

SOME REMARKS IN RETROSPECT

P. J. DEN BOER

Biological Station of the Agricultural University (Wageningen), Kampsweg 27, 9418 PD
Wijster, The Netherlands

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Evolution, as the unifying concept of biology, is the result of an immense collection of generally unique historical processes, which have left only very few direct records. Moreover, the records we need to reconstruct some of the more interesting parts of these histories are usually lacking. On the other hand, evolutionary processes will not be restricted to the past, and if we support the 'principle of topicality' (according to Occam's razor), we should still be able to study such processes as they are occurring at present. If we are interested in the evolution of behaviour this is even the only way to get some insight, since behaviour only in exceptional circumstances leaves any direct fossil records. There remains one major difficulty, however: significant evolutionary changes, as they occurred in the past, apparently took an enormous amount of time. Hence, once again we have to use Occam's razor: important evolutionary changes are assumed to result from an accumulation of smaller changes as these are actually studied by population biologists.

This very concise formulation of the necessary presuppositions for the realