of the young female {male} cohort); (3) the coefficient of variation (CV) of the absolute weight of "very soft" females and males; (4) the mean body size (length) of young females and males; (5) the CV of the body size of young females and males; and (6) the mean duration of the sclerotization process "very soft - soft" (the values for females and males are pooled) (**Table 11**).

Table 11 Linear regressions of the arcsine transformed probability of females and males to survive from autumn i to the following spring (i+1) on the abundance of young animals (Aai, abundance of females and males pooled, **Table 1**) and expression of post-ecdysial traits. Significance levels are corrected for the number of independent variables tested (k = 6).

independent variables	females	males
abundance of young animals (Aai)	+, p = 0.624, r^2 = 4.2 % n = 8	+, p = 0.686, r^2 = 2.9 % n =8
size-standardized mean weight of very soft animals	+, p = 0.219, r^2 = 23.9 % n = 8	+, p = 0.274, r^2 = 23.2 % n = 7
CV of weight of very soft animals	+, p = 0.589, r^2 = 5.1 % n = 8	+, p = 0.760, r^2 = 2.0 % n = 7
mean body size of young animals	**+, p = 0.084, r^2 = 41.6 %** p_{corr} = 0.410 n = 8	**+, p = 0.084, r^2 = 41.7 %** p_{corr} = 0.408 n = 8
CV of body size of young animals	-, p = 0.306, r^2 = 17.2 % n = 8	**-, p = 0.001, r^2 = 83.8 %** **p_{corr} = 0.008** n = 8
mean duration of sclerotization "very soft - soft" (values of females and males pooled)	**-, p = 0.083, r^2 = 83.1 %** p_{corr} = 0.407 n = 4	-, **p = 0.087, r^2 = 83.3 %** p_{corr} = 0.422 n = 4

The regression of survival of young females and males on the abundance of the young is not significant; the sign is positive. This unexpected result does not support the view that the beetles compete for food in autumn (see also below chapter C. VI. 2.). - The mean body size of females and males weakly affects their survival; after correction the significance level is > 0.10. As expected in the case of an effective influence the sign is positive in females and males. - Similarly the regressions of survival on the size-standardized mean weight of very soft animals and the CV of their absolute weight are positive (but not significant). - On the other hand, the sign of the regression on the mean duration of sclerotization is negative (as expected), and weakly significant in females and males (before correction). - There is only one regression of survival on a trait for which the significance level is still significant after correction: the CV of the body size of young males highly significantly affects their survival; the sign of the regression is negative (as expected): the larger the CV, the lower the survival; however, it has to be stressed that the significance disappears when one generation (1995) is eliminated (**Fig. 14**). - In summary, it is possible that traits of the freshly emerged animals affect their survival from autumn i until spring i+1. The lack of significance may be due to the small number of values (n = 7 - 8 or even only 4 ; **Table 11**).



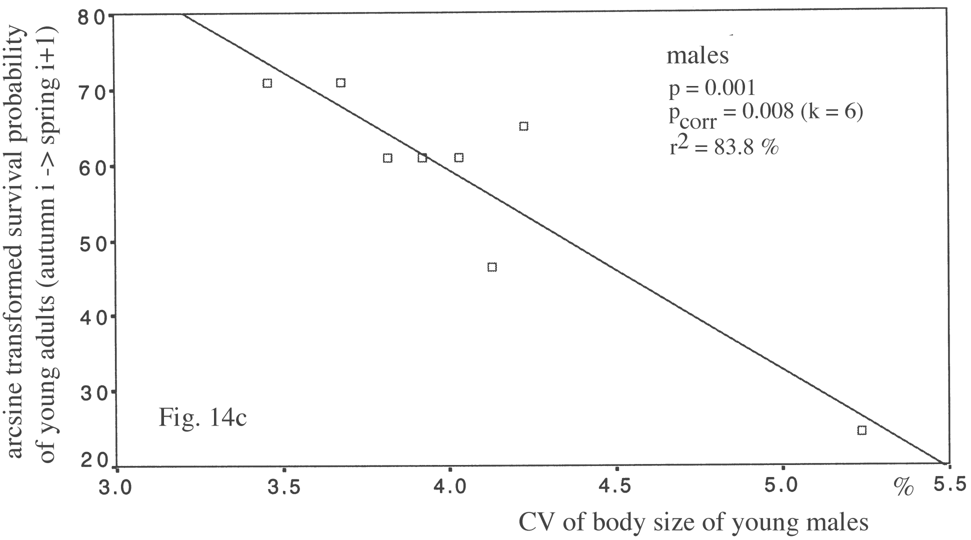


Fig. 14 Linear regression of the arcsine transformed probability of young females (**Fig. 14a**) and males (**Fig. 14b**) surviving from the season of emerging (autumn i) until spring i+1 on the average of the mean daily temperature in the 2nd decade of May in spring i (cf. **Table 13**). **Fig. 14a**: The regression of the survival of females remains weakly significant when the lowest value for survival is omitted (uncorrected: p = 0.0622, r^2 = 53.4 %). **Fig. 14b**: The regression of survival of males remains significant when the lowest value for survival is omitted (uncorrected: = 0.0162, r^2 = 71.7 %).
Fig. 14c. Regression of the survival of young males on the coefficient of variation (CV) in young male body size; the significance disappears when the lowest value for survival is omitted: -, p = 0.124 (uncorrected), r^2 = 40.6 % (cf. **Table 11**).

C. VI. 2. Relationship between abundance of young and their traits

We also check for possible effects of the abundance of the freshly emerged beetles (number of females plus males, **Table 1**) on traits of the young stock. Traits like relative emerging weight, body size and the CV of these parameters might be influenced by crowding among larvae. We do not know the abundance of the larvae, but it is reasonable to assume that the abundance of the young beetles is positively correlated with that of the preimaginal stages. - On the other hand, post-ecdysial development could be directly influenced by the abundance of young beetles, for example by competition for food. The regressions are on the total abundance (numbers of females and males pooled, cf. chapter C. VI. 1.). - In no case is a regression unambiguously significant (**Table 12**); in some cases the uncorrected significance levels are < 0.10: but the sign of the regression coefficients does not support the assumption that the larvae are crowded. - As the duration of cuticle sclerotization depends on food supply after emerging (Klenner, 1989; Weber & Heimbach, 2001) the missing regression of this parameter on the abundance of the young beetles leads to the assumption that at least over the range of abundances observed freshly emerged adults in autumn do not compete for food (even the sign of the insignificant regression is unexpectedly negative; see also the interpretation of the regression of the survival of the young on their abundance in chapter C. IV. 1.).

Table 12 Linear regression of the traits of the young generation on the number of young beetles that emerged (number of females and males pooled; **Table 1**). Significance levels are corrected using k = 5 (= number of independent variables tested).

dependent variables	trait of young females	trait of young males
size-standardized mean weight of very soft animals	+, **$p = 0.020$, $r^2 = 37.5$ %** **$p_{corr} = 0.096$**, $n = 14$	+, **$p = 0.023$, $r^2 = 41.9$ %** $p_{corr} = 0.109$, $n = 12$
CV of absolute weight of very soft animals	+, $p = 0.799$, $r^2 = 5.6$ % $n = 14$	+, $p = 0.988$, $r^2 = 0.0$ % $n = 12$
mean body size of of young animals	+, **$p = 0.067$, $r^2 = 25.3$ %** $p_{corr} = 0.291$, $n = 14$	+, $p = 0.537$, $r^2 = 3.3$ % $n = 14$
CV of body size of of young animals	-, **$p = 0.089$, $r^2 = 22.2$ %** $p_{corr} = 0.372$, $n = 14$	-, $p = 0.207$; $r^2 = 12.9$ % $n =14$
	values for young females and males pooled	
mean duration of sclerotization "very soft - hard"	-, $p = 0.591$, $r^2 = 4.3$ % $n = 9$	

C. VI. 3. Dependence of survival of young in autumn i on temperature in spring i

The reproductive success of the population under study depends on the net reproductive rate (as defined in chapter B. I. 3.) and survival of the young. In the following it is tested whether the variability in the (arcsine transformed) probability of freshly emerged females and males of surviving from autumn i to spring i+1 depends on temperature factors in spring i (**Table 13**). - Only the temperature in the 2nd decade of May (TM2i) affects the survival of young females and males distinctly (after two corrections the significance level is still weakly significant in females and highly significant in males): the higher this temperature the higher the survival (**Fig. 14**). This dependence is remarkable as there is no evident influence of PTi, although Prigge's interval and the 2nd decade of May overlap.

The influence of TM2i seems to be stronger on male than female survival: in females b_i is +4.2514, males +5.3682, r^2 is 81.2 % in females and 91.9 % in males (**Table 13**). We assume that TM2i affects the embryonic and early larval development, and thus determines much of the variability in the fitness of young adults. The different dependence of the fitness of young females and males on TM2i significantly affects the sex ratio in spring (chapter C. IV. 8).

In chapter C. VI. 1. it is shown that the CV of young male body size highly significantly affects their survival (**Table 11**). As expected from this result, the CV of young male body size depends on TM2i in spring: the higher the TM2, the lower the CV (**Table 14**). There is also a negative regression on PTi. In the bifactorial stepwise regression TM2i is influential whereas PTi is eliminated:

stepwise regression of CV of young male body size:

TM2i: -, $p = 0.011$, $r^2 = 42.9$ %

PTi: -, $p = 0.661$

Table 13 Regression of arcsine transformed probability of young females and males surviving from autumn i to spring i+1 on abiotic and biotic factors in spring i. n = 8 in all cases. The abundance parameters refer to female abundance of the plateau-phase in spring (**Table 1**). Significance levels are corrected using the formula $1 - (1 - p)^k$ according to the number of functions, and respectively, the number of independent variables tested. $p_{func/corr}$: k = 11 (in case of non linear functions); $p_{corr/1}$: k = 7 (in case of TM2: temperature in the 1st, 2nd and 3rd decade of April, 1st, 2nd and 3rd decade of May and June is tested); $p_{corr/2}$: k = 5 (= number of independent variables tested, in some cases this is a 2nd correction). + / - sign of the coefficient of linear regression, (+) S-function: rising, (±) quadratic function: convex viewed from above.

independent variables	surviving of young females	surviving of young males
PTi	linear, + $p = 0.141$, $r^2 = 32.3$ %	quadratic function: **convex (±)** **$p_{func/corr}$: = 0.097, $r^2 = 84.6$ %** $p_{corr/2} = 0.399$
TM2i	linear, + **$p = 0.002$, $r^2 = 81.2$ %** **$p_{corr/1} = 0.015$** **$p_{corr/2} = 0.074$**	linear, + **$p < 0.001$, $r^2 = 91.9$ %** **$p_{corr/1} = 0.001$** **$p_{corr/2} = 0.007$**
Bi	linear, + $p = 0.346$, $r^2 = 14.8$ %	S-function **(+)** **$p_{func/corr} = 0.056$, $r^2 = 75.3$ %** $p_{corr/2} = 0.249$
abundance	Ai: linear, - $p = 0.125$, $r^2 = 34.7$ %	Ai: linear, **-** **$p = 0.075$, $r^2 = 43.5$ %** $p_{corr/2} = 0.324$
BEVi	linear, + **$p = 0.051$, $r^2 = 49.7$ %** $p_{corr/2} = 0.229$	linear, + $p = 0.103$, $r^2 = 38.2$ %

Table 14 Linear regressions of the CV of male body size on biotic and abiotic factors in spring i. n = 14 in all cases. Cf. legend of **Table 13**. Correction of significance levels: corr/1: k = 2 (= number of parameters of abundance tested); corr/2: k = 5 (= number of independent variables tested; for BEVi see chapter C. VII.1.).

independent variables	statistics
PTi	-, **$p = 0.028$, $r^2 = 34.1$ %** $p_{corr/2} = 0.134$
TM2i	-, **$p = 0.011$, $r^2 = 42.9$ %** **$p_{corr/2} = 0.054$**
Bi	-, **$p = 0.047$, $r^2 = 28.9$ %** $p_{corr/2} = 0.215$
abundance (Ai-1)	+, **$p = 0.012$, $r^2 = 42.5$ %** **$p_{corr/1} = 0.023$** $p_{corr/2} = 0.110$
BEVi	**-, $p = 0.043$, $r^2 = 30.0$ %** $p_{corr/2} = 0.196$

C. VI. 4. Dependence of survival of young on biotic factors affecting the parental stock

We investigate the influence of Bi and female abundance in the plateau-phase of spring (**Table 1**) on the survival of the young (**Table 13**) and the CV of young male body size (**Table 14**), the only trait of the young that could possibly affect their survival to spring i+1 (**Table 12**). Concerning the abundance, the a priori assumption is that Ai will have an effect (cf. chapter B. I. 3.).

The survival of young females does not regress on Bi or the abundance of females in spring (**Table 13**). For young males both their survival and the CV of body size show some dependence on Bi and a parameter of spring abundance in monofactorial tests (**Table 14:** remarkably, the density parameter Ai-1 is more influential than Ai).

It seems that the dependence of young male survival and CV of body size on PTi, abundance and Bi are due to an effect of TM2 on both traits (cf. chapter C. VI. 3.):

(1) regression of young male survival on (cf. **Table 13**):

TM2i: +, $p = 0.016$

PTi: -, $p = 0.284$

Ai: -, $p = 0.966$

Bi: -, $p = 0.952$

$p_{mult} = 0.022$, $r_{mult}^2 = 95.7$ %

(2) stepwise regression of young male CV on (cf. **Table 14**):

TM2i: -, $p = 0.011$, $r^2 = 42.9$ %

PTi: -, $p = 0.661$

Bi: -, $p = 0.305$

Ai-1: +, $p = 0.107$

When in (2) instead of Ai-1 the quotient "TM2 / Ai-1" is used as the independent variable, the influence of TM2 dominates (+, $p = 0.011$, $r^2 = 42.9$ %). However, the inverse quotient dominates in stepwise regression (+, $p = 0.002$, $r^2 = 55.6$ %).

In summary, the temperature in the 2nd decade of May has a strong effect on the survival of young females and males (when TM2 in spring i is low, the probability of surviving from autumn i until spring i+1 is reduced; **Table 13 & 14**). In contrast, net reproductive rate, abundance of young and parental abundance have no effect. However, in case of the CV of body size of young males an effect of Ai-1 cannot be excluded (cf. chapter C. VII. 5.).

C. VI. 5. Do parental females affect the reproductive investment of 0.5 year old females?

The results presented in chapter C. V. indicate that there is no density-dependent limitation of food in the population under study: rather, in spring i reproduction and reproductive investment of females are probably affected by density-dependent "mutual interference" in spring i-1 (chapter C. V. 1. & D. III. 4.). Concerning the surviving females we assume that the interference experienced in spring i-1takes effect in spring i. Concerning the 0.5 year old beetles we assume that density-dependent mutual interference in spring i-1 causes an inhibition of the gonadal development of the female offspring in spring i (chapter C. V. 1.). This assumption has still to be checked. We have no information on the contribution of the particular generations to Bi; however, the reproductive investment of females of a particular generation can be estimated from their relative mean weight ("mean weight of the females divided by the mean weight of the males") developed in the 1st decade of May (chapter C. I. 2.).

If there is a density-dependent inhibition of the development of the gonads of the 0.5 year old females by the parental females, their relative mean weight that develops in the 1st decade of May of spring i should regress negatively on the density parameter Ai-1 of females (abundance parameter in **Table 1** are used as independent variable): indeed, the regression is negative and weakly significant (-, $p = 0.068$, $r^2 = 51.8$ %, $n = 7$). The regression on the density parameter Ai is also negative, but not significant (-, $p = 0.350$, $r^2 = 17.5$ %). - Is "Prigges paradox" (chapter C. IV. 3.) demonstrable? As expected, the sign of the regression is positive but not significant ($p = 0.184$, $r^2 = 32.2$). In stepwise regression on Ai-1 and PTi, the influence of Ai-1 is significant with $p = 0.068$. - However, the relative mean weight of 0.5 year old females in the first decade of May regresses significantly on mean daily temperature in the 2nd decade of April (by an inverse function). When the weight parameter is regressed on Ai-1 and the fitted value of the weight parameter (fitted by the indicated inverse function), the latter is significant. When the weight parameter is stepwise regressed on Ai-1, the fitted value and the quotient "fitted value / Ai-1", the quotient remains in the function ($p = 0.007$; $r^2 = 79.8$ %), and the other independent variables are excluded. However, the inverse quotient has no influence, and TA2 remains in the equation. - Nevertheless, we maintain the hypothesis (chapter C. V. 6.) that not only the reproductive investment of the surviving females in spring i is due to density-dependent mutual interference operating in spring i-1, but also the reproductive investment of the F1 females in spring i (cf. also chapter D. III.4.).

C. VII. The expectation periodicity - an endogenous adaptation to the 4 year periodicity in the temperature critical for early development (PTi)?

C. VII. 1. The phenomenon

Robert Baumgartner calculated the mean 4 year period of PTi values known since 1891 by means of the cubic regression function (**Fig. 8**), and regressed the Bi values measured since 1982 on the sequence of the values of the mean 4 year period. As expected due to the 4 year periodicity in PTi, this regression is highly significant (**Table 15a**): the sequence of the values of the mean 4 year period and PTi are highly significantly correlated (+, 1982 - 2001: $r^2 = 43.7$ %, $p = 0.002$). **Table 16** gives the sequence of the values of the mean period and PTi for the years of this study.

However, unexpectedly, both the corresponding value i of the mean period and PTi significantly and independently affect the variability in Bi, as shown by the bifactorial regression (**Fig. 15**; **Fig. 16; Table 15b**). The partial coefficient of determination of both, value i of the mean period and PTi, is about 30 %, the coefficient of multiple determination is as high as 73.4 %. Bi regresses on the product "PTi x value i of the mean period" with a coefficient of determination of 68.9 % (**Fig. 16).**

Also the significant influence of the value i of the mean period on Bi is not abolished when the most influential abundance parameter (cf. chapter C. V. 2.) is introduced as a 3rd independent factor:

PTi: +, $p = 0.031$

value i of mean period: +, $p = 0.022$

Ai-1: -, $p = 0.070$

$p_{mult} < 0.001$, $r_{mult}^2 = 78.8$ %

Table 15 Regression of net reproductive rate (Bi), parameter of reproductive activity of females and males and survival probability of females and males (spring i -> spring i+1; irrespective of age) on Prigge's critical temperature (PTi) and Baumgartner's Expectation Value (BEVi).

Table 15 a Monofactorial regression on BEVi

dependent variable	**sign**	**p**	**p_{corr} (k = 4)**	**r^2 (%)**	**n**
Bi	+	**<0.001**	**<0.001**	**62.5**	20
female rel. mean weight in 1st decade of May	+	**0.016**	**0.063**	**32.8**	17
male activity	+	**0.010**	**0.041**	**63.4**	9
female survival	+	0.757		1.7	8
male survival	-	0.210		24.8	8

Table 15 b Bifactorial enter regression on PTi and BEVi

dependent variable	**influential factor**	**p**	**p_{mult}**	**r_{mult}^2 (%)**
Bi	PTi	**0.017**		
	BEVi	**0.008**	**<0.001**	**73.4**
female rel. mean weight	PTi	0.167		
in 1st decade of May	BEVi	0.280	**0.023**	**41.7**
male activity	PTi	**0.018**		
	BEVi	0.329	**0.002**	**86.7**
female survival	PTi	**0.081**		
	BEVi	0.127	0.180	49.7
male survival	PTi	0.650		
	BEVi	0.226	0.438	28.1

Table 15 c Bifactorial enter regression on PTi and the product BEVi x PTi

dependent variable	**influential factor**	**p**	**p_{mult}**	**r_{mult}^2 (%)**
female rel. mean weight	PTi	0.608		
in 1st decade of May	BEVi x PTi	0.281	**0.023**	**41.7**
male activity	PTi	0.882		
	BEVi x PTi	0.312	**0.002**	**86.8**
female survivial	PTi	**0.078**		
	BEVi x PTi	0.105	0.155	52.9

Table 15 d. Bifactorial stepwise regression on PTi and the product BEVi x PTi. For female survival probability stepwise regression is not calculated.

dependent variable	**influential factor**	**p**	**r_{mult}^2 (%)**
female rel. mean weight	PTi	0.609	
in 1st decade of May	BEVi x PTi	**0.006**	**40.5**
male activity	PTi	0.882	
	BEVi x PTi	**< 0.001**	**86.8**

Table 16 Prigge's temperature, PT_i, for 1982 - 2001 and Baumgartner's value of the expectation periodicity BEVi. (BEVi is the value of the mean 4 year period of Prigge's temperature corresponding to spring i; the mean 4 year period is calculated from the PTi values known since 1891.

year	PT_i (^oC)	BEV_i (^oC)
1982	14.8	12.89
1983	11.5	12.18
1984	11.0	12.78
1985	14.9	13.69
1986	14.3	12.89
1987	9.9	12.18
1988	14.8	12.78
1989	15.1	13.69
1990	12.2	12.89
1991	10.6	12.18
1992	16.9	12.78
1993	15.2	13.69
1994	12.9	12.89
1995	11.1	12.18
1996	10.7	12.78
1997	13.7	13.69
1998	14.3	12.89
1999	12.4	12.18
2000	13.1	12.78
2001	14.8	13.69

The effect of the value i of the mean period of PTi on the population dynamics of *C. auronitens* is a major achievement of our research. We call the mean 4 year period of PTi "Baumgartners Expectation Periodicity", the value i of the expectation periodicity corresponding to the year i is abbreviated as BEVi (for the underlying model see chapter C. VII. 3.). It seems that BEVi represents an unknown factor or a complex of unknown factors, which affect Bi and other parameters of the population under study (see chapter C. VII. 3., C. VII. 4. & C. VII. 6.).

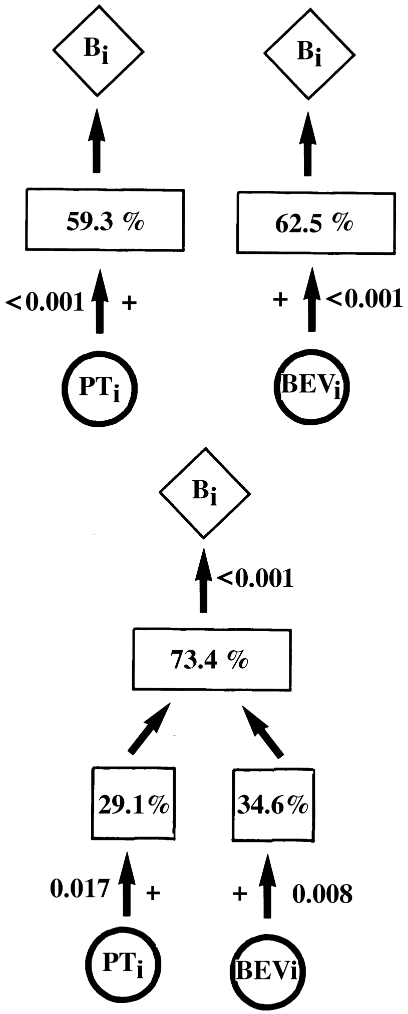
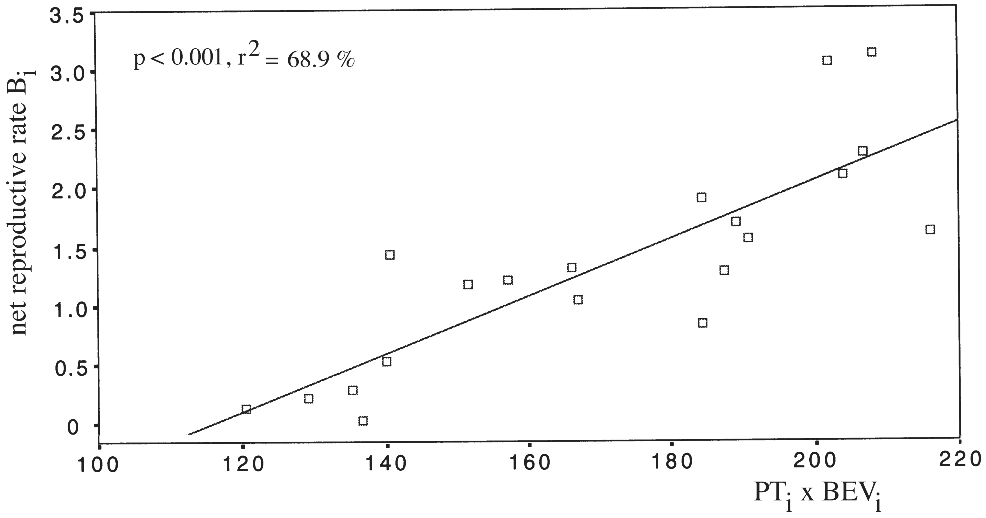


Fig. 15 Regression of net reproductive rate, Bi, on Prigge's temperature, PTi, and Baumgartner's value of the expectation periodicity, BEVi. Significance levels, signs of regression and coefficients of partial and multiple determination are given. Bi = +0.222 x PTi + 0.794 x BEVi - 11.778; $p_{b0} = 0.001$. Correlation of PTi and BEVi: +, p = 0.002, $r^2 = 43.7$ %. n = 20.



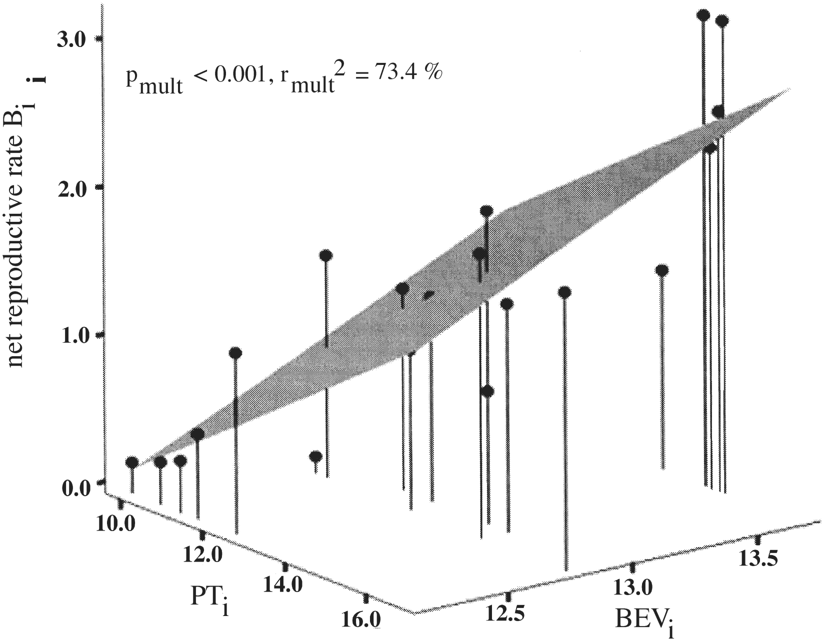


Fig. 16 Above: linear regression of the net reproductive rate, Bi, on the product PTi x BEVi. - Below: multiple linear regression of Bi on PTi and BEVi. Cf. chapter C. VII. 1. and **Fig. 15**. - PTi: Prigge's critical temperature; BEVi: Baumgartner's Expectation Value.

C. VII. 2. Critical tests of the distinct influence of the expectation periodicity on Bi

Finding a significant and distinct influence of PTi and BEVi on Bi was unexpected because both refer to the same interval in spring, and are highly correlated with each other (cf. chapter C. VII. 1.). Could the influence of BEVi represent a strong effect of PTi on Bi? To test this Bi is regressed on PTi and PTi^2. The unifactorial regression of Bi on PTi^2 is highly significant (+, $p < 0.001$, $r^2 = 57.3$ %; as is the quadratic function of Bi on PTi: $p_{func} < 0.001$, $r^2 = 63.3$ %). In the bifactorial regression on PTi and PTi^2, however, both are not significant, and in a stepwise regression PTi is influential, whereas PTi^2 is eliminated (data not shown). When, however, Bi is regressed on PTi, BEVi and the product BEVi x PTi, the product is most influential in stepwise regression (+, $p = 0.005$), the influence of PTi is weaker (-, $p = 0.070$; $p_{mult} < 0.001$, $r_{mult}^2 = 74.6$ %; remarkably, the influence of PTi is negative) and BEVi is eliminated. At least in part the influence of BEVi on Bi is not due to the dependence of Bi on PTi (appendix 4).

PTi is the mean temperature of an interval in May with variable limits. Does BEVi reflect the influence of May temperatures that are not represented by PTi? Indeed, BEVi is highly correlated with mean temperature in the 2nd decade of May: +, $p = 0.002$, $r^2 = 41.1$ %). BEVi is not correlated with mean temperature in the 1st and 3rd decade of May. The multiple regression of Bi on BEVi, PTi and the mean temperature in the 2nd decade of May (TM_2) again reveals a distinct and highly significant influence of BEVi on Bi:

regression of Bi on PTi, TM2 and BEVi

PTi: +, $p = 0.025$

TM2: -, $p = 0.308$

BEVi: +, $p = 0.006$

$p_{mult} < 0.001$; r_{mult}^2: 75.1 %

Even if Bi is regressed on TM2, PTi, BEVi and additionally on the temperature in the 1st and 3rd decade of May (TM1, TM3), BEVi has a significant distinct influence on Bi (data not shown).

The estimate of Bi for the period before the study site was enclosed with a beetle-proof fence is probably less accurate than that for the subsequent period (1993-2001):

- In an open area re-trapping rates are smaller, and thus, Jolly-Seber estimates are less reliable.
- Jolly-Seber estimates refer to an area that is larger than the area actually sampled: some beetles emigrate and re-immigrate; the range of the actual trapping area is unknown both in spring and autumn. In autumn the trapping area is probably smaller than in spring (freshly emerged beetles are less active than reproducing beetles; moreover, the autumn season is considerably shorter than the spring season, Weber & Heimbach, 2001). This difference, in particular, reduces the accuracy of the estimate of Bi for the period 1982 - 1992.

One critical aspect is whether in both periods, 1982 - 1992 (when the area was not surrounded by a beetle-proof fence) and 1993-2001 (when it was closed), BEVi affected Bi. In unifactorial regressions the influence of BEVi and PTi is demonstrable in each case.

	PTi	BEVi
1982 - 1992	$p = 0.002$	$p < 0.001$
	$r^2 = 66.5$ %	$r^2 = 81.9$ %
1993 - 2001	$p = 0.004$	$p = 0.026$
	$r^2 = 71.9$ %	$r^2 = 53.2$ %

Between 1982 and 1992 Bi was affected by both BEVi and PTi:

1982 - 1992:
PTi: $p = 0.031$
BEVi: $p = 0.002$
$p_{mult} < 0.001$, $r_{mult}^2 = 90.2$ %

Between 1982 and 1992 Bi is calculated using two series of autumn abundances (**Table 1**). Up to now the Bi values not set in brackets in **Table 1** have been used (chapter B. I. 2.). When the Bi values in brackets are used the statistical parameters of the bifactorial regression are nearly identical (not shown).

In the bifactorial regression using the Bi values calculated for the interval 1993 - 2001 the effect of PTi is weakly significant, that of BEVi is not significant; however, the coefficient of multiple determination is significant:

1993 - 2001:
PTi: $p = 0.073$
BEVi: $p = 0.536$
$p_{mult} = 0.018$, $r_{mult}^2 = 73.8$ %

This means that both factors probably have a distinct effect on Bi. This is demonstrated by regressing Bi on PTi, BEVi and the product PTi x BEVi. The effect of the product is weakly significant ($p = 0.094$), while that of PTi and BEVi is not significant. Again, the coefficient of multiple determination is significant ($p = 0.015$; $r^2 = 85.8$ %). In the stepwise regression the product is influential, but not PTi and BEVi :

1993 - 2001:
PTi x BEVi: $p = 0.002$, $r^2 = 75.0$
PTi: $p = 0.981$
BEVi: $p = 0.822$

Obviously, also over the period 1993 - 2001, both PTi and Bi independently affected the variability in Bi.

That the regression of Bi on BEVi is rather unaffected by inaccurate estimates of Bi, is also shown by the following tests (1-4).

(1) Bi values are ranked (1-20); the rank is regressed on BEVi and PTi:
regression of the rank of Bi on PTi: $p < 0.001$, $r^2 = 64.4$ %;
regression of the rank of Bi on BEVi: $p < 0.001$, $r^2 = 56.1$ %;
bifactorial regression of the rank of Bi and PTi: $p = 0.004$, BEVi: $p = 0.024$;
$p_{mult} < 0.001$; $r_{mult}^2 = 74.7$ %.

(2) When Bi is rounded to the next integer (0, 1, 2, 3) the influence of BEVi on the "Bi-number" is significant in the bifactorial regression ($p = 0.030$), the influence of PTi is highly significant ($p = 0.001$); $p_{mult} < 0.001$, and $r_{mult}^2 = 76.8$ %.

(3) When Bi values are allocated to classes with a width of 0.3 (0 - 0.3, 0.3 - 0.6 etc.; 11 classes) or to classes with a width of 0.8 (0 - 0.8, 0.8 - 1.6, etc; 4 classes), the influence of both, BEVi and PTi, is significant in the bifactorial regression (data not shown). In the case of 4 classes one value (1992: 1.60) is at the limit of a class; if this value is allocated to class 2 instead of class 3, the significance of BEVi is maintained.

(4) When only two classes are distinguished (class 1: 0.01 - 1.54, 13 values; class 2: 1.60 - 3.11, 7 values) the influence of BEVi is not significant in the bifactorial regression with PTi; however, in the stepwise regression the product PTi x BEVi is influential ($p < 0.001$; $r^2 = 58.3$ %), and that of PTi and BEVi is not.

An unexpected relationship is revealed when the variability of Bi is analysed separately for years with PTi values above 14 ^{0}C ($n = 9$) and below 14 ^{0}C ($n = 11$). In years when PTi < 14 ^{0}C PTi has a highly significant, BEVi has a weakly significant influence in the unifactorial regression. However, BEVi is not influential in the bifactorial regression (neither in the regression on PTi nor on the product $PTi_{<14 \text{ degrees}}$ x BEVi, data not shown). - On the other hand, in years when PTi >14 ^{0}C only BEVi is significant in the monofactorial regression. PTi is not influential even if Bi is bifactorially regressed on BEVi and the product ($PTi_{>14 \text{ degrees}}$ x BEVi) (data not shown). This result is highly important for our model (cf. chapter C. VII. 3.).

C. VII. 3. The model

We assume that responding to the expectation periodicity is adaptive: the yearly expectation value indicates the most likely conditions for reproduction (early development) at a critical interval (Prigge's interval) later in spring; thus by responding to the expectation beetles might be able to anticipate the conditions in the critical period and adapt their reproductive investments: when poor conditions are predicted reproductive investments (mate searching, oogenesis) are reduced in early spring, which increases the individual probability of survival. When good conditions are predicted reproductive investments are increased in early spring in order to utilize the expected favourable conditions for reproduction, even when the actual conditions in early spring are relatively unfavourable. Thus, it is likely that "Prigge's paradox" (the anticipatory influence of PTi on female weight development in early spring: chapter C. IV. 3.) is in response to a factor that is a predictor of the conditions in Prigge's critical interval. The relatively precise periodicity of Prigge's critical temperature (chapter D. III. 5.) is prerequisite for evolution of such an adaptation.

When Bi is controlled by both PTi and BEVi, the 4 year periodicity in Bi should be more precise than that in PTi, which is the case (chapter C. IV. 2., **Fig. 6**). Whatever the biological basis for this ability to predict conditions in late spring, it follows from the more precise periodicity in Bi that such prediction can only be made with a certain probability: when the prediction is negative, PTi may unexpectedly be relatively high; conversely, when it is positive, PTi may unexpectedly be relatively low. In chapter C. VII. 2. it is shown that in years with a mean temperature above 14 ^{0}C in Prigge's interval, Bi regressed on BEVi, but not on PTi. Conversely, in years with PTi values below 14 °C, Bi regressed on PTi, but not on BEVi. Obviously, in years with a high (optimum) PTi value (above 14 ^{0}C) the prediction was relatively frequently wrong, and thus the variability of Bi strongly depended on BEVi. In years with a low (adverse) PTi value, the prediction was more frequently correct, namely negative, and the variability in Bi was mainly influenced by PTi and less by BEVi, which was negative in most cases. Consequently, because of the relatively high frequency of wrong predictions in years with PTi values >14 ^{0}C there is no correlation between PTi and BEVi in these years ($p = 0.825$; $r^2 = 0.7$ %; $n = 9$), whereas in years with PTi values <14 ^{0}C there is a significant positive correlation ($p = 0.026$; $r^2 = 43.9$ %, $n = 11$). It is of special interest that type-1 errors (negative prognosis - good conditions in Prigge's interval) occur more frequently than type-2 errors (positive prognosis - adverse conditions). Type-2 errors could be more serious, as the population is harmed in two ways: by a reduction in net reproductive rate (because of the adverse weather in the critical interval) and possibly also by a reduction in probability of survival (because of - wasted - reproductive investments; assuming that the "reward" hypothesis holds; see below and chapter C. VII. 6.).

The expectation value, BEVi, is a virtual factor incorporating three categories of biological factors: (1) "target factors" that enable the animals to ensure their genetic persistence (reproduction and survival); (2) "realisation factors" that enable the beetles to adapt the target factors; (3) "information factors" that in early spring inform the population of the conditions that are likely to prevail during the critical period in early development.

(1) Both net reproductive rate and survival could be target factors: the model makes sense if the beetles are "rewarded" for a reduction in reproductive effort in anticipation of an adverse weather event. If more resources are allocated to somatic maintenance, the "reward" could be an increase of individual survival (i.e. an increase in the probability of reproducing in the following years when better conditions are more likely to occur). Thus, in terms of life history theory (Stearns, 1992; Futuyma, 1998) we postulate a trade-off between reproductive investment and survival. Therefore one question is: does the expectation periodicity affect the target factors (reproduction and survival) in a contrary manner (cf. chapter C. VII. 4.)? The positive influence on reproduction was shown in chapter C. VII. 1. The assumed negative influence on survival from spring i until spring i+1 is analysed in chapter C. VII. 4. Whether the probability of the young to survive from autumn i until spring i+1 is a target factor of the expectation periodicity is analysed in chapter C. VII. 5.

(2) Also, in chapter C. VII. 4. we determine the parameters of the population, which are the realisation factors postulated by our model. Realisation factors should be associated with the value of expectation. Realisation factors are thought to operate in early spring. It is expected that they are influenced also by early spring temperature. The question is: does BEVi affect the variability of potential realisation factors independently of early spring temperature? - It is logical to assume that realisation factors involve decisions regarding reproductive investment: oogenesis (chapter C. I. 2.) and the search for mates by males (chapter C. I. 3.).

(3) Finally, the nature of the information factors is analysed in chapter C. VII. 6. and C. IX. 1. and discussed in chapter D. III. 2. We assume that information is given by biotic factors that fluctuate synchronously with PTi, e.g. the abundance and/or generation structure of the spring stock.

C. VII. 4. Are reproductive investment and the probability of survival of females and males under the influence of BEVi?

Female reproductive investment is oogenesis measured as female relative mean weight ("mean weight of the females divided by the mean weight of the males") in the 1st decade of May (chapter C. I. 2.). Male reproductive investment is in mate searching activity measured as the probability of being trapped in the plateau-phase in spring (chapter C. I. 3.).

Both female and male reproductive investment regress positively and significantly on BEVi; after correcting the significance level for the number of dependent variables tested, the regression for females is weakly, and that for males is significant (**Table 15a** in chapter C. VII. 1.).

In the bifactorial regression of female relative mean weight in the 1st decade of May on PTi and BEVi, neither PTi nor BEVi is significant (**Table 15b**); in stepwise regression only PTi is influential with $p = 0.010$ and $r^2 = 36.4$ %. Also in the bifactorial regression of female relative mean weight in the 1st decade of May on PTi, and the product BEVi x PTi no factor is significant (**Table 15c**); in stepwise regression, however, the product is influential, whereas PTi is eliminated (**Table 15d**). Obviously, BEVi has a distinct influence on female reproductive investment. However, like abundance (chapter C. V. 3.) the influence of BEVi does not explain "Prigge's paradox": the anticipatory influence of PTi on the female reproductive investment is only partly replaced by BEVi.

Does a concerted effect of abundance and BEVi account for "Prigge's paradox"? To answer this two tests are performed: (1) female relative mean weight in the 1st decade of May is regressed on PTi, female abundance Ai-1 (cf. **Table 1**) and BEVi; (2) the coefficient of determination of female relative mean weight in the 1st decade of May on PTi is compared with the partial coefficients of determination when Ai-1 and/or BEVi are controlling factors:

(1) enter regression of female relative mean weight in the 1st decade of May on PTi, Ai-1 and BEVi :

PTi: +, $p = 0.252$

Ai-1: -, $p = 0.087$

BEVi: +, $p = 0.440$

$p_{mult} = 0.015$, $r_{mult}^2 = 53.8$ %

stepwise regression of female relative mean weight in the 1st decade of May on PTi, Ai-1 and BEVi:

PTi: +, $p = 0.052$

Ai-1: -, $p = 0.055$

$p_{mult} = 0.006$, $r^2 = 51.6$ %

BEVi: +, $p = 0.440$

(2) coefficient of determination of female relative mean weight in the 1st decade of May by PTi:

coefficient of determination in monofactorial regression on PTi: 36.4 %, $p = 0.010$ (**Table 7**)

partial coefficient of determination, controlling factor Ai-1: 24.3 %, $p = 0.052$

partial coefficient of determination, controlling factor BEVi: 13.2 %, $p = 0.167$

partial coefficient of determination, controlling factors BEVi and Ai-1: 10.0 %, $p = 0.252$

We conclude that "Prigge's paradox" is explained (possibly not completely, cf. stepwise regression (1) above) by the effect of Ai-1 and BEVi on female reproductive investment. - However, BEVi is a virtual factor; so what is - besides Ai-1 - a further real factor or the complex of factors behind BEVi? For the model of the expectation periodicity see chapter C. VII. 3. and for the discussion of "Prigge's paradox" see chapter C. VII. 6.

Male reproductive investment is in mate searching activity in spring (chapter C. I. 3.). The probability of being trapped in the plateau-phase in spring regresses also highly significantly on PTi (chapter C. IV. 4., **Fig. 9**) and significantly on BEVi (**Table 15a**). In the bifactorial regression PTi is significant, BEVi is not significant (**Table 15b**). When stepwise regressed on PTi and the product PTi x BEVi, the product is highly influential, and PTi is eliminated (**Table 15 c, d**). These analyses suggest that both PTi and BEVi significantly affect male reproductive investment. - When the male trapping probability is bifactorially regressed on BEVi and Ai-1 (female abundance, cf. **Table 1**) the first factor is highly significant (+, $p = 0.005$), and the latter is significant (-, $p = 0.016$; $p_{mult} = 0.002$; $r_{mult}^2 = 87.0$ %). - However, when PTi, BEVi and Ai-1 are treated as independent variables in a stepwise regression PTi is influential, BEVi and Ai-1 are not ($r^2 = 84.2$ %); the same result is obtained when PTi and the quotient "Ai-1 / BEVi" or the inverse quotient are used. These results do not exclude a distinct influence of BEVi on male reproductive investment; however, they lessen the probability that this is the case (remember that the parameter of abundance does not significantly affect the male activity in the bifactorial regression with PTi ; cf. chapter C. V. 4).

The survival of females and males (irrespective of age) does not regress on BEVi; for males, as expected, the sign is negative; for females, however, it is positive (**Table 15a**).

For the relevance of these results for the model see chapter C. VII. 6.

C. VII. 5. Is the survival of the young affected by BEVi?

The probability of freshly emerged females surviving from autumn i until spring i+1 regresses weakly significantly on BEVi (after correcting the significance level the regression is no longer significant: **Table 13**). In a bifactorial regression including the temperature in the 2nd decade of May (TM2), which affects the survival of young (chapter C. VI. 4.), BEVi is not significant; when, however, female survival is regressed on TM2 and the product "BEVi x TM2" the product is influential in bifactorial regression and TM2 is not:

stepwise regression of the probability of young females surviving from autumn i until spring i+1

BEVi x TM2: +, $p = 0.002$, $r^2 = 83.1$ %

TM2: +, $p = 0.922$

The probability of the freshly emerged males of surviving does not regress on BEVi (**Table 13**). However, the CV of young male body size, which influences survival, regresses significantly on BEVi (again after correcting the significance level the regression is no longer significant: **Table 14**). In a trifactorial regression incorporating TM2, PTi and BEVi (cf. **Table 14**), and bifactorial regression incorporating TM2 and the product "PTi x TM2 x BEVi" BEVi does not have an effect; statistics not shown).

The survival of young males also regresses weakly significantly on a parameter of female abundance in spring (Ai; **Table 1**); the significance disappears after correction (**Table 13**); the significance is also abolished when TM2 is incorporated in a bifactorial regression (chapter C. VI.4.). The CV of young male body size also regresses on a parameter of abundance (Ai-1; **Table 14**). This is also not significant when corrected; however, as already mentioned, an effect of this abundance parameter can not be excluded with certainty (chapter C. VI. 4.).

We conclude that the survival of young females could be influenced by the expectation periodicity: the larger BEVi the larger the probability that young females will survive from autumn i until spring i+1. However, this dependence cannot be interpreted as an adaptation to the weather in spring i: when adverse weather is "predicted" reproductive investment is reduced (interpreted as an adaptation; chapters C. VII. 4., C. VII. 6. & D. III. 2.), but the survival of the fewer young produced may also be reduced (a mis-adaptation?, cf. chapter D. III. 2.). - An effect of BEVi on the survival of young males is not apparent. There could be some influence of the abundance in spring i-1 on the CV of young male body size (chapter C. VI. 4.). The sign is positive: if such an influence really exists the CV of body size would be larger (and consequently, survival probability smaller) when beetles are abundant in spring i-1. Again, such a dependence could hardly be interpreted by the model of an expectation periodicity by which the population dynamics is adapted to periodically occurring adverse weather in spring.

C. VII. 6. Do the empirical data fit the model?

Target factors of the expectation periodicity

In chapter C. VII. 3. we assume that (1) net reproductive rate and (2) survival are target factors of the expectation periodicity. (1) Net reproductive rate is assumed to regress positively and (2) survival to regress negatively on BEVi. Indeed, net reproductive rate regresses highly significantly and positively on the yearly value of the expectation periodicity (cf. the results outlined in chapters C. VII. 1. & C. VII. 2.). On the other hand, the above assumption regarding female and male survival is not fulfilled: survival does not regress on BEVi (C. VII. 4.) and is not correlated with Bi (chapter C. III.). However, both Bi and female survival regress distinctly on the parameter of abundance: Bi negatively (chapter C. V. 2.), and female survival positively (chapter C. V. 4.). Probably this is relevant as abundance seems to be an information factor of the expectation periodicity (see above). Thus, our data indirectly reveal a correlation of the correct sign between Bi and female survival, which fits the model: the reward hypothesis is weakly founded. - Moreover, in chapter C. IX. 2. it is shown that female survival is more strikingly negatively correlated with another measure of Bi ($B_{i,\ without\ 1.5}$ calculated assuming that the 1.5 year old females are reproductively inactive). That the data do not reveal the assumed inverse dependence on BEVi could be due to the rather small data set for survival and/or to the fact that BEVi may not fully represent the expectation periodicity (see below).

Realisation factors of the expectation periodicity

We conclude that reproductive investment (female relative mean weight in the 1st decade of May and male activity level in the plateau-phase in spring) may be realisation factors of the expectation periodicity: (1) net reproductive rate, Bi, is strongly influenced by these parameters (chapters C. I. 2. & C. I. 3.), (2) both biotic factors distinctly regress on BEVi, respectively on the product PTi x BEVi, in the bifactorial regression (with PTi as the second independent variable; chapter C. VII. 4.).

Information factors of the expectation periodicity

The biggest problem is to identify the information factors. It is realistic to assume that biotic parameters that fluctuate synchronously with PTi inform the females and males in early spring whether good or bad conditions are likely in Prigge's critical interval. Such parameters could be the abundance and the population structure. We will analyse whether parameters of the female stock inform on the expectation: the total female abundance in spring (values from **Table 1** are used) and the female generation structure in spring (abundances and proportions of generations calculated from **Table 2:** cf. chapters C. VIII. & C. IX.).

If total abundance is an information factor then (1) abundance should fluctuate synchronously with PTi, (2) abundance should indirectly influence the target factors Bi and survival (Bi negatively and survival positively), (3) abundance should directly influence the supposed realisation factors (female relative mean weight in the 1st decade of May and male activity level), (4) BEVi should regress on abundance.

(1) The most influential parameter of abundance (Ai-1) is weakly negatively correlated with PTi; like PTi, abundance shows a minimum at 4 years in the periodogram, which, however, is not significant (chapter C. V. 2.).

(2) Abundance distinctly negatively influences Bi (chapter C. V. 2.) and positively female survival (chapter C. V. 5.) as expected (see above).

(3) Abundance probably distinctly affects female reproductive investment (chapter C. V. 3.); but not the activity level of males (chapter C. V. 4).

(4) Does BEVi distinctly regress on the parameter of abundance? This remains to be analysed. As is expected BEVi negatively regresses on Ai-1, but only weakly significantly ($p = 0.073$, $r^2 = 17.7$). In the bifactorial regression of BEVi on PTi and Ai-1, and respectively, PTi and the quotient "Ai-1 / PTi", PTi is significant, but Ai-1 and the quotient are not so:

bifactorial regression of BEVi on PTi and Ai-1

PTi: +, $p = 0.007$

Ai-1: -, $p = 0.372$

$p_{mult} = 0.005$, $r_{mult}^2 = 48.1$ %

bifactorial regression of BEVi on PTi and Ai-1 / PTi

PTi: +, $p = 0.041$

Ai-1 / PTi: -, $p = 0.478$

$p_{mult} = 0.006$, $r_{mult}^2 = 47.1$ %

A similar result is obtained when the inverse quotient is used.

It may be concluded from (1) - (3) that abundance is an information factor, which is, at least partly, represented by BEVi; result (4), however, does not support this conclusion.

Several results support the assumption that abundance (if at all) is only one of a complex of factors that constitute the information resource of the expectation periodicity (1-4):

(1) When Bi is regressed on PTi, BEVi and Ai-1 the effect of BEVi is significant, and the parameter of abundance weakly significant (PTi is significant; chapter C. VII. 1.).

(2) Ai-1 does not replace the anticipatory influence of PTi on female relative mean weight in the 1st decade of May, but seems to weaken this influence (chapter C. V. 3.).

(3) The coefficient of determination of the regression of BEVi on Ai-1 is only 17.7 % (see above).

(4) When male reproductive investment is regressed on Ai-1 and BEVi the influence of Ai-1 is significant, and that of BEVi still highly significant (chapter C. VII. 4.).

We conclude that abundance is only partly represented by BEVi. This conclusion is well illustrated by the regression of Bi on BEVi and Ai-1:

BEVi: +, $p < 0.001$, $r_{part}^2 = 55.1$ % (monofactorial: $r^2 = 62.5$ %)

Ai-1: -, $p = 0.050$, $r_{part}^2 = 21.8$ % (monofactorial: $r^2 = 35.1$ %)

$p_{mult} < 0.001$, $r_{mult}^2 = 70.9$ %;

and also by the regression of female relative mean weight in the 1st decade of May on BEVi and Ai-1:

Ai-1: -, $p = 0.056$, $r_{part}^2 = 23.6$ % (monofactorial: $r^2 = 36.0$ %)

BEVi: +, $p = 0.084$, $r_{part}^2 = 19.8$ % (monofactorial: $r^2 = 32.8$ %)

$p_{mult} = 0.009$, $r_{mult}^2 = 48.7$ %

Obviously, BEVi does not represent all the information incorporated in the expectation periodicity (1 - 3):

(1) BEVi does not affect female and male survival probability (chapter C. VII. 4., **Table 15a**);

(2) The influence of BEVi does not completely account for "Prigge's paradox" (the anticipatory influence of PTi on female reproductive investment) although BEVi distinctly affects female relative mean weight in the 1st decade of May (chapter C. VII. 4., **Tables 14 b - d**): in the bifactorial regression on PTi and BEVi no factor is significant, p_{mult}, however, is significant ; this points to an influence of both factors (the influence of PTi prevails); indeed in the bifactorial regression on PTi and the product BEVi x PTi, the influence of the product prevails.

(3) Tables 14 b - d indicate that the influence of PTi on male activity is not completely abolished by BEVi. In this case, however, the influence of PTi may not be anticipatory (mimicked) but may reflect the effect of the actual temperature on locomotion.

The information lacking in BEVi is partly, but not completely supplied by abundance. Especially "Prigge's paradox" indicates that there is more anticipatory information than is included by BEVi and Ai-1: they do not completely explain the anticipatory influence of PTi (as shown in chapter C. VII. 4.).

In summary, these analyses confirm that (1) net reproduction is a target factor of the expectation periodicity; concerning the female survival this conclusion is also justified: this parameter does not regress on BEVi, but distinctly on the parameter of abundance which gives some anticipatory information. - (2) Oogenesis (measured as female relative mean weight in the 1st decade of May) and male mate searching activity (measured as the trapping probability in the plateau-phase in spring) seem to be realisation factors of the expectation periodicity. - (3) Abundance is an information factor; however, the effects of abundance and BEVi on the realisation and target factors partly overlap: abundance is only partly represented by BEVi, and BEVi contains more information than is given by abundance. Additional information factors have to be assumed which are (completely and /or partly) represented by BEVi.

Possibly, the generation structure of the population is an additional information factor of the expectation periodicity. The generation structure can only be measured in a beetle-proof enclosure. Our study area was enclosed in the summer of 1992 (chapter B. I. 2.). As the female stock in spring is composed of several generations the complete generation structure is unknown until 1997. Thus, there are insufficient empirical data for analysis. Therefore, we will try to simulate the population structure underlying the number of freshly emerged beetles recorded since 1982 and the observed survival of the female generations (chapters C. IV. 7. & C. V. 5.): if a distinct influence of BEVi on Bi is simulated we will use the result of this simulation to analyse by regression what parameters may be behind BEVi (chapter C. VIII. 4.). - By simulating Bi (additionally based on temperature and/or abundance dependence of Bi) we will try to reveal the relevance of PTi and female abundance for the expression of a distinct influence of BEVi on Bi (chapters C. VIII. 1. - 3.).

C. VIII. Simulation of the expectation periodicity and female population structure

C. VIII. 1. Conditions for simulating the expectation periodicity (simulations A - E)

We made a series of simulations assuming the following conditions (for general assumptions cf. chapter B. I. 4.).

Simulation A

(A1) Net reproductive rate, Bi, depends on PTi and Ai-1 (cf. chapter C. V. 2.):

$$Bi = 0.2946 \text{ x } PTi - 0.0043 \text{ x } Ai\text{-}1 - 1.7039;$$

$$p_{b1} = 0.001, p_{b2} = 0.040, p_{b0} = 0.148$$

$$p_{mult} < 0.001, r_{mult}^2 = 69.6 \%$$

(A2) The proportion of freshly emerged females is always 55 % (chapter C. IV. 8.).

(A3) The probability of young females surviving from autumn i until spring i+1(y) depends on the temperature in the 2nd decade of May in spring i (TM2i) (chapter C. VI. 3.; the probability is not arcsine transformed, cf. chapter B. I. 4.):

$$y = 0.0689 \text{ x } TM2i - 0.3165$$

$$p_{b1} = 0.001, p_{b0} = 0.141$$

$$r^2 = 83.8 \%$$

(A4) The (not arcsine transformed) probability of the 0.5 year old females ($y_{0.5}$) surviving from spring i until spring i+1 depends on Ai-1 (cf. chapter C. V. 5.):

$y_{0.5} = 0.0013 \text{ x } Ai\text{-}1 + 0.3631$

$p_{b1} = 0.073$, $p_{b0} = 0.026$

$r^2 = 50.5\ \%$

(A5) The (not arcsine transformed) probability of the 1.5 year old females ($y_{1.5}$) surviving from spring i until spring i+1 depends on Ai-1 (cf. chapter C. V. 5.):

$y_{1.5} = 0.0019 \text{ x } Ai\text{-}1 + 0.1515$

$p_{b1} = 0.003$, $p_{b0} = 0.075$

$r^2 = 91.6\ \%$

(A6) The probabilities of the older females surviving from spring i until spring i+1 are density-independent and have the following constant values (chapter C. V. 5.):

2.5 year old females: 0.5853
3.5 year old females: 0.2950
4.5 year old females: 0.1257
(not arcsine transformed)

Using the conditions A1 - A6 a distinct influence of BEVi on Bi is not simulated.

(B) In an attempt to strengthen the influence of the independent variables on the simulation of an expectation periodicity we simulated the dynamics of the population after eliminating the non significant constants in the formulae (A1) and (A3).

(B1) Bi depends on PTi and Ai-1 as indicated by the following formula:

$Bi = 0.1953 \text{ x } PTi - 0.0063 \text{ x } Ai\text{-}1$

$p_{b1} < 0.001$, $p_{b2} = 0.001$

$p_{mult} < 0.001$

(B2) Like (A2).

(B3) The probability of the young females surviving from autumn i until spring i+1(y) depends on TM2i as indicated by the following formula:

$y = 0.04825 \text{ x } TM2i$

$p < 0.001$

(B4) Like (A4).

(B5) Like (A5).

(B6) Like (A6)

Also using the conditions B1 - B6 a distinct influence of BEVi on Bi is not simulated.

(C) In a 3rd simulation we assumed that 1.5 year old females are not reproductively active: Bi refers to the abundance of females younger and older than 1.5 years in the plateau-phase of spring i (= $B_{i,\text{without } 1.5}$, moreover, the abundance of 1.5 year old females does not affect the reproduction of the other females.

The density influence on survival of 0.5 and 1.5 year old females is the same as in simulations (A) and (B) (see below). The difference to simulation (A) and (B) is based on the observation that $B_{i,with\ 1.5}$ does not regress on the relative mean weight of the 1.5 year old females in the 1st decade of May (chapter C. I. 2.). – The constant is eliminated from the formula of the regression function of $B_{i,without\ 1.5}$, (see below; when the constant is not eliminated, PTi and $A_{i-1,\ without\ 1.5}$ do not influence $B_{i,without\ 1.5}$).

Below (simulations E / I and E / II) we use results from simulation H (simulation H is based only on assumptions concerning the survival of young and the older generations; cf. chapter C. VIII. 4.). However, $B_{i,without\ 1.5}$ from simulation H does not regress on the parameter $A_{i-1,without\ 1.5}$ (see chapter IX. 1. - point 4b). Therefore, simulation C is based on the field data although their number is small, and the constant in the regression of $B_{i,without\ 1.5}$, has to be eliminated. It has to be stressed that we expect an influence of BEVi on the simulated Bi, which refers to the abundance of the total female stock in spring i ($B_{i,with\ 1.5}$).

(C1) $B_{i,\ without\ 1.5}$ depends on PTi and $A_{i-1,without\ 1.5}$ as indicated by the following formula :

$B_{i,without\ 1.5} = 0.2508 \text{ x PTi} - 0.0133 \text{ x } A_{i-1,without\ 1.5}$

$p_{b1} = 0.007$, $p_{b2} = 0.056$

$p_{mult} = 0.011$

(C2) Like (A2) and (B2).

(C3) Like (B3).

(C4) Like (A4) and (B4).

(C5) Like (A5) and (B5).

(C6) Like (A6) and (B6).

Using assumptions C an influence of BEVi is simulated. $B_{i,with\ 1.5}$ regresses on BEVi with high significance:

$p_{b1} < 0.001$

$p_{b0} < 0.001$

$r^2 = 57.0\ \%$

Also in the bifactorial regression with PTi the influence of BEVi on $B_{i,with\ 1.5}$ is distinct:

BEVi: +, $p = 0.016$, $r_{part}^2 = 29.4\ \%$

PTi: +, $p = 0.071$, $r_{part}^2 = 17.9\ \%$

$p_{mult} < 0.001$, $r_{mult}^2 = 64.7\ \%$

The expression of an expectation periodicity which is adapted to the 4 year periodicity in PTi seems to be because 1.5 year old females are reproductively spent. This implies that generation structure is an essential information factor of the expectation periodicity. However, a reproductive relaxation of 1.5 year old females could be disadvantageous as outlined in chapter D. III. 2.

In model C it is assumed that 1.5 year old females are reproductively inactive: they do not produce eggs and do not participate in the density-dependent inhibition of egg production. On the other hand, they affect the survival of 0.5 year old females, and the survival of 1.5 year old females is affected by the abundance of the total female stock (assumptions C4 and C5). These assumptions are questionable, as they do not fit a simple reward hypothesis (chapters C. VII. 3. & C. IX. 1.). However, the probability of the female generations surviving from spring i to spring i+1 does not significantly depend on the abundance of the females younger and older than 1.5 years in spring i-1 ($A_{i-1,\text{without }1.5}$); only the survival of the total female stock regresses weakly significantly on this parameter of abundance (+, $p = 0.089$, $r^2 = 55.6$ %).

In order to check for the relevance of density-dependent survival in the expression of the expectation periodicity, also constant survival for the 0.5 and 1.5 year old females is assumed (simulation D):

(D4) 0.5 year old females: $p = 0.624$

(D5) 1.5 year old females: $p = 0.594$

The other assumptions are as in simulations B and C.

A distinct influence of BEVi on $B_{i,\text{with }1.5}$ is also found in simulation D:

BEVi: +, $p = 0.002$, $r_{part}^2 = 43.1$ %

PTi: +, $p = 0.021$, $r_{part}^2 = 27.7$ %

$p_{mult} < 0.001$, $r_{mult}^2 = 76.7$ %

Density-dependent survival does not appear to be essential for the expression of the expectation periodicity.

Models C and D have a serious weakness: the bifactorial determination of the net reproductive rate, $B_{i,\text{without }1.5}$, by PTi is not significant, when the constant in the regression formula is considered (compare above). Therefore, we test the possibility that an expectation periodicity can be simulated by ignoring any effect density might have on reproduction and survival (two simulations - E / I and E / II - are carried out). The other assumptions are as in simulations B, C and D.

(E / I) The net reproductive rate, $B_{i,\text{without }1.5}$, measured in the field between 1993 and 2001 depends on PTi as indicated by the following formula:

$B_{i,\text{without }1.5} = 0.656 \times PTi - 6.881$

$p_{b1} = 0.059$, $p_{b0} = 0.109$, $r^2 = 47.5$ %, $n = 8$;

Even after ignoring any possible density effects the simulation E / I indicates a distinct influence of BEVi on $B_{i,\text{with }1.5}$:

BEVi: +, $p = 0.053$, $r_{part}^2 = 20.3$ %

PTi: +, $p < 0.001$, $r_{part}^2 = 68.4$ %

$p_{mult} < 0.001$, $r_{mult}^2 = 85.8$ %

BEVi x PTi: +, $p = 0.036$, $r_{part}^2 = 23.4$ %

PTi: -, $p = 0.755$, $r_{part}^2 = 0.6$ %

$p_{mult} < 0.001$, $r_{mult}^2 = 86.4$ %

As in formula (E / I), the influence of PTi is only weakly significant and the constant is not significant (probably both due to the small number of observations), we also simulate $B_{i,without\ 1.5}$ based on the results of simulation H (C. VIII. 4.), in which the generation structure is based on the observed abundance of the freshly emerged beetles and observed survival. This simulation is called "simulation E / II".

(E / II): The net reproductive rate, $B_{i,without\ 1.5}$, simulated in H depends on PTi as indicated by the following formula:

$B_{i,without\ 1.5} = 0.459 \times PTi - 4.500$

$p_{b1} < 0.001$, $p_{b0} = 0.002$, $r^2 = 60.8$ %, n = 15

The result of simulation E / II is nearly the same as predicted by E / I. $B_{i,with\ 1.5}$ regresses significantly on BEVi:

BEVi: +, $p = 0.048$, $r_{part}^2 = 21.0$ %

PTi: +, $p < 0.001$, $r_{part}^2 = 71.3$ %

$p_{mult} < 0.001$, $r_{mult}^2 = 87.2$ %

Simulations E / I and E / II indicate that reproductive inactivity of 1.5 year old females is the minimum condition for the expression of an adapted expectation periodicity. Obviously, in year 1 of the 4 year cycle when an adverse weather event is likely, the abundance and proportion of 1.5 year old females is high so that net reproductive rate (referring to the total female population) is small, even if PTi is relatively high. Indeed, the arcsine-transformed proportion of 1.5 year old females and PTi are negatively correlated in the data sets produced by these simulations:

E / I: -, $p = 0.079$, $r^2 = 16.1$ %

E / II: -, $p = 0.062$, $r^2 = 18.1$ %

This relationship is confirmed by simulation H (chapter C. VIII. 4.). Also in the observed data, there is a negative correlation between PTi and the proportion of 1.5 year old females in spring i (-, $p = 0.066$, $r^2 =$ 45.7 %).

The prediction of simulations E / I and E / II raises the question whether the assumption of a negative density-dependence of the net reproductive rate, $B_{i,with\ 1.5}$, is necessary at all in order to describe the adaptation of the population to the 4 year cycle in PTi. This critical question will be analysed in detail in chapter C. VIII. 5. by comparing the predictions of simulations C, D, E / I, E / II and H and the analyses of the field data (cf. also chapter C. IX. 1.).

C. VIII. 2. The steady state (simulation F)

How does the simulated population behave when temperature is kept constant? Are there periodic fluctuations in Bi and Ai; is the periodicity self-sustained or does the population stabilize at a level dependent on net reproductive rate and density? To answer this PTi and the mean daily temperature in the 2nd decade of May where kept constant (14°C in both cases), all other assumptions regarding population dynamics are as in simulation C. Starting with the population structure simulated for 2000 and 2001 the fluctuations in $B_{i,with\ 1.5}$ and $A_{i,with\ 1.5}$. dampen out within approximately 4 periods, and then a steady state of net reproductive rate (**Fig. 17**) and abundance is reached. There is no influence of the 4 year period of BEVi on $B_{i,with\ 1.5}$ before the steady state is reached (the sign of regression is even negative: -, $p = 0.515$), possibly because the period length of the outdamping fluctuation of net reproductive rate (**Fig. 17**) and abundance is not 4, but 5 years (not shown).

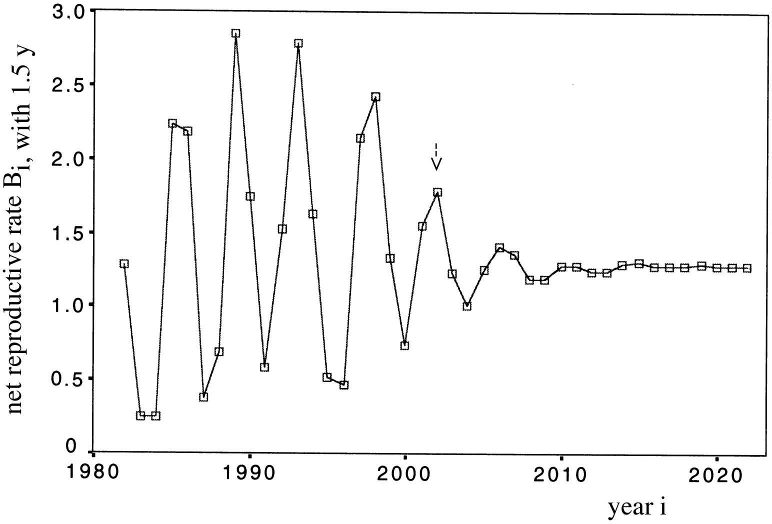


Fig. 17 Simulation of net reproductive rate, Bi (of total female stock), for the period 1982 - 2001 (simulation C), and under constant temperature operating from the arrow mark (simulation F: PTi and TM2 = 14^0C; cf. chapter C. VIII. 2.).

C. VIII. 3. Is an adapted expectation periodicity expressed when the period of PTi is longer than 6 years (simulation G)?

We simulate a 6 year periodicity in PTi by adding two temperature values to each observed 4 year cycle (chapter C. IV. 2.). Let "year 1" be the low temperature year within a 4 year cycle, and add an additional value after that for year 2, 3 and/or 4. The two years after which a value is added are determined of chance. Only high temperatures are added (two values out of the respective 4 year cycle). It is a matter of chance what high temperature value is added after the years determined by chance. Not only the PTi of an added year but also the mean daily temperature in the 2nd decade of May of the respective year is used to simulate the population dynamics under a 6 year periodicity in the influential temperature. The simulated PTi series comprises 30 years; the cubic regression of PTi on the phases of the 6 year cycle is highly significant ($p = 0.002$); also the periodogram analysis indicates a period of 6 years ($p < 0.05$). Over the time span of the field study (1982 - 2001) PTi also regresses on the phases of the 4 year cycle with an significance level of $p = 0.012$, and the periodogram analysis indicates a period with an significance level of $p < 0.05$ (chapter, C. IV. 2.). - The other assumptions of simulation G are as in simulation C (chapter C. VIII. 1.)

The simulated net reproductive rate, $B_{i,\text{with }1.5}$, regresses on PTi with high significance ($p < 0.001$, $r^2 = 57.5$ %), and as expected there is a significant regression on the mean value i of the 6 year period of PTi ($p = 0.006$, $r^2 = 23.7$ %). However, in the bifactorial regression on PTi and the mean value i of the 6 year period only the influence of PTi is significant (appendix 5):

PTi: +, $p < 0.001$

mean value i of the 6 year period: -, $p = 0.950$

$p_{mult} < 0.001$, $r_{mult}^2 = 57.5$ %

Also, $B_{i,with\ 1.5}$ of simulation G does not regress on the value of the 4 year expectation periodicity, BEVi (monofactorial: $p = 0.207$. $r^2 = 5.6$ %).

Thus, an expectation periodicity of 6 years is not expressed when there is a 6 year periodicity of PTi; probably, the adaptation to a distinct temperature cycle presupposes adapted differences in the reproductive activity of the different generations of females, and an adapted density effect on reproduction (cf. chapter D. III. 5.).

C. VIII. 4. Simulation of the generation structure (simulation H)

The generation structure of the female stock is simulated using.the estimated number of freshly emerged beetles (**Table 1**; a constant female proportion of 0.55 is assumed). The survival of the freshly emerged females from autumn i to spring i+1 depends on the temperature in the 2nd decade of May in spring i (the constant in the regression formula is eliminated). Constant survival probabilities from spring i to spring i+1 are assumed not only for the older females, but also for the 0.5 and 1.5 year old females (as in simulation D, chapter C. VII. 1.);

The simulated generation structure is complete in 1988 (6 generations); however, the simulation of net reproductive rate is started 1987, when the 6th generation, which is rather small in other years, is still absent (**Table 17**).

Table 17 The simulated female generation structure (simulation H; for conditions of simulation cf. text). The abundance of the female generations and total abundance of females are given. Deviations between the sum of females of different age and the total abundance are due to rounding the abundances to whole numbers.

year	0.5	1.5	2.5	3.5	4.5	5.5	total
1983	143	?	?	?	?	?	?
1984	33	89	?	?	?	?	?
1985	61	21	53	?	?	?	?
1986	129	38	12	31	?	?	?
1987	134	80	23	7	9	?	253
1988	6	84	48	13	2	1	154
1989	113	4	50	28	4	0	199
1990	170	71	2	29	8	0	281
1991	122	106	42	1	8	1	281
1992	14	76	63	24	0	1	179
1993	132	9	45	37	7	0	230
1994	226	82	5	26	11	1	351
1995	143	141	49	3	8	1	345
1996	22	89	84	29	1	1	225
1997	1	14	53	49	8	0	125
1998	71	0	8	31	14	1	126
1999	55	44	0	5	9	2	115
2000	47	34	26	0	1	1	111
2001	23	29	20	15	0	0	88

As can be expected, the simulated $B_{i,\text{with 1.5}}$ regresses monofactorially with high significance on BEVi (+, $p = 0.002$, $r^2 = 53.1$ %) and PTi (+, $p < 0.001$, $r^2 = 74.1$ %).

In the bifactorial regression of $B_{i,\text{with 1.5}}$ on PTi and BEVi the influence of BEVi is not significant:

PTi: +, 0.002

BEVi: +, p = 0.124

$p_{mult} < 0.001$, $r_{mult}^2 = 78.9$ %

Nevertheless, there is a distinct influence of BEVi. When the product "PTi x BEVi" is used the product is influential, whereas PTi is eliminated in the stepwise regression:

PTi x BEVi: +, $p < 0.001$, $r^2 = 79.2$ %

PTi: -, p = 0.619

We test the quality of simulation H by correlating observed and simulated parameters (**Table 18**): all ($B_{i,\text{with 1.5}}$, total female abundance and absolute abundance of each female generation, proportion of each female generation in the total female abundance) are highly correlated (r^2 is at least 80.0 % and p = 0.003). Thus, the simulated structure of the female stock is realistic, and this simulation can be used to determine the degree of determination of BEVi by parameters of the female stock.

Table 18 Correlation between observed and simulated values (simulation H; observed Bi from **Table 1**; observed total abundance from **Table 1** and **Table 2**; observed abundance of female generations and observed proportion of generations in the female stock from **Table 2**). Proportions are not arcsine transformed. Significance levels are corrected using k = 11.

	sign	p	p_{corr}	r^2	n
$B_{i,\text{with}}$ (1987 - 2001)	+	**<0.001**	**<0.001**	**83.6**	15
abundance of females in spring					
total abundance					
1987 - 2001 (Table 1)	+	**<0.001**	**<0.001**	**87.0**	15
1993 - 2001 (Table 2)	+	**<0.001**	**<0.001**	**89.1**	9
abundance of generations					
0.5 year old (1993 - 2001)	+	**<0.001**	**<0.001**	**98.3**	9
1.5 year old (1994 - 2001)	+	**<0.001**	**0.001**	**94.5**	8
2.5 year old (1995 - 2001)	+	**0.003**	**0.029**	**85.8**	7
3 year old and older (1995 - 2001)	+	**0.003**	**0.036**	**84.6**	7
proportion of generations in total abundance in spring					
0.5 year old (1993 - 2001)	+	**0.001**	**0.012**	**80.0**	9
1.5 year old (1994 - 2001)	+	**<0.001**	**0.001**	**92.6**	8
2.5 year old (1995 - 2001)	+	**0.002**	**0.018**	**88.3**	7
3 years and older (1995 - 2001)	+	**0.002**	**0.017**	**88.4**	7

The absolute abundance of 1.5 year old females in spring i and 0.5 year old females in spring i-1 are the most influential (negatively, **Table 19**). Both parameters show a pronounced 4 year periodicity: in the case of 0.5 year old females the maximum is in the year before that in which an adverse weather event is likely to occur (**Fig. 18**), and because of constant survival the maximum of 1.5 year old females is in the year in which the adverse weather event is likely (**Fig. 18**). This fits the hypothesis that 1.5 year old females have a special significance in the development of the population's expectation periodicity (cf. chapter C. VIII. 1.): the low net reproductive rate in year 1 of the cycle (when an adverse weather event is likely) is, at least partly, due to the high proportion of 1.5 year old females in that year. This result is important as in simulation H nothing in particular is assumed about the female generations.

Table 19 Monofactorial regressions of BEVi on parameters of the female population structure in spring simulated in simulation H. Proportions are arcsine transformed. Levels of significance are corrected using k = 20. n = 15 in each case.

independent parameter	**sign**	**p**	**p_{corr}**	**r^2 (%)**
total abundance in spring i ($A_{i,\text{with } 1.5}$)	-	0.184	0.983	13.2
total abundance in spring i-1 ($A_{i-1,\text{with } 1.5}$)	-	0.144	0.956	16.9
abundance of females younger and older than 1.5 year in spring i ($A_{i,\text{without } 1.5}$)	-	0.978	1.000	0.0
abundance of females younger and older than 1.5 year in spring i-1 ($A_{i-1,\text{without } 1.5}$)	-	**0.017**	0.2917	**38.9**
absolute abundance of 0.5 year old females in spring i	-	0.299	0.999	6.3
absolute abundance of 1.5 year old females in spring i	-	**<0.001**	**0.010**	**53.9**
absolute abundance of 2.5 year old females in spring i	+	0.412	1.000	4.5
absolute abundance of ≥ 3.5 year old females in spring i	+	**0.021**	0.346	**34.6**
absolute abundance of 0.5 year old females in spring i-1	-	**<0.001**	**0.010**	**53.9**
absolute abundance of 1.5 year old females in spring i-1	+	0.412	1.000	4.5
absolute abundance of 2.5 year old females in spring i-1	+	**0.002**	**0.035**	**51.2**
absolute abundance of ≥ 3.5 year old females in spring i-1	-	0.125	0.932	18.4
proportion of 0.5 year old females in spring i	-	0.552	1.000	2.8
proportion of 1.5 year old females in spring i	-	**0.028**	0.430	**32.1**
proportion of 2.5 year old females in spring i	+	0.107	0.896	18.7
proportion of ≥ 3.5 year old females in spring i	+	**0.014**	0.253	**37.9**
proportion of 0.5 year old females in spring i-1	-	**0.008**	0.141	**46.1**
proportion of 1.5 year old females in spring i-1	+	**0.065**	0.737	**25.6**
proportion of 2.5 year old females in spring i-1	+	**0.002**	**0.045**	**55.3**
proportion of ≥ 3.5 year old females in spring i-1	-	0.379	1.000	6.5

When all parameters are considered in a multifactorial stepwise regression of BEVi, the following parameters are influential:

stepwise regression of BEVi on:

absolute abundance of ≥ 3.5 year old females in spring i-1: -, p = 0.001

proportion of 1.5 year old females in spring i: -, p = 0.031

proportion of 2.5 year old females in spring i-1: +, p = 0.024

$p_{mult} < 0.001$, $r_{mult}^2 = 87.8$ %

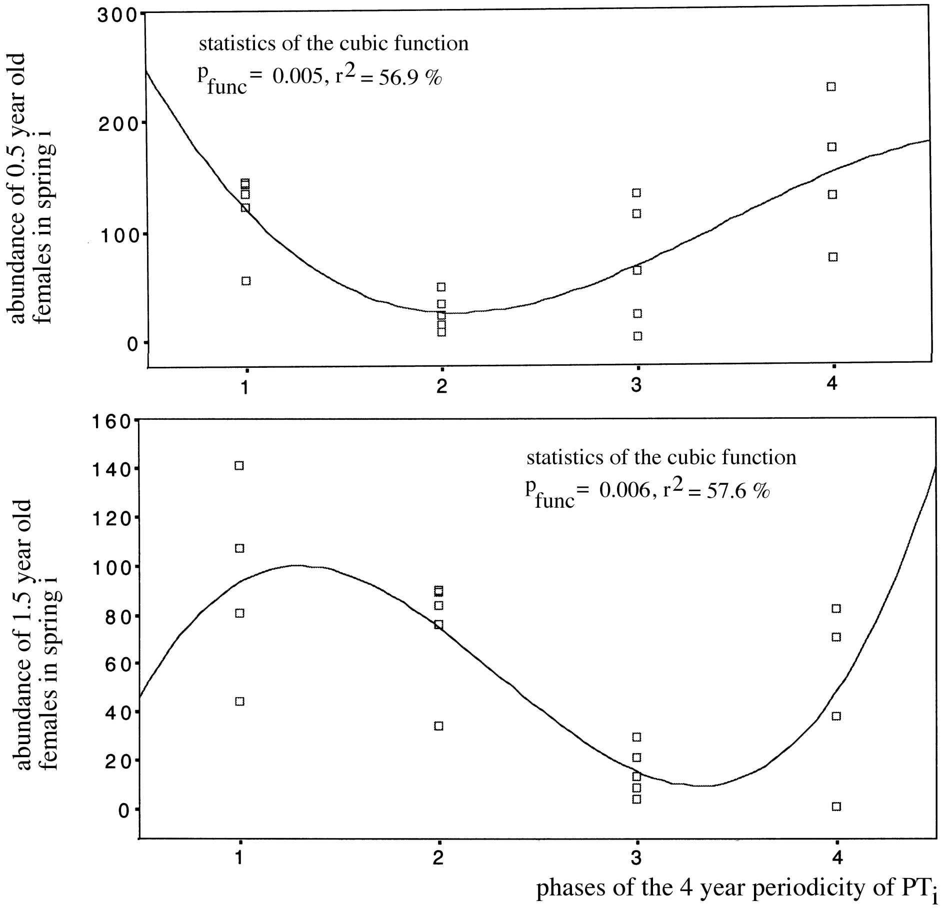


Fig. 18 Cubic regression of the simulated abundance of 0.5 year old females (above) and 1.5 year old females (below) on the phases of the 4 year periodicity in PTi (the phases are identical to those in **Fig. 7**: in year 1 low temperature is likely to occur in Prigge's interval). After simulation H (cf. chapter C. VIII. 4.).

When only parameters of the absolute abundance are considered the coefficient of determination is even larger:

stepwise regression of BEVi on:

abundance of females younger and older than 1.5 years in spring i-1 ($A_{i-1,\text{without } 1.5}$): -, $p = 0.002$

absolute abundance of 1.5 year old females in spring i: +, $p = 0.002$

absolute abundance of ≥ 3.5 year old females in spring i: +, $p = 0.002$

absolute abundance of ≥ 3.5 year old females in spring i-1: +, $p = 0.006$

$p_{mult} < 0.001$, $r_{mult}^2 = 95.5$ %

Surprisingly, in this case the abundance of 1.5 year old females in spring i has a positive effect, although simulations C and D (chapter C. VIII. 1.) indicate that the reproductive inertness of 1.5 year old females is an essential precondition for the expression of an adapted 4 year expectation periodicity.

In summary, simulation H indicates that parameters of the female generation structure may be used to predict the conditions that are likely to occur in the critical period in May. Which aspects of female generation structure may be the most important in determining the expectation periodicity are discussed in chapter C. IX. 1. Definitively the effective information factors (cf. chapter C. VII. 3.) can only be resolved by field experiments (chapter D. IV).

C. VIII. 5. Comparison of the simulations

In simulations C, D, E / I, E / II and H BEVi has a distinct influence on the net reproductive rate, $B_{i,with\ 1.5}$. Which of these simulations best describes the dynamics in nature? To answer this question, the degree of determination of $B_{i,with\ 1.5}$ by BEVi in the simulations is compared with that in nature; moreover, the simulated parameters $A_{i,with\ 1.5}$ and $B_{i,with\ 1.5}$ are regressed on those measured in nature (**Table 20**).

For the field data, the coefficient of partial determination of $B_{i,with\ 1.5}$ by BEVi is 34.6 % (PTi is the controlling factor) (**Fig. 15** in chapter C. VII. 1.); the coefficient produced by simulation C comes nearest to this value (29.4 %); that predicted by simulation D is somewhat higher (43.1 %), those predicted by simulations E / I, E / II and H are lower (18.6 - 21.0 %) (**Table 20**).

Table 20 Comparison of simulated and observed parameters of population dynamics.

coefficient of partial determination of reproductive rate ($B_{i,\ with\ 1.5}$)*			**regression of the simulated value (y) on the measured value (x)**							
	BEVi	**(BEVi x PTi)**	**abundance ($A_{i,\ with\ 1.5}$)**				**reproductive rate ($B_{i,\ with\ 1.5}$)**			
simulation	**r_{part}^2 (%)**	**r_{part}^2 (%)**	**formula**	**p_{b1}**	**p_{b0}**	**r^2 (%)**	**formula**	**p_{b1}**	**p_{b0}**	**r^2 (%)**
C	29.4	30.9	y = 0.138 x + 127.791	0.350	<0.001	4.9	y = 0.654 x + 0.504	0.001	0.080	44.6
D	43.1	45.4	y = 0.289 x + 125.166	0.067	<0.001	17.4	y = 0.740 x + 0.267	<0.001	0.312	53.6
E / I	20.3	23.4	y = 0.442 x + 420.565	0.481	0.003	2.8	y = 0.950 x + 0.174	<0.001	0.552	60.2
E / II	21.0	23.8	y = 0.453 x + 141.227	0.029	0.002	23.9	y = 0.697 x + 0.280	<0.001	0.195	60.8
H	18.6	21.5	y = 0.934 x + 26.368	<0.001	0.227	87.0	y = 0.718 x + 0.193	<0.001	0.187	83.7

* controlling factor: PTi

When regressing a simulated parameter on that observed a regression coefficient (b1) of 1 ($p_{b1} << 0.10$) and a constant (b0) of 0 ($p_{b0} > 0.10$) are expected in a perfect simulation. As expected, $A_{i,with\ 1.5}$ and $B_{i,with\ 1.5}$ are best mimicked by simulation H (the coefficients of determination are as high as 87.0 %, and 83.7 % respectively, and the regression functions are close to expectation; **Table 20**). However, simulation H is not critical as nothing is assumed regarding the reproduction dependence (this simulation is based on the observed number of freshly emerged beetles, chapter C. VIII. 4.).

In simulation E / I, the parameter b0 of the abundance regression deviates marked from expectation (b0 amounts to 420.565); moreover, in simulation E / I and also in C, the parameter b1 of the abundance regression is not significant. The simulations that come closest to observation are D and E / II: the parameters of the reproduction regression are similar; in the abundance regression b1 is smaller than 1 and b0 larger than 0 in both simulations; b1 is larger in E / II than in D, and b0 is smaller in D than in E / II.

C. VIII. 6. Conclusions and critical questions

The simulations reveal that an expectation periodicity influencing net reproductive rate, and adaptive changes in reproductive effort relative to expected temperature conditions are expressed when specific assumptions about the reproductive behaviour of the females are made. The indispensable and even sufficient condition for the expression of an expectation periodicity is that 1.5 year old females are reproductively spent (cf. chapter C. VIII. 1.). In simulations E / I and E / II there are no density-dependent effects on reproduction or survival, nevertheless an expectation periodicity is expressed. Obviously, in year 1 of the 4 year temperature cycle, when adverse weather is likely to occur, the simulated proportion of 1.5 year old females is relatively high so that reproductive rate referred to the total female stock is relatively small, even though PTi should be relatively high.

Thus, the simulations raise questions about the validity of the model outlined in chapters C. VII. 3. & C. VII. 6. Is abundance one of the information factors of the expectation periodicity? Are there any density-dependent effects on net reproductive rate, female reproductive investment and survival (chapter C. V. 5.)? Is it possible to justify the metaphorical terminology we used ("expectation periodicity", "information factors", "reward hypothesis")? Are the density-dependent effects (chapter C. V.) the consequence of nothing more than a correlation between abundance in spring i-1 and the proportion of 1.5 year old beetles in spring i? This will be critically discussed in chapter C. IX. 1.

C. IX. The field data in the light of the simulation results

C. IX. 1. Should the hypothesis regarding the role of density-dependence be maintained?

In chapters C. VII. 3. & C. VII. 6. the hypothesis is presented that the population can adapt to periodical changes in critical temperature conditions prevailing during early development by means of an endogenous expectation periodicity. A complex of information factors is used as cues that enable females to adjust their reproductive investment to the temperature conditions that are likely to occur. Reduced reproductive investment is associated with an increase in adult survival, which is also a target factor of the adapted expectation periodicity.

In our model, abundance in spring is an information factor: Ai-1 (the female density in the plateau-phase) influences (1) net reproductive rate (negatively; chapter C. V. 2.); (2) reproductive investment of females (negatively; chapter C. V. 3.) and (3) female survival (positively; chapter C. V. 5.). These influences are separate from those of temperature. However, simulations (chapter C. VIII.) indicate that the indispensable and even sufficient condition for the expression of an expectation periodicity is that 1.5 year old females are reproductively spent. Does this mean that the observed density-dependent effects are irrelevant?

There are several reasons for keeping the hypothesis of a density-dependent expectation periodicity (analyses 1 - 4 a-d). - In these analyses the influences of the parameter "abundance of the females younger and older than 1.5 years in spring i-1 ($A_{i-1,\text{without } 1.5}$), and thus the assumption that only reproducing females contribute to the density effects is checked.

Parameters of female generation structure in spring (abundances, and respectively, proportions made up of the generations in the total female abundance) are calculated from **Table 2** (cf. also chapter C. IX. 2.)

(1) In simulations E / I and E / II (chapter C. VIII. 1.) an expectation periodicity is generated in the absence of density-dependence. In simulation E / I, however, the density fluctuates at a much higher level than was observed in nature; in simulation E / II the fluctuations are like those observed in nature. The reproduction functions in E / I and E / II (containing only PTi as an independent variable) are similar (**Fig. 19**). This means that a limiting population growth by means of the periodically fluctuating PTi and different reproductive contributions of the different female generations would require a rather subtle adaptation of the net reproductive rate (referred to the females younger and older than 1.5 years) to the cycling temperature conditions. This is unlikely. Therefore, it is assumed that both the population structure is adaptively associated with the temperature conditions and that non-spent females adjust their reproductive investment to the expected weather conditions. This mechanism could be a negative density-dependence of the reproductive investment of females that are reproductively active.

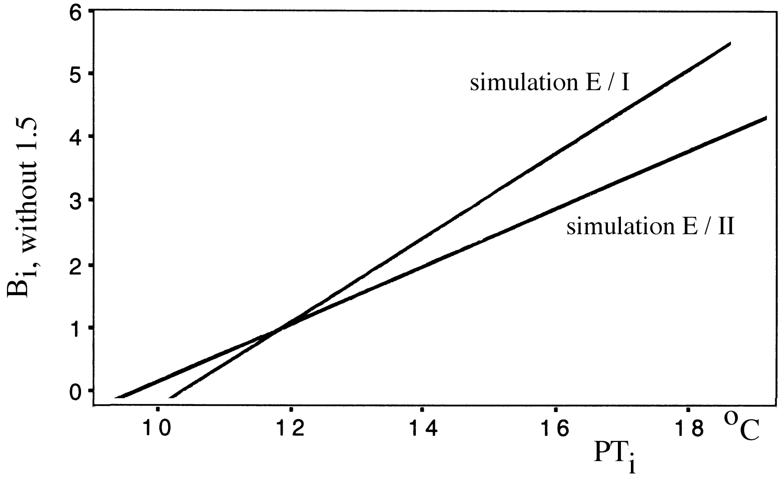


Fig. 19 The reproduction functions used for simulation: E / I and E / II. E / I: $B_{i,\text{without } 1.5} = 0.6558 \times PTi - 6.881$; E / II: $B_{i,\text{without } 1.5} = 0.4591 \times PTi - 4.500$

(2) In chapter C. VIII. 5. we asked whether the density-dependence observed (chapter C. V.) was the consequence of nothing more than the correlation between abundance in spring i-1 ($A_{i-1,\text{with } 1.5}$) and the proportion of 1.5 year old beetles in spring i ($P_{i,1.5}$)? In the 1994 - 2001 field data there is no correlation between $A_{i-1,\text{with } 1.5}$ and $P_{i,1.5}$ (+, $p = 0.543$, $r^2 = 6.5$ %). - In simulation H for which the correspondence of observed and simulated data is good (**Table 18**; chapter C. VIII. 4.; simulated data are available from 1986: $n = 16$) this correlation is weakly significant (+, $p = 0.082$, $r^2 = 23.1$). -The missing, and respectively, weak significance indicates that in nature not only population structure but also abundance is an important information factor.

(3) Point (2) is an argument against the assumption that the anticipatory reduction in reproductive investment of females in early spring when weather is likely to be bad ("Prigge's paradox"; chapter C. IV. 3.) is only caused by a high proportion of 1.5 year old (spent) females in the spring stock in these years. One should discuss "Prigge's paradox" in the context of the observation that the survival of the females positively depends on density. Importantly, in chapter C. IV. 7. & C. V. 4, we show that better survival is not a simple consequence of reduced activity in cold years. Both phenomena - Prigge's paradox and the positive dependence of female survival on density - make sense in light of our model, specifically in terms of a trade-off between reproduction and survival (cf. chapter C. VII. 4 & C. VII. 6.). However, the observation that the survival of 1.5 year old females is also positively dependent on density (**Fig. 14** in chapter C. V. 5.), although we assume that these females are reproductively spent, raises a problem. This can be resolved by assuming that 1.5 year old females are not reproductively inactive, but produce fewer eggs than females of other generations, and that also the 1.5 year old females have higher survival when they reduce egg production further in expectation of adverse weather.

(4 a-d) The number, and thus the proportion of 1.5 year old females in the field is not known for years before 1994. Nevertheless, are there any hints that the density of females younger and older than 1.5 years ($A_{i-1,\text{without }1.5}$) in addition to the influence of the proportion of the 1.5 year old females in spring i ($P_{i,1.5}$) and PTi influences the expectation periodicity (4 a), net reproductive rate (4 b), reproductive investment (4 c) and survival (4 d) in the field? Additionally the analyses (4a), (4 b) and (4 c) are based on the density and proportion parameter predicted by simulation H {cf. point (2)}.

(4 a) What biotic factors constitute the expectation periodicity and inform the individuals? - In the field the density of the females younger and older than 1.5 years in spring i-1 ($A_{i-1,\text{without }1.5}$) and the (arcsine transformed) proportion of the 1.5 year old females in spring i ($P_{i,1.5}$) are not correlated (+, p = 0.597, r^2 = 6.0 %). BEVi does not regress on $A_{i-1,\text{without }1.5}$ or on $P_{i,1.5}$, either monofactorially (-, p = 0.131, r^2 = 39.4 %; respectively: -, p = 0.231, r^2 = 22.7 %) or bifactorially; however, as expected the sign is negative in both cases, and BEVi regresses weakly significantly on the product $A_{i-1,\text{without }1.5}$ x $P_{i,1.5}$ (p = 0.080, r^2 = 48.9 %). As over the period 1994 - 2001, PTi and BEVi as well as PTi and the product are correlated (+, p = 0.061, r^2 = 47 %; respectively: -, p = 0.001, r^2 = 92.3 %), a stepwise regression of BEVi on PTi, $A_{i-1,\text{without }1.5}$, $P_{i,1.5}$ and the product $A_{i-1,\text{without }1.5}$ x $P_{i,1.5}$ is performed; the product dominates:

$A_{i-1,\text{without }1.5}$ x $P_{i,1.5}$: -, p = 0.080, r^2 = 48.9%

PTi: +, p = 0.897

$A_{i-1,\text{without }1.5}$: -, p = 0.855

$P_{i,1.5}$: +, p = 0.910

In the following analysis the generation structure predicted by simulation H, which simulates natural conditions rather well, is used (chapter C. VIII. 4., **Table 18**). $A_{i-1,\text{without }1.5}$ and (arcsine transformed) $P_{i,1.5}$ are weakly positively correlated (+, p = 0.070, r^2 = 24.7 %). BEVi regresses monofactorially on $A_{i-1,\text{without }1.5}$ (-, p = 0.017, r^2 = 38.9 %) as well as on $P_{i,1.5}$ (-, p = 0.028, r^2 = 32.1 %). In the tetrafactorial stepwise regression on PTi, $A_{i-1,\text{without }1.5}$, $P_{i,1.5}$ and the product $A_{i-1,\text{without }1.5}$ x $P_{i,1.5}$, the product is dominant:

$A_{i-1,\text{without }1.5}$ x $P_{i,1.5}$: -, p = 0.005, r^2 = 49.5 %

PTi: +, p = 0.187

$A_{i-1,\text{without }1.5}$: +, p = 0.951

$P_{i,1.5}$: -, p = 0.887

Thus, the analysis of both the field data and that generated by simulation H indicate a distinct negative influence of the abundance of the females younger and older than 1.5 years on the expectation periodicity, as is expected if the population adapts to the weather periodicity both by means of a fluctuating population structure and abundance of reproducing females.

In simulations C and D a distinct influence of $A_{i-1,\text{without }1.5}$ on BEVi was expected, but not in simulations E / I and E / II. To test this, the same analyses on simulations C, D, E / I and E / II are performed. – $A_{i-1,1.5}$ and $P_{i,1.5}$ simulated by C and D are highly positively correlated (+, r = 0.682, p = 0.001; respectively: +, r = 0.757, p < 0.001). In C BEVi regresses highly significantly on $A_{i-1,1.5}$, but does not on $P_{i,1.5}$ (monofactorial regressions: -, p < 0.001, r^2 = 53.6 %; respectively: p = - 0.125, r^2 = 12.5 %). Regressed on $A_{i-1,1.5}$, $P_{i,1.5}$, the product of both and PTi, $A_{i-1,1.5}$ is significant, both in enter and stepwise regression (enter: -, p_{part} = 0.047, p_{mult} = 0.002, r^2 = 61.8 %; stepwise: p < 0.001, r^2 = 53.6 %). The same is the case for simulation D (enter: -, p_{part} = 0.075, p_{mult} = 0.001, r^2 = 70.2 %; stepwise: p < 0.001, r^2 = 61.4 %). - In simulation E / I and E / II $A_{i-1,1.5}$ and $P_{i,1.5}$ are also correlated (+, r = 0.644, p = 0.003; respectively: r = 0.720, p = 0.001). In simulation E / I in the tetrafactorial stepwise regression only PTi is significant:

PTi: +, $p = 0.002$, $r^2 = 45.3$ %

$A_{i-1,1.5}$: -, $p = 0.360$

$P_{i,1.5}$: -, $p = 0.109$

product: -, $p = 0.219$

In simulation E / II in the tetrafactorial stepwise regression PTi and $P_{i,1.5}$ are significant:

PTi: +, $p = 0.011$, $r^2 = 45.3$ %

$P_{i,1.5}$: -, $p = 0.074$

$p_{mult} = 0.001$, $r_{mult}^2 = 55.5$ %

$A_{i-1,1.5}$: -, $p = 0.756$

product: +, $p = 0.819$

Thus, simulations C, D , E / I and E / II support our assumptions: depending on the simulation conditions there is a distinct influence of $A_{i-1,1.5}$ on BEVi in C and D , but not in E / I and E / II. The result of the regression analysis of simulations E / I and E / II is important as it supports a distinct influence of parameter $A_{i-1,\text{without } 1.5}$, measured in the field and simulated in H, on BEVi.

(4 b) In the field $B_{i,\text{without } 1.5}$ regresses negatively and significantly on $A_{i-1,\text{without } 1.5}$: -, $p = 0.031$, $r^2 = 63.9$ %. The influence is distinct as in a stepwise bifactorial regression PTi is eliminated (PTi: +, $p = 0.881$). In spite of the small amount of field data the analysis indicates that the abundance parameter $A_{i-1,\text{without } 1.5}$ has a distinct influence on net reproduction. - However, in simulation H $B_{i,\text{without } 1.5}$ does not regress on $A_{i-1,\text{without } 1.5}$: -, $p = 0.255$, $r^2 = 10.6$ %.

(4 c) Does the observed density parameter $A_{i-1,\text{without } 1.5}$ also influence female and male reproductive investment (chapter C. I. 2. & C. I. 3.)? The regression of the relative mean weight of the total female stock and that of particular female generations in the 1st decade of May is negative, but not significant (this may be due to the small number of values: $n = 7$ in case of the total female stock, $n = 5$ or 6 in case of particular generations). Tentatively the relative mean weight of the total female stock in the 1st decade of May is regressed on the simulated density parameter $A_{i-1,\text{without } 1.5}$: also this regression is negative, but not significant (-, $p = 0.156$, $r^2 = 16.0$ %).

The regression of the (arcsine transformed) probability of males being trapped on the observed parameter $A_{i-1,\text{without } 1.5}$ is negative and even more highly significant than the regression on $A_{i-1,\text{with } 1.5}$: -, $p = 0.003$, $r^2 = 85.3$ %, $n = 7$ (cf. **Table 10** in chapter C. V. 4). The influence of $A_{i-1,\text{without } 1.5}$ is distinct in the trifactorial stepwise regression with PTi (+, $p = 0.180$) and the observed parameter (arcsine transformed) $P_{i,1.5}$ (-, $p = 0.536$) (the analysis in chapter C. V. 4 indicates that the influence of $A_{i-1,\text{with } 1.5}$ on probability of males being trapped is not distinct). - The regression of the male trapping probability on the simulated parameter $A_{i-1,\text{without } 1.5}$ is also significant: -, $p = 0.032$, $r^2 = 50.3$ %. In the trifactorial stepwise regression, however, the parameter $A_{i-1,\text{without } 1.5}$ is eliminated:

PTi: +, $p_{part} = 0.000$

$P_{i,1.5}$: +, $p_{part} = 0.029$

$p_{mult} < 0.001$; $r^2 = 93.3$ %

$A_{i-1,\text{without } 1.5}$: +, $p = 0.626$

(4 d) The probability of females and males surviving from spring i to spring i+1 does not depend on the abundance of the females younger and older than 1.5 years in spring i-1: only the survival of all females regresses weakly significantly on this parameter of abundance (+, $p = 0.087$, $r^2 = 56.0$ %). To critically test this a multifactorial stepwise regression is performed using (arsine transformed) $P_{i,1.5}$, PTi and $TM2_{i-4}$ (cf. chapter C. V. 5.): the influence of $A_{i-1,\text{without } 1.5}$ remains, the other factors are eliminated.

In summary, there are several indications that the density parameter $A_{i-1,\text{without } 1.5}$ has distinct effects on population parameters as our reward hypothesis assumes: i. e. the assumption of density-dependences should not be rejected. However, a density-dependent influence of the females in spring i-1 on those in spring i could cause also a remarkable disadvantage as is outlined in chapter D. III. 2. - For further support of the reward hypothesis see chapter C. IX. 2.

In addition to abundance and more or less completely reproductive inertness of the 1.5 year old females are there other biotic factors in the information complex of the expectation periodicity? For example, another possibility is that all female generations regularly differ in their reproductive investment (chapter D. III. 2.).

C. IX. 2. Further support for the "reward" (trade-off) hypothesis: negative correlations between reproduction and survival

In chapter C. III. it is stated that net reproductive rate, $B_{i,\text{with } 1.5}$, and survival are not significantly correlated. Nevertheless, the "reward" (trade-off) hypothesis was proposed, which assumes that when poor conditions are predicted in late spring females reduce their reproductive investment in early spring; this strategy is "rewarded" by an increase in individual survival (chapter C. VII. 3.).

Interestingly, net reproductive rate, $B_{i,\text{without } 1.5}$, is more strikingly correlated with female survival than $B_{i,\text{with } 1.5}$, which is used in chapter C. III.:

total female stock (irrespective of age): -, $p = 0.034$, $r^2 = 62.5$ %, $n = 8$
0.5 year old females: -, $p = 0.020$, $r^2 = 77.5$ %, $n = 7$
1.5 year old females: -, $p = 0.066$, $r^2 = 61.1$ %, $n = 6$
2.5 year old females: -, $p = 0.309$, $r^2 = 33.2$ %, $n = 5$
3.5 year old females: -, $p = 0.306$, $r^2 = 48.1$ %, $n = 4$

It has to be conceded that the significance levels are > 0.10 when corrected for the number of tests ($k = 5$), nevertheless the correlations reinforce the reward hypothesis. - For an interpretation of the negative correlation between $B_{i,\text{without } 1.5}$ and survival of the 1.5 year old females see chapter C. IX.1.: it is reasonable to assume that these females are not completely reproductively inactive, and could also profit - in terms of individual survival - by a further reduction in oogenesis.

The survival of males is not correlated with $B_{i,\text{without } 1.5}$. Even the uncorrected significance levels are > 0.10; however, all signs are negative as for females (not shown).

Summarizing the conclusions of chapters C. IX. 1. and C. IX. 2. answers the question asked in chapter C. VIII. 6.. The assumed density-dependences operating in the *Carabus auronitens* population are not rejected by the analyses, and thus, the metaphorical terminology used to describe the population dynamics of this *Carabus auronitens* population can be retained. - However, further research on *Carabus auronitens* (and other carabid species) should be directed towards testing the reward hypothesis by field experiments (chapter D. IV.).

D. Discussion

D. I. Criticisms of field studies and simulations

We used four well-proven methods in our long-term investigation of a *Carabus auronitens* population (1 - 4).

(1) The measurement of net reproductive rate defined as "number of individuals emerging in late summer/autumn divided by the number of females in the plateau-phase of the spring of the same year". In his studies on the population dynamics of carabids Den Boer (2002) also uses the term "net reproductive rate", but defines it as the total number of adults captured in year i+1 divided by that captured in year i. He confesses that this term is a black box (Den Boer, 1985), which includes survival of adults, rate of egg laying, survival of preimaginal stages and young adults as well as migration of adults. For the quotient used by Den Boer the term "fluctuation rate" or "population growth rate" would be more adequate. However, it must be conceded that the quotient "number of adults captured in year i+1 divided by that captured in year i" is the only appropriate parameter when a larger number of sites and species are investigated. In the case of *Carabus auronitens* the parameter "net reproductive rate" is not such a black box as it includes the rate of egg laying and survival of the preimaginal stages, but not the survival of old individuals. Our approach allows one to test for a relationship between net reproductive rate (in our sense) and adult survival; such a relationship probably exists in the population studied and is a key factor in our model of "density-dependent reinforcement of risk spreading" (see chapter D. III. 6.).

(2) The second point concerns the estimate of the abundance of the beetles using the Jolly-Seber method. We used this method before and after the area was enclosed by a beetle-proof fence (Weber & Heimbach, 2001). It is evident that the estimates for the open area are less reliable as they include immigration and emigration of beetles, and thus refer to an area larger than that on which the pitfalls were placed. Unfortunately, we do not know the dimension of this area. This uncertainty was a reason for enclosing the area. For an enclosed area the density calculated by the Jolly-Seber method is also not identical with the actual density, when the estimates for all trapping days in a season are averaged: the beetles leave their winter resting places and pupation sites and start to rest asynchronously. Therefore we only use the average of Jolly-Seber estimates for the "plateau-phase of a season" (Weber & Heimbach, 2001). In the enclosed area the total number of individuals trapped during a season could also be used as measure of abundance. However, animals that die early in spring would be classed as having survived throughout the season and reproduced. Because of early spring mortality the number of beetles estimated for the plateau-phase in spring is expected to be lower than the total number of individuals present in spring. This is indeed the case:

total abundance (females plus males): $y = 0.9036\,x - 6.9058$; $p < 0.001$, $r^2 = 99.5\ \%$

female abundance: $y = 0.8533\,x - 0.3742$; $p < 0.001$, $r^2 = 98.6\ \%$

y = Jolly-Seber estimates for the plateau-phase in spring i (**Table 1**)

x = total number of individuals present in spring i (1993-2001; **Table 2**)

On the other hand, the number of marked individuals can be used to estimate the number of beetles emerging in late summer/autumn (in the enclosed area) and to calculate the net reproductive rate.

The other critical question is whether the mean abundance estimated for the plateau-phase in spring after the area was surrounded by a beetle-proof fence differs from that previously (when the area was surrounded by a not beetle-proof fence, Weber & Heimbach, 2001). Neither the means nor their standard deviations differ significantly (two-sample-t- and F-test; Sachs, 1992):

1982 - 1992 (fence not beetle-proof): mean = 354.54, SD = 89.83, SE = 27.08

1993 - 2001 (fence beetle-proof): mean = 288.67, SD = 169.63, SE = 56.54

The reason for this could be that also between 1982 and 1992 the possibility to emigrate and immigrate into the area of investigation was reduced. In short, in contrast to Nelemans et al. (1989) experience with the carabid *Nebria brevicollis*, our Jolly-Seber estimates for the not completely beetle-proof area seem to be good measures of the actual density in the area of investigation.

(3) Only individual marking can be used to determine the longevity of individuals and the age structure of the population. Coding individuals by abrading marks on their sclerotized elytra is easy; elytra perforations (by drilling or branding) should be avoided (cf. Weber & Heimbach, 2001). However, durable marking of very soft individuals by abrading marks is difficult and requires some experience.- In several population studies the age pyramid and the age of specimens were determined using the degree of mandible wear (Butterfield, 1986; Houston, 1981; Wallin, 1987, 1988; Wallin et al., 2000). In our team Doris Koch (2001; cf. chapter B. I. 5.) regressed the degree of mandible wear in *Carabus auronitens* on age, which is known because of the individual marking (cf. chapter B. I. 2.). The degree of mandible wear of males regresses positively on age; however, the coefficient of determination is rather small (19.8 %); in females it is not significant (**Fig. 20**). Thus for this population of *Carabus auronitens* the degree of mandible wear is not a reliable indicator of the age of individuals and the age structure of the population.

(4) The beetle-proof fence and our investigation routines (the number of pitfalls, the program of opening and closing them) are tried. In our experience a 0.2 ha area is large enough for a long-term investigation of a group of *Carabus auronitens* isolated inside a beetle-proof fence, and - on the other hand - small enough to study the enclosed group by a small team of researchers.

However, the simulations are unsatisfying because they are based on a rather small data set:

- In simulations A, B, C, (D, F, G), net reproductive rate regresses negatively on density over the whole range of densities observed (cf. chapter C. VIII.). However, in natural populations there is probably a critical minimum density below which the net reproductive rate regresses inversely on density: i.e. net reproductive rate becomes the smaller the more the density decreases. The reason for this might be that below the critical minimum density the probability of females and males to meet decreases when the density becomes smaller (see chapter A).

- The threshold of Prigge's critical temperature, PTi, below which the population stops reproducing independent of density seems to be around 10^{O}C (cf. **Fig. 5**). Somewhat above this threshold the temperature dependence of net reproductive rate is probably not linear. The existence of an upper threshold is also probable: our data indicate that above 14 - 15 ^{0}C net-reproductive rate no longer increases linearly with increasing PTi, but levels off (cf. **Fig. 5**). On higher, supraoptimal PTi, net reproductive rate may even decrease.

A more satisfying model of the population dynamics of *Carabus auronitens* needs data from a longer investigation of a population fenced in a beetle-proof enclosure (around 20 years or more). Such data sets might make it possible to formulate non-linear regression models with regression coefficients and intersection points with narrow confidence limits.

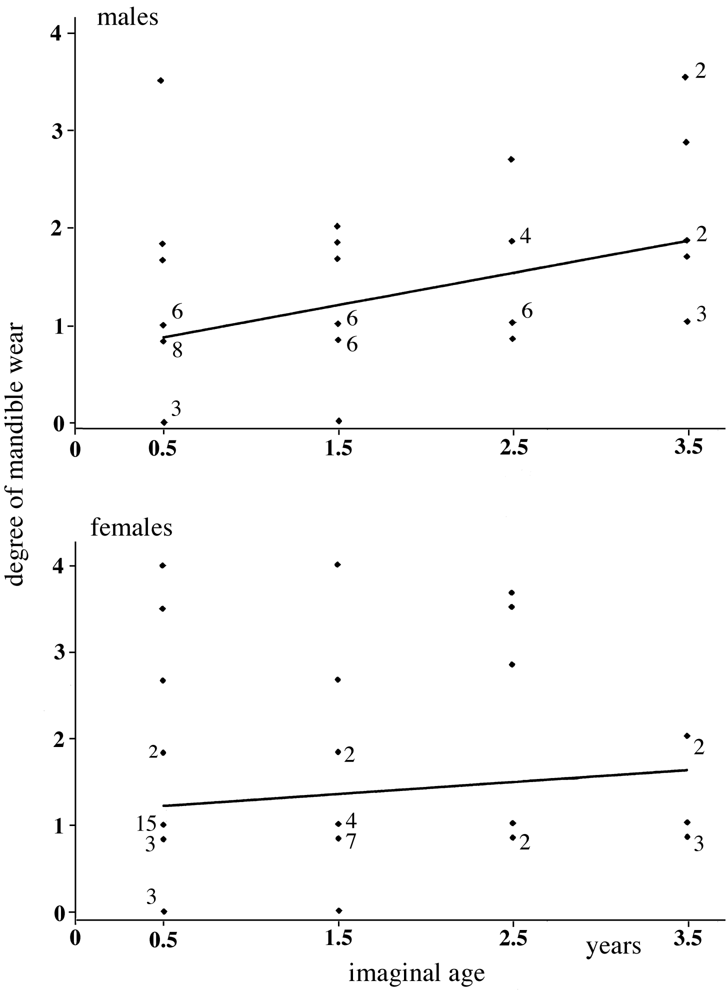


Fig. 20 Regression of the degree of bilateral mandible wear (weighted mean) on imaginal age at first capture in spring 2001. Males: $y = 0.317x + 0.717$, $p < 0.001$, $r^2 = 19.8$ %; females: $y = 0.129x + 1.154$, $p = 0.305$, $r^2 = 2.0$ %.

D. II. Density-dependent dynamics in carabid populations?

In the ecological literature on carabids there is a long-lasting debate on whether density-dependent processes influence the abundance of individuals and persistence of populations. Especially Den Boer (1985, 1986, 1991, 1998, 2002) has argued that the density of carabid populations fluctuates because of the strong influence of density-independent factors and thus usually remains far below the carrying capacity; the danger of extinction of populations due to the net reproductive rate becoming smaller than the mortality rate is ever present, but following Den Boer is reduced by effective strategies of risk spreading (chapter A).

This provoked stimulating controversy between Den Boer and Baars & Van Dijk twenty years ago. The question was how do populations of the carabid beetles *Pterostichus coerulescens* (= *versicolor*) and *Calathus melanocephalus* persist in time and space: by density regulation around equilibrium densities or random restrictions and spreading of risk strategies. Baars & Van Dijk (1984 a) could not satisfactorily simulate density fluctuations in subpopulations of *Pterostichus coerulescens* and *Calathus melanocephalus* using weather data and dispersal alone, but including regulating density-dependences gave a better fit to field data. In both species there is a negative relationship in the field between the number of breeding beetles and egg production per female over the reproductive season (fecundity). In addition, in *Pterostichus coerulescens* the number of recruits per female in year i+1 regresses significantly positively on the mean fecundity in year i; in *Calathus melanocephalus* this relationship is not significant. According to their hypothesis egg production is density-dependent. The authors found that in enclosures the number of eggs produced per female increased with additional food, and by manipulating the density of beetles in enclosures they found that average egg production was always smaller at highest density than at lowest densities (Baars & Van Dijk, 1984 b). This suggests that both interference and competition for food could be density-dependent and that intraspecific competition for food is effective in both species at high densities. - The density-dependence of egg production in these two species is not questioned by Den Boer (1986), but he argued that "... in a peak year it is not the possibly reduced fecundity that reverses the course of density ... ..., the reduction is too small for that" (p. 365), " ... variation in the mean density of young adults as well as variation in the survival of old adults ... ... are much greater than variation in mean fecundity between years" (p. 368). - Nevertheless, it is important that Baars & Van Dijk (1984 a, b) have demonstrated density-dependent food limitation; if food limitation is effective, it could also negatively affect the quality and quantity of yolk incorporated into eggs, and thus developmental rates of embryos and young larvae. Indeed, Van Dijk (1996) showed for the carabid *Bembidion tetracolum* that the quality of food not only influences the number, but also the quality of the eggs produced (represented by their nitrogen and carbon content). - The effect of density-dependent competition for food on egg production was confirmed by Van Dijk (1994, 1996), both the quantity and quality of food influence the fecundity in carabids, however, within different individual ranges that are possibly genetically fixed (Den Boer, 2002).

In our opinion, to argue that populations could persist in the absence of density-dependent processes is no proof that such processes do not exist. Hypotheses based on field observations can only be falsified by field experiments and not by proposing a contrary hypothesis.

In carabid ecology there are several interesting field experiments showing the existence of density-dependence. These experiments should not be forgotten. They will be referred to in the following review (cf. also the enclosure experiments of Baars & Van Dijk discussed above). The occasional field observation, evaluation of pitfall trapping in open areas and laboratory experiments on density dependence are not considered. They were compiled, albeit not exhaustively, in our publication (Weber & Heimbach, 2001).

Heessen (1980) manipulated densities of *Pterostichus oblongopunctatus* inside fenced areas (5 x 5 m and 2.5 x 5 m) of natural habitat and observed that higher densities had a significant negative effect on egg production per female. From the results of feeding pairs of beetles kept in small boxes exposed on the ground in a forest he concluded that the amount of food available per beetle influenced the number of eggs produced. Brunsting & Heessen (1984) concluded from so-called convergence experiments in field enclosures that regulation is effective, probably via density-dependent egg production and cannibalism of the larvae - i.e. by intraspecific competition and antagonism in the struggle for food.

Lenski (1984) kept the naturally co-existing *Carabus limbatus* and *Carabus sylvosus* together in field enclosures. Adults of *Carabus limbatus* were provided with food every time they were caught, whereas those of *Carabus sylvosus* were not fed. This resulted in an increase in the average body mass and reproductive rate of *Carabus limbatus*, and depressed their activity compared to conspecifics in control plots. The co-existing individuals of *Carabus sylvosus* profited indirectly: they showed a significant weight increase compared to conspecifics in control plots; possibly their foraging success increased because of the reduced interspecific competition for food. - In another experiment Lenski (1982) kept different numbers of *Carabus limbatus* in enclosures and observed that there was a significant reduction in mean body mass at the higher densities (this is important, as Lenski stressed, as in *Carabus limbatus* there is a positive relationship between body mass and the number of eggs in females).

An important experiment of this type, unfortunately not mentioned by us in our 2001 publication (Weber & Heimbach) is Loreau's (1990 a, b) 4-year enclosure experiment using *Abax ater* and *Pterostichus madidus*. Two enclosures contained *Abax ater*, two *Pterostichus melanarius*. For each species the density was normal in one enclosure and double this in the other. In two further enclosures both species were present, in one at normal, and in the other at double this density. *Pterostichus madidus* naturally absent from the study site was introduced from a nearby region. The aim of the investigation was to test whether intraspecific competition occurred (in the enclosures with increased density) and whether the absence of *Pterostichus madidus* could be due to exclusion by *Abax ater*, the dominant species at this site. - The evidence for intraspecific competition in *Abax ater* was ambiguous as in one of the two high density enclosures the population increased whereas in the other it decreased as predicted. Surprisingly there was a negative correlation between individual locomotory activity and population density in males, but not females of *Abax ater*. Probably, at high densities males found mates more quickly. Nevertheless the body mass of males was lower at the high densities, an observation that is consistent with competition for food, at least in males (females and males of *Abax ater* use a somewhat different prey spectrum). - The populations of *Pterostichus madidus* developed poorly in all enclosures: mortality was high and recruitment was low. It seems that the population dynamics of both species was dominated by spatial heterogeneities at the micro-local scale (heterogeneous prey distributions?) and local adaptations. However, in *Abax ater* intraspecific competition could not be excluded with certainty.

Niemelä et al. (1997) used enclosures to study over four years whether the invasive carabid species, *Pterostichus melanarius*, had a negative effect on the native carabid assemblage in South Canada. The alien did not affect population size or body mass of the native species, however, the two most abundant native species appeared to be more active in the enclosures with *Pterostichus melanarius*.

We did not find any evidence for interspecific competition between co-existing *Carabus auronitens* and *Carabus nemoralis* (however, males of both species are attracted to females of the other species, see Dörr, 2001, chapter B. I. 5.; and Weber & Heimbach, 2001, chapter 4.9.) or for intraspecific competition for food (density-dependent food shortage; chapter C. V. 1. & C. VI. 2. of the present paper), either in the adult spring stock, adult autumn stock or larval stock. Nevertheless, in the final analyses of our 20 year study of *Carabus auronitens* there are indications of a density-dependent effect on egg production and adult survival; unexpectedly, these effects are inverse (as outlined in chapter C. VII. 6. & chapter C. IX. II. of the present paper).

D. III. A new synthesis: density-dependent enhancement of risk spreading

D. III. 1. Exogenous key factors in the dynamics of the *Carabus auronitens* population

The (non-climatic) habitat in the Westphalian Lowlands is favourable for *Carabus auronitens*. Prey seems to be abundant, at least in oak-hornbeam forests (chapter D. II.; cf. also our "Lenski experiments": Weber & Heimbach, 2001); furthermore the level of the ground water is high at most sites implying that the soil does not completely dry out even in summers with little rain. Additionally, at our study site, the Forst Tinnen, near the city of Münster, there is no competition from other *Carabus* species: here *Carabus auronitens* co-exists only with the non-competing *Carabus nemoralis* (Weber & Heimbach, 2001). At other sites in the Westphalian Lowlands *Carabus auronitens* co-exists with *Carabus problematicus*, *Carabus coriaceus* and/or *Carabus purpurascens*.

On the other hand, climatic conditions are not always favourable for *Carabus auronitens* populations in the Westphalian Lowlands. The dynamics of the population seems to be governed by temperature in spring: - that in mid April may affect oogenesis (the physiological basis for this is obscure, see chapter C. IV. 3., **Table 7**); - that in mid April affects also the 75 % mark of CNL of females and probably also males (chapter C. IV. 6., **Fig. 10**); - that in mid May the fitness of the offspring and thus the sex ratio in spring (chapter C. IV. 8., **Fig. 11** and chapter C. VI. 3., **Table 13**); and that in Prigge's interval in mid and late May affects net reproductive rate, possibly via the developmental rate of the eggs (chapter C. IV. 1., **Fig. 5**).

Temperature in Prigge's interval, PTi, has an especially powerful influence on the dynamics of the population. PTi fluctuated with a periodicity of 4 years during the course of this study: every few years PTi was so low that the reproductive rate was drastically reduced (cf. chapter C. IV. 1.). It seems that in the Westphalian Lowlands the beetle has evolved a peculiar way of surviving this climatic inclemency (see chapters D. III. 2. & D. III. 6.). - Moreover, surprisingly, there are traits of the young beetles that seem to be under the control of abiotic conditions operating during the breeding season in spring (chapter C. VI. 3.), and that this dependence determines much of the variability in sex ratio in spring (chapter C. IV. 8.). It seems that low temperature in mid May reduces the fitness of the young beetles and negatively affects the relative number of offspring if low temperatures persist for longer (Prigge's critical 17 day interval; cf. chapter C. IV. 1.).

The existence of critical periods may be due to the gating of reproductive processes by photoperiod (Thiele, 1977): temperature prevailing during rather narrow gates becomes critical. The narrowness of these gates is surprising; this may be the consequence of an adaptation to former climatic conditions (cf. chapter D. III. 5.).

D. III. 2. Is there an endogenous mechanism in the *Carabus auronitens* population, which adapts the dynamics to a periodically fluctuating exogenous key factor?

We hypothesize that the Westphalian Lowlands populations of *Carabus auronitens* have evolved a means of surviving climatic inclemency: an endogenous mechanism links the population dynamics to the periodically fluctuating temperature parameter (PTi), which affects the early development of the offspring (chapter C. IV. 1.). The hypothesized mechanism is based on "information factors" that "inform" the population in early spring about the critical temperature to be expected later in spring. "Information factors" directly control "realisation factors" (reproductive investment: oogenesis in females and mate searching in males) and thus indirectly influence "target factors" (net reproductive rate and survival of the parental spring stock). We metaphorically describe this mechanism as an "expectation periodicity": it results in the reproductive investment of the population adjusting to the periodic fluctuations in temperature that occurs during the critical period in early development. If the temperature conditions are likely to be unfavourable, the realisation factors are influenced by the information factors in such a way that the beetles restrict their investment in reproduction in early spring and as a consequence have an increased probability of the survival: thus, temporal risk spreading based on adult longevity is enhanced (chapter C. VII. 3., cf. also chapter D. III. 6.).

The realisation factors, oogenesis and mate searching in males, both regress on a parameter (Baumgartner's Expectation Value: BEVi; chapter C. VII. 1.) which is derived from the long-term periodic fluctuations in temperature that occurs in the period critical for the early development of the offspring. BEVi seems to partially reflect the adaptive influence of information factors. - However, BEVi does not include all the information available to the population about the conditions that are to be expected during the critical period in early development: BEVi is not able to completely replace the anticipatory influence of PTi on female reproductive investment in early spring (chapter C. VII. 5.); moreover, BEVi does affect survival of the parental females and males (chapter C. VII. 4.).

It is important to know which "information factors" modify BEVi and which "information factors" are not reflected by BEVi. - It was possible to check our field data whether abundance could act as an information factor (chapter C. VII. 6.). Indeed, abundance distinctly influences (1) the net reproductive rate, Bi, (C. V. 2.); (2) female survival (chapter C. V. 5., **Fig. 13;** Bi and female survival probability are influenced by density with opposite signs); and (3) probably female reproductive investment (chapter C. V. 3.). - However, the effect of abundance and BEVi on realisation and target factors overlap only partly: abundance is only partly represented by BEVi, and BEVi contains more information than is given by abundance (chapter C. VII. 6.). It is likely there are more information factors.

The field data indicate that the generation structure of the population could be a further information factor of the expectation periodicity. It is possible that 1.5 year old females are reproductively inactive or less active than females of other ages (C. I. 2.). The proportion of 1.5 year old females in spring stock is on average high in the years in which adverse conditions are likely to occur during the critical period for development in late spring (chapters C. VIII. 4. & chapter C. IX. 1., **Fig. 18**). Simulations show that BEVi has an influence on net reproductive rate similar to those observed in the field only when 1.5 year old females are reproductively spent (chapters C. VIII. 1. & C. IX. 1.). - However, also the survival of 1.5 year old females increases with increasing abundance (chapter C. V. 5., **Fig. 13**), which indicates the "reward" hypothesis (see below) also applies to 1.5 year old females, possibly because they are not completely reproductively spent and their reproductive investment is also affected by the expectation periodicity (chapter C. IX. 2.). - Moreover, it may not be excluded a priori that other generations also differ in terms of reproductive effort.

The assumption that 1.5 year old females are spent or reproductively less active than females of other generations has consequences. In years when Prigge's temperature is likely to be adverse (year 1 of the temperature cycle) the proportion of 0.5 year old females is relatively high (**Fig. 18**). This is advantageous as the young females have a high survival. However, this results one year later (year 2 of the cycle) in a high proportion of 1.5 year old females (**Fig. 18**), and a low overall reproductive rate (**Fig. 7**). The consequence is that on average abundance is lowest in year 3 of the cycle and recovery of the population is retarded by one year (**Fig. 12**). - Further, as the density of females in spring i-1 influences reproductive investment in spring i, is such an effect also exerted by the females preparing for an adverse weather event in spring 1 (when BEVi is minimal, and an adverse weather event is likely to occur)? **Fig. 12** shows that in spring 1 the abundance is relatively high: i.e. the females in spring 1 of the cycle could negatively influence reproduction in spring 2, when the probability of an adverse weather event is on average lower. Also this effect would retard the recovery of the population by one year (appendix 6). However, **Fig. 7** reveals that in year 2 of the cycle a low temperature is sometimes recorded, which would weaken this disadvantage. - The existence of such disadvantages needs to be tested by experiments in the field (chapter D. IV.).

A further possible disadvantage is the way the traits of the young in autumn i seem to be influenced by the biotic conditions in spring (chapter C. VII. 5.). This is probably a consequence of the underlying adaptive mechanism: when poor weather is indicated there is a reduction in the number of ripening oocytes in the ovaries and synthesis of vitellogenin and lipids in the fat body destined for the growing oocytes (Postlethwait & Giorgi, 1985; Dettner & Peters, 1999); if these processes are not balanced, the eggs could be provisioned suboptimally.

D. III. 3. Possible physiological mechanisms of the "reward", a trade-off between reproduction and longevity

The "reward" (trade-off) hypothesis is well supported by empirical data (chapters C. VII. 4. & C. IX. 2.): net reproductive rate, Bi, and female survival regress inversely on abundance, and $B_{i,without\ 1.5}$ and survival are negatively correlated. However for males reproductive investment regress negatively on density, and only survival of the 0.5 year old males regresses weakly on density (positively as in females). - In our 2001 paper (Weber & Heimbach, 2001) a significant association between net reproductive rate and survival of 0.5 year old females is reported, but assumed to be the consequence of a low PTi in years of low reproduction. The larger data set now available does not support the assumption that temperature mimics the dependence of female survival rate on a biotic factor: abundance (chapter C. V. 5.).

The postulated relationship between reproductive investment and survival appears to be a physiological trade-off. Such trade-offs are the consequence of a flexible allocation of limited resources to two competing functions (Stearns, 1992; Futuyma, 1998). A frequently described physiological trade-off is that between investment in reproduction and somatic maintenance (survival): sperm production, egg production and mating are costly because nutrient reserves are limited (Dixon & Kundu, 1997; Yanagi & Miyatake, 2003). In *Drosophila melanogaster* there is a negative relationship between early reproduction and longevity (and postponed reproduction) due to the way lipid and carbohydrate reserves are allocated (Djawdan et. al., 1996; Simons & Bradley, 1997). Lipids and carbohydrates are used to fuel metabolic and locomotory activities, and stored in the yolk of eggs for embryonic and early larval nourishment (Postlethwait & Giorgi, 1985).

The "reward" hypothesis excludes the possibility that risky dispersal is increased at high density (i.e. emigration from high density sites: density-dependent dispersal is often assumed to be an effective means reducing the negative consequences of high abundance; Denno & Peterson, 1995). We exclude density-dependent dispersal in the *Carabus auronitens* population studied, as the probability of trapping males depends inversely on female abundance; moreover, the probability of trapping females and the end of the spring season for females and males are not influenced by abundance (chapters C. V. 4. & C. V. 5.).

The existence of a trade-off between reproductive investment and survival in carabids has often been questioned. According to Van Dijk (1979 a, 1994, 1996) there is no trade-off between egg production and survival of females in *Calathus melanocephalus* and *Pterostichus coerulescens*, and to Lenski (1984) in *Carabus limbatus*, whereas Murdoch (1966) reports high adult survival followed poor breeding and vice versa in *Agonum fuliginosum* and *Agonum thoreyi* in the field (this relationship was not confirmed for South German *Agonum* populations, Wasner, 1979). Murdoch (1966) used the number of eggs present in females collected in the field as an estimate of total egg production per female. This assumption is not supported by direct observations on *Calathus melanocephalus* and *Pterostichus coerulescens*, especially the latter (Van Dijk, 1979 b). On the other hand, Heessen (1980) found a strong relationship between the mean weekly egg production and the mean number of eggs in the ovaries in *Pterostichus oblongopunctatus*.

In *Carabus auronitens* it is questionable, whether egg production is the only factor affecting survival. Possibly, in both females and males it is the change in locomotory behaviour that occurs at high density that increases the probability of survival. When this change in locomotory behaviour is expressed the risk of individual predation may be reduced, but not harvesting of food must not! This is supported by the positive regression of the probability of trapping (activity level) of males on Bi (chapter C. I. 3.; **Fig. 3**), which seems to be caused by a temperature-independent positive response to BEVi (chapter C. VII. 4.). - Moreover, mating may also be costly and reduce longevity (Chapman et al., 1995; Orsetti & Rutowski, 2003; Yanagi & Miyatake, 2003). - A further possibility is that the increased longevity is due to density-dependent mild stress: in *Drosophila melanogaster* larvae a heat shock protein is expressed in cultures kept at moderately high densities, which increases the longevity of adult females and males (Sørensen & Loeschke, 2001).

D. III. 4. The pheromone mediated interference hypothesis

What is the mechanism underlying the negative affect of density on the reproductive investment of females (oogenesis)? Is it food shortage at high densities? This is unlikely as female survival increases with abundance (chapter C. V. 5.), and post-reproductive "recreation" does not depend on density, which would be expected if there is a density-dependent food shortage (chapter C. V. 5.). Therefore, we favour the hypothesis that the density-dependent effects are triggered by mutual interference (chapter C. V. 1., C. V. 6. & C. VI. 5.) which is dependent on the release of a pheromone. Reproductive investment could be reduced when a threshold concentration of the inhibiting pheromone in the habitat is reached (thus, contact is not required); the threshold is reached at a density that is below the carrying capacity of the habitat. However, the suggestion that there is density-dependent interference via a pheromone in *Carabus auronitens* is rather speculative. The only fact we know is that females are olfactorially attractive to males: males react to pitfall traps containing a female (Baumgartner, 2000; cf. Luff's, 1986, experiment on sexual olfactory attraction in the carabid *Pterostichus madidus* and mate location by volatile sex pheromones in several non-carabid beetles; Jacobson, 1974; Vanderwel, 1994; Zhang et al., 1997).

On the basis of pitfall trap captures in *Carabus arcensis* Grüm (1990) developed a model of "female-to-female repulsion" mediated by "encountering" or "chemical signals" (i.e. pheromones). The intensity of such a reaction - if it exists - should be density-dependent. In *Carabus auronitens*, "female-to-female repulsion" is unlikely (trapping rate of females does not regress on the female abundance, chapter C. V. 4; moreover, Baumgartner, 2000, found that females are caught in similar percentages in pitfalls baited with a female or a male, or are unbaited). - We assume mutual inhibition of oocyte growth and attractiveness by the female pheromone when the density of females is high (but still below the carrying capacity of the habitat). Inhibition of sexual maturation by pheromones is well known in social hymenoptera and termites (Jacobson, 1974; Bückmann, 1995). - Inhibiting mutual interference was observed by Klomp and Gruys in the Pine Looper, *Bupalus piniarius* (Klomp, 1964; Gruys, 1970; Schwerdtfeger, 1979, p. 360): caterpillars that meet during a nocturnal activity phase regorge gut fluid, which inhibits growth, and thus, the resultant adults are smaller and less fertile; this "interference" is density-dependent and - as assumed by us in *C. auronitens* - operates at densities below carrying capacity. - Density-dependent interference, which is not a consequence of competing for food, but adjusts population density to "expected" food availability is observed in the ladybird beetle, *Adalia bipunctata*: in the presence of conspecific larvae gravid females are more likely to leave an area and lay fewer eggs (Hemptinne et al., 1992). - A complex system of pheromone mediated reproductive behaviour and physiology was described by Happ (1969) for the non-carabid beetle *Tenebrio molitor*. Both females and males produce sex pheromones. Male pheromones are of two distinct types: (1) an excitant pheromone that attracts females; and (2) an anti-aphrodisiac pheromone, which inhibits the response of other males to female scent. A male emits the inhibitory pheromone only after stimulation by female sex pheromone. The male transfers some of his anti-aphrodisiac pheromone to the female during mating, thus reducing her attractiveness to other males (see also Haynes & Birch, 1985, for courtship inhibiting pheromones in other insects). - That pheromone production and release can depend on density is also known for some non-carabid Coleoptera. When the Red Flour Beetle, *Tribolium castaneum*, is crowded, benzoquinones are released that suppress the effect of an aggregation pheromone and cause the insects to disperse (Faustini & Burkholder, 1982; for antiaggregation pheromones in other Coleoptera see Borden, 1985; Tamaki, 1985; and Pureswaran et al., 2000; see Klomp (1964) for more examples of regulation by mutual interference mediated by contact and/or secretion of volatile substances). - In summary, research on pheromones indicates that the operation of auto-regulative feed-back loops in non-social insects can not be ruled out (Huffaker et al., 1971: pp. 22/23).

In *Carabus auronitens*, females seem mutually to control the intensity of oogenesis by release of a pheromone. Possibly, the old females present in spring i "remember" whether the density in spring i-1 was relatively low or high. The physiological condition of the young beetles reproducing for the first time in spring i may be influenced by the density of their parents as there is a weakly significant effect of female abundance in spring i-1 on the reproductive investment of their daughters in spring i (cf. chapter C. VI. 5.). Delayed density-dependent processes are known (Solomon, 1949; May, 1980) in which the effect extends to the generation following the generation that experienced the high density. Eggs of the lepidoptera, *Panolis flammea* and *Bupalus piniarius*, develop at a reduced rate when the parental generation experienced crowding (Schwerdtfeger, 1979, p. 360). In case of the Pine Looper it operates via density-dependent mutual interference between the caterpillars of the parental generation (see above). Such long-delayed density effects resemble the phenomenon of photoperiodic "telescoping": for example in aphids a photoperiodic effect may be manifested a full generation (or more) later (Beck, 1980, p. 105). It has to be stressed that in the case of *Carabus auronitens* this maternal effect is restricted to the first spring season of their offspring.

D. III. 5. The likelihood of an expectation periodicity evolving

Simulation G (chapter C. VIII. 3.) indicates that the population under study is unlikely to express an expectation periodicity if the temperature cycle lasts 6 years. The expression of a 4 year expectation periodicity seems to be dependent on several biological phenomena (1, 2a, 2b, 3). (1) A rather long adult life: the maximum life expectation in *Carabus auronitens* (5.5 years: **Table 2**) is exceeded only in cavernicolous carabid beetles (Rusdea, 1998); (2) despite their long life, reproductive activity of young (0.5 year old) females is rather high (2a) and does not affect life expectancy, but does result in a reduction in reproductive activity in the 2nd spring (2b); (3) females influence each other (and possibly also the males) in such a way - possibly by a pheromone (cf. chapter D. II. 4.) - that reproductive investment is reduced after a few years of population growth, i.e. in year 1 of the cycle when the next adverse weather event is likely to occur in the critical interval in May.

In our model the negative density-dependence in reproductive investment is not associated with carrying capacity of the habitat but a 4 year periodicity in the climate. The periodicity of PTi is demonstrable in the climate data recorded for the region since 1891 (chapter C. IV. 2.; **Fig. 8**). The question is, how could such an adaptive mechanism have evolved? A probable mechanism is the ability of the beetles to influence one another by pheromone-mediated interference. This ability was adapted to the maximum densities that can be reached on average in the course of one cycle in the periodically fluctuating abiotic key factor (PTi). The other two necessary phenomena (differences between female generations concerning the cost of reproduction and the trade-off between reproduction and longevity) could also be preadaptations which were optimized under the climate conditions at the northern limit of the distribution of *Carabus auronitens*. Thus the evolution of a "density-dependent reinforcement of risk spreading" could be based on preadaptations and distinct adaptations to regional conditions, as simulation G shows (chapter C. VIII. 3.). Whether the evolution of an adapted expectation periodicity was dependent on group (for example between successive founder populations) or individual selection (Futuyma, 1998) has to be clarified.

Wynne-Edwards' model (Stearns & Hoekstra, 2000, p. 50) of group selection can be excluded in the case of *Carabus auronitens*. In this model social behaviours, such as flocking, is important; for example, it is assumed that breeding in colonies is a means of obtaining information on population density. If overpopulation threatens the individuals in the colony reduce reproduction so that there will be enough food for all of the offspring. In the model presented here, the individual beetles profit from reducing reproductive investment when adverse weather is likely to occur. Individuals not practising this strategy are at a twofold selective disadvantage as they are likely to produce few (or even no) offspring and have a reduced longevity.

Why is the seasonality of *Carabus auronitens* in the Westphalian Lowlands synchronized in such a way (probably by photoperiod as in other carabids; Thiele, 1977) that embryonic and early larval development can be negatively influenced by a low mean temperature in a critical interval in May? In June, temperature is high enough to ensure early development every year. If the early stages occur in June, however, the new generation of beetles would emerge so late that they would be in danger of not completing post-ecdysial maturation if winter starts early. The beetles need to feed after emergence; 80 % will die if unable to feed for 10 days after emerging, even if fed ad libitum thereafter (Klenner, 1989; Weber & Heimbach, 2001). The dependence of *Carabus auronitens* on photoperiodic gating could reflect adaptations to former climatic conditions. For example, it is likely that *Carabus auronitens* survived the Little Ice Age (1550 - 1850) in the Westphalian Bay at the northern fringe of the distribution of the species. In the Lowlands of Northwest Europe (England) the growing season was as much as 5 weeks shorter in the 17th century (Growe, 1990, p. 412-415). The photoperiodic control of the seasonal development of *Carabus auronitens* in the Westphalian Lowlands probably evolved under the climatic influence of the Little Ice Age.

In the absence of long-term investigations it is unknown whether populations of *Carabus auronitens* in other regions have also evolved a weather expectation. (1) It is unlikely that the reproductive rate of *Carabus auronitens* populations living in high mountains depends on the temperature in the same critical interval (cf. chapter C. IV. 1.) as populations in the Westphalian Lowlands (Weber & Heimbach, 2001). (2) If in other populations there is also a critical period in early development, it is questionable whether the climatic conditions then cycle with a periodicity to which population traits could adapt by the evolution of an expectation periodicity. It is more likely that populations in other regions use the interference phenomena to adapt via an equilibrium density to the carrying capacity of their habitats. The outcome of simulation F (constant temperature assumed) indicates that the evolution of adapted equilibrium densities is possible: negative feedback loops seem to be effective in the population dynamics of *Carabus auronitens* (chapter C. VIII. 2., **Fig. 17**). - The challenge is now to compare the dynamics of conspecific populations, not only of *Carabus auronitens*, in regions with differing climatic conditions.

Finally, have similar phenomena been observed in other carabid species? Unfortunately there are only few long-term investigations. Den Boer and co-workers recorded the density of *Calathus melanocephalus* and *Pterostichus coerulescens* in the Netherlands between 1959 and 1985 (see also chapter D. I.). The fluctuations Ai+1/Ai at several sites show some periodicity (Baars & Van Dijk, 1984 a; Van Dijk & Den Boer, 1992). The periodogram analysis of the fluctuations recorded at 3 sites over 20 - 22 years (Den Boer & Reddingius, 1996) indicates a significant periodicity of 7 years ($p < 0.05$) at one site and weakly significant periodicities of 11 and 7 years ($p > 0.05$) at the two other sites in *Calathus melanocephalus*. In *Pterostichus coerulescens* there was a periodicity of 5 years at one site and a 7 year periodicity at another site ($p < 0.05$). Baars & Van Dijk (1984 a) suggest that - at least in part - a cyclic weather pattern might have induced these fluctuation cycles. "The variation on recruitment or survival rate, 'explained' by variation in weather, ranges from 50% to 100%" (p. 381). Thus, it is possible that weather fluctuates with a periodicity of 5, 7 and 11 years in the habitats occupied by *Calathus melanocephalus* and *Poecilus coerulescens* in this region. However, neither the influential factors nor their annual values are published by the authors: thus, it is not possible to do a periodogram analysis. Nevertheless, it is questionable whether the *Calathus melanocephalus* and the *Pterostichus coerulescens* populations studied are adapted to cycles in weather in the same way as *Carabus auronitens* appears to be, as in years with low rates of egg production survival is not relatively high (chapter D. III. 3.).

D. III. 6. A concise description of the model of "density-dependent reinforcement of risk spreading"

The *Carabus auronitens* population is adapted to a 4 year periodicity in temperature in late spring when the early stages of the species probably develop. On average, in every 1st year of this cycle the temperature (PTi) is so low that reproduction more or less fails. The population survives such events because the adults are long lived and temporal risk spreading is possible (chapter A). The population seems to be specifically adapted to the 4 year periodicity by a mechanism described here for the first time, of "density-dependent reinforcement of risk spreading". This hypothesis is supported by empirical observations. Fundamental to our hypothesis is that the net reproductive rate depends not only on PTi but also the value i of the mean 4 year periodicity in PTi. The latter is interpreted as the influence of an endogenous "expectation periodicity" (BEVi).

Two factors that could be imported for the apparent adaptive feature of the reproductive activity are: (1) 1.5 year old females are more or less reproductively inactive (spent); (2) the investment in vitellogenesis in early spring i of the reproductive females depends negatively on the density of reproductive females in the previous spring (i-1). - In every 4th year, when an adverse weather event is likely to occur, the proportion of 1.5 year old females is relatively high, and in the previous year the density of the non-spent females is relatively high. This results in the average reproductive investment of females in early spring i being low, even when the actual conditions are optimal. (It is also possible that the locomotory behaviour of females and males is reduced when an adverse weather event is likely to occur; chapter C. V. 4.). - As a consequence of the reduced reproductive investment, survival from spring i to spring i+1 is increased (the "reward" or "trade-off" hypothesis). The stimulus for the assumed physiological (and behavioural) conversion could be density-dependent mutual interference, mediated via pheromones. There is no conclusive evidence of density-dependent food shortage among larvae or imagines in spring or autumn (cf. chapter C. V. 1.). This means that the density-dependence, which is essential for our model becomes effective at densities far below the carrying capacity of the habitat (i.e., below densities at which competition - "density-dependent food shortage" as defined by Weber & Heimbach, 2001 - is expected to occur). That is at one and the same density the reproductive rate is reduced and adult survival increased. At the carrying capacity one would expect adult survival to be reduced by food shortage.

D. IV. Possibilities of experimental falsifications

It is now important to test the essential assumptions of our model in the field: (1) that reproductive investment is negatively density-dependent far below the carrying capacity of the habitat (cf. chapters C.

V. 3. & C. V. 4.); and (2) that there is a trade-off between reproductive investment and survival (cf. chapters C. V. 5., C. VII. 3., C. IX. 2., D. III. 2., 3. & 6.).

A first experimental test was done by so-called "Lenski experiments" with artificially enlarged densities in enclosures of 20 m in diameter (Table 3.6.-7 in Weber & Heimbach, 2001). Half of the animals in experimental enclosures were fed after every capture, the other half was not like all animals in control enclosures. The percentage by which the densities were increased was 21 - 61 % of the density in the 0.2 ha enclosure in the same year. The maximum increased density was 124 % of the highest density observed in the 0.2 ha enclosure (in spring 1995; **Tables 1 & 2**). Weight increase did not differ essentially between experimental and control enclosures. As predicted by our hypothesis net reproductive rate in year i was low in 5 of 6 enclosures with artificially enlarged densities compared with the net reproductive rate recorded in the 0.2 ha enclosure in the same year and mortality was rather low, which accords well with the reward (trade-off) hypothesis. - However, it has to be stressed that our "Lenski experiments" are not a critical field test of our model: (1) control enclosures of the same size with natural densities were not established; (2) the generation structure of the enclosed groups is unknown; (3) the enclosed populations were established not earlier than in spring i; (4) unfortunately, in one spring (1994) there was a severe caterpillar outbreak in the Forst Tinnen, where the experiments were carried out; (5) beetles were not checked in spring i+1 whether really - as we assume in chapter C. V. 1. - high density in spring i does not influence weight development in spring i+1 as a consequence of density-dependent food shortage in spring i. - Improved "Lenski experiments" at high densities need to be done to determine the carrying capacity.

A key stone of our model is the assumption that high densities have an opposite effect on reproduction and survival: this is important for the spreading of risk strategy (chapters A. and D. III. 6.). Below are some of the experiments which could be used to falsify the hypothesis of "density-dependent reinforcement of risk spreading".

Our model makes several assumptions, based on analyses of the *Carabus auronitens* time series, which have yet to be experimentally tested:

(1) Reproductive investment of females (vitellogenesis) is lower at high than low population densities, but this is not due to competition for food.

(2) Adult survival increases at high densities by reducing reproductive investment.

(3) The density in spring i-1 influences phenomena 1 and 2.

(4) 1.5 year old females are more or less reproductively inactive (spent) and at later age participate in reproduction again. Do females of other generations also differ with respect to reproductive investment?

(5) Are 1.5 year old females actively involved in the assumed interference effect in spring i-1?

(6) If the density-dependent effect operates in spring i-1, the question arises whether this effect is caused also by females preparing for an adverse weather event by reducing their reproductive investment.

These assumptions and questions should be tested by field experiments. Such an experiment should start in a year after an adverse weather event. Let us number this year as 1. Beetle-proof enclosures, at least 20 m in diameter, need to be erected. As soon as possible in spring 1 enclosure populations are established. Animals are taken from the natural habitat, thus, their age is unknown; however, the enclosure populations should be so large that random differences in generation structure between the enclosed populations can be excluded. In experimental enclosures the density should be equivalent to the highest observed in the field, and in control enclosures the lowest (**Fig. 12**). The animals introduced into the enclosures, as well as young beetles emerging in the enclosures, should be marked individually and regularly trapped to measure their body weight, activity level and survival and the actual density (by the

Jolly-Seber method). These populations should be monitored until the year with the next adverse weather event.

Let us assume the next adverse weather event does not occur earlier than in year 3, and that a caterpillar outbreak does not occur. Then we should be able to answer the following questions:

- Are the relative weights (mg / mm) of females and males less in the high density enclosures?

- Is the level of activity of females and/or males less in the high density enclosures?

- Is net reproductive rate in the experimental enclosures smaller already in spring 1?

- Is net reproductive rate in the experimental enclosure reduced not earlier than in spring 2?

- Is the survival of adults high in those enclosures where net reproductive rate is low?

If the relative weights of females and males are less in the high density enclosures, critically is especially the end of the spring season, the assumption that there is no competition for food would be falsified. - Also, if net reproductive rate is not reduced in spring 1 or spring 2 and survival of the adults is not high in the high density enclosures after a year when the reproductive rate was low compared with the control enclosures, our assumption about density-dependent traits in the *Carabus auronitens* population would be falsified. - If in the experimental enclosures net reproductive rate is reduced in spring 1, the survival hypothesis can be tested in spring 2, if reduced not earlier than spring 2, the experiment has to be continued till spring 3 in order to test the assumption about survival. In any case, the experiment should be continued until the next adverse weather event.

In order to test the assumption and question (4) above we have to establish enclosures, which contain (1) only 0.5 year old females, (2) only 1.5 year old females, (3) only 2.5 year old females, (4) only 3.5 year old females and (5) a mixture of the female generations typical for the year in which this experiment is carried out. In order to exclude the influence of male age, which we have not previously considered, the composition of the male stock in each enclosure should resemble that in nature in the year in question. For this large numbers of young beetles need to be marked in a big enclosure during the previous years.

Testing questions (5) and (6) will be the most demanding and should be performed when the answers to the other questions are positive. For testing (5): the density-dependent effect on reproduction of enclosed populations containing only 1.5 year old females has to be compared with that in enclosures containing females of other ages. Testing for (6) makes sense when the density effect in spring i is due to the density of females in spring i-1. For this experiment high and low density enclosures need be established in a year with an adverse weather event.

Performing these experiments will require a lot of work, but methods exist for erecting beetle-proof enclosures, successfully marking individuals and monitoring their weight, locomotory behaviour and survival (Weber & Heimbach, 2001). Ecologists should (more than they have done in the past) realize the possibilities offered by carabids for doing "experiments in nature" (Brandmayr & Weber, 1981).

E. Appendices

Appendix 1

The body size of females and males varies from generation to generation. The smallest females and males were observed in autumn 1999 (females: 22.87 mm; males: 20.84 mm), the biggest in autumn 2001 (females: 24.34 mm; males: 22.08 mm). Thus, the quotient "mean weight of females divided by mean weight of males" can only be used as a measure of egg production of a stock of mixed generations, when the quotient "body size of females divided by body size of males" is independent of the absolute body size of females and males. As the body size quotient does not regress on the absolute size of females (+, $p = 0.285$; $r^2 = 9.5$ %; $n = 14$) and males (-, $p = 0.336$; $r^2 = 7.7$%) the relative difference between the body size of females and males is fairly constant.

Appendix 2

The 4 year periodicity in climate seems to be associated with a corresponding periodicity in the Annual North Atlantic Oscillation (NAO), which reflects differences in air pressure between Iceland and the Azores. The periodogram analysis of the NAO values measured between 1891 and 2000 (published by Hurrell: http://www.cgd.ucar.edu/~jhurrell/nao.html; 2002) shows a significant 4 year periodicity, as well as significant 2, 5, 8, 10 and 16 year periodicities; regression analysis confirms the existence of a significant 4 year periodicity for the period 1891 – 2000 (**Fig. 21**). Whether the 2 and 4 year minima indicated by the periodogram analysis represent a periodicity of their own or are subminima of the 8 year periodicity is questionable (the analogous question arises concerning the 5 year minimum with respect to the 10 year periodicity). - Also, for the NAO values measured since 1982, periodogram analysis indicates a minimum of 4 years, which does not deviate significantly from background (minima at 2 and 8 years deviate with $p < 0.10$ from background, data not shown). - PTi is positively correlated with the NAO value in year i+1 (1891 - 2000: $r^2 = 7.7$ %, $p = 0.003$; 1982 - 2000: PTi and NAO values are not significantly correlated).

Several authors have described the influence of directional NAO trends on population dynamics of aquatic and terrestrial species in Europe (Post & Stenseth, 1999; Straile, 2000; Hüppop & Hüppop, 2002); however, the consequences of climatic periodicities in the range of a few years have not been recorded.

Appendix 3

We observed that the minimum absolute weight of the females as measured in the 1st, 2nd or 3rd decade of April between 1985 and 1998 depends with weak significance on PTi (linear regression: +, $p = 0.057$, $r^2 = 27.0$ %). This result is confirmed by analyzing the whole series of investigation (1985 - 2001; linear regression: +, $p = 0.059$, $r^2 = 21.8$ %).

Appendix 4

When Bi is regressed on PTi^2 and BEVi, the influence of both factors is significant: PTi^2: $p = 0.020$; BEVi: $p = 0.006$; $p_{mult} < 0.001$, $r_{mult}^2 = 73.0$ %. – When Bi is regrssed on PTi, PTi^2 and BEVi, the influence of BEVi is significant ($p = 0.017$), whereas PTi and PTi^2 are not ($p = 0.513$ and 0.660) ($p_{mult} > 0.001$; $r_{mult}^2 = 73.8$ %); in stepwise regression PTi and BEVi are influential, and PTi^2 is eliminated.

Fig. 21a

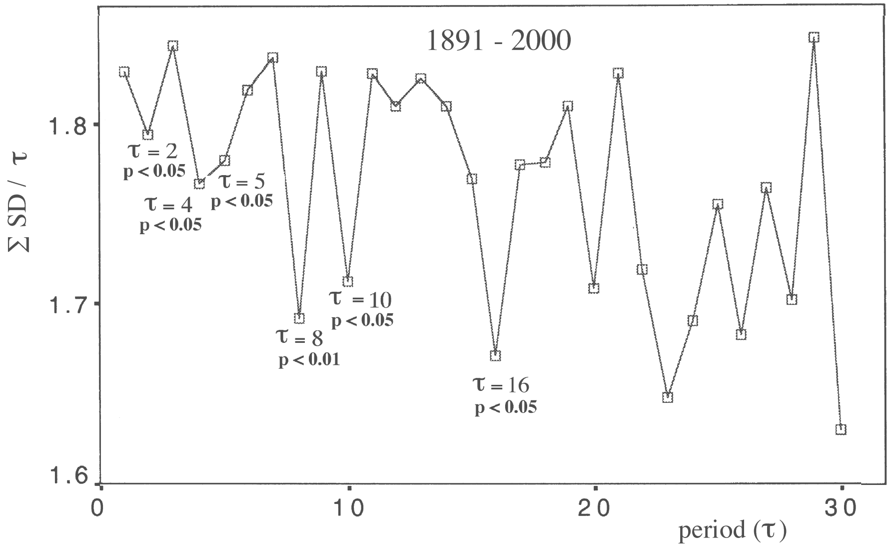


Fig. 21b

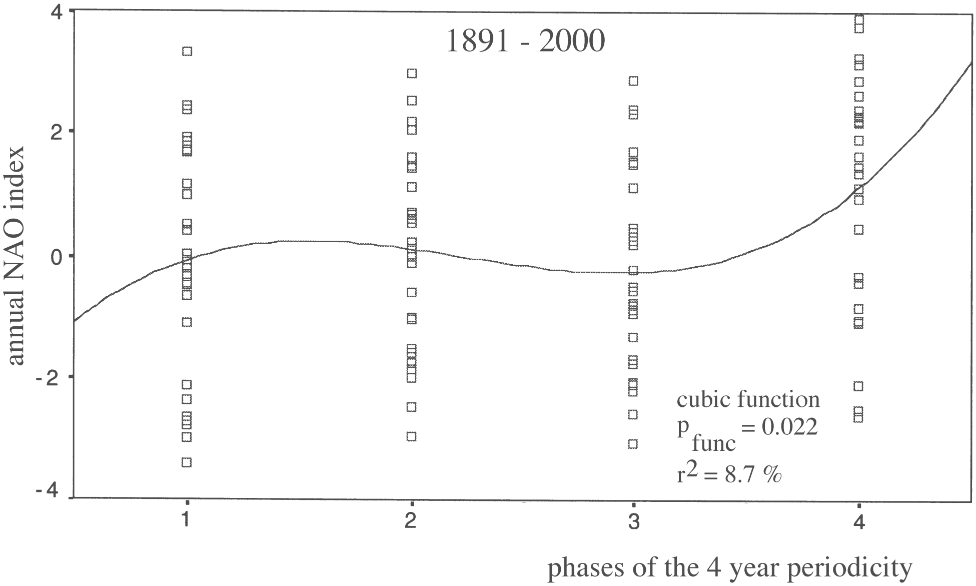


Fig. 21 **Fig. 21a**: periodogram analysis (after Lamprecht & Weber, 1970) of the annual NAO index 1891-2000 (Hurrell's data from www, cf. appendix 2). Statistics after Sokolove & Bushell (1978). **Fig. 21b**: cubic regression of the annual NAO index for 1891 - 2000 on the phases of the 4 year periodicity. Phases are identical to those in **Figs. 6, 7, 8, 12 & 18**.

Appendix 5

Baumgartner's Expectation Value, BEVi, is the value i of the mean 4 year period in PTi calculated from the PTi series for 1891 - 2001. The mean for the 6 year period was determined on the basis of 30 years only. Therefore, in a critical test "BEVi" was also calculated from the PTi values measured from 1982 - 2001. The statistics of the regression of Bi (related to the total female stock) on PTi and "BEVi" reveal a significant distinct influence of both independent variables:

PTi: +, $p = 0.021$

"BEVi": +, $p = 0.045$

$p_{mult} < 0.001$, $r_{mult}^2 = 68.1$ %

Appendix 6

If the females in spring of year 1 of the cycle (when BEVi is minimal, and an adverse weather event is likely to occur) do not influence the reproductive rate in the following year by a density-dependent inhibitory effect, the coefficient of determination of $B_{i,with\ 1.5}$ by Ai-1 should become larger when the density values of the year 1 are omitted from the regression analysis. When this is done the coefficient of determination becomes marginally larger (-, $p = 0.0137$, $r^2 = 40.9$ %, $n = 14$; r^2 equals 35.1 % when all values are considered: **Table 10**). Thus, the test does not allow any conclusion concerning the possibility of a disadvantage.

F. Summary

In a field study, based on the capture of individually marked adults, the fluctuations in density and net reproductive rate, Bi, of a Westphalian Lowland *Carabus auronitens* population were measured between 1982 and 2001. In 1992 the 0.2 ha study area was surrounded by a beetle-proof fence, which made it possible to measure also the mortality rate of the adults. - In the Westphalian Lowlands, *Carabus auronitens* is a univoltine spring breeder with two seasons of activity per year. The maximum life span of adults is 5.5 years. The teneral beetles emerging in the late summer / autumn of year i are the descendants of the beetles active in the spring of year i. In late summer / autumn almost exclusively freshly emerged beetles are active; old beetles surviving from spring remain in dormancy until the following spring i+1. - As much as 73.4 % of the variation in Bi (number of freshly emerged beetles in autumn i divided by number of females in spring i) is determined by the temperature (PTi) in a critical period of early development in late spring and an "expectation value" (BEVi). In the Westphalian Lowlands PTi shows a 4 year periodicity, which seems to be correlated with a respective periodicity in a climate parameter, the Annual North Atlantic Oscillation Index (NAO). BEVi is the value of the mean 4 year period of PTi corresponding to spring i. The influence of the expectation value on the population dynamics is interpreted as an adaptation of the population to the 4 year periodicity in PTi. Net reproductive rate and survival fitness are the "target factors" of the expectation periodicity. - When according to the 4-year periodicity low temperatures are likely to occur during the critical period in late spring, the beetles appear to reduce their investment in reproduction (vitellogenesis in females and mate searching in males) in early spring, even if the conditions in early spring are not suboptimal. Reduction in reproductive investment seems to be associated with an increase in female individual survival probability. - A model is developed that explains how the beetles may be "informed" anticipatorily whether the temperature during the critical period will be optimal or suboptimal. An important "information factor" seems to be the abundance of females: in each 4th spring the critical temperature (PTi) is likely to be unfavourable; in this and the previous spring, the density of females is relatively high. There is no indication of a density-dependent food-shortage within the range of abundance observed in spring: the carrying capacity of the habitat seems to be much higher than the densities, that trigger females and males to reduce investment in reproduction. Thus, density-dependent reactions are probably caused by pheromone-mediated interference. This is a precondition that in the same year reproductive investment is reduced and survival probability is increased. Simulations reveal that the generation structure of the female stock in spring i may be a further information factor of the expectation periodicity: females of different ages seem to differ in terms of their reproductive investment (there is some empirical support for 1.5 year old females being more or less reproductively spent). - Improved individual survival probability after reproductive failure is essential for population survival: it is a strategy of temporal risk spreading. If by using "information factors" beetles avoid unprofitable investments in reproduction, and so individual survival is increased, the strategy of temporal risk spreading is reinforced. This mechanism is referred to as "density-dependent reinforcement of risk spreading".

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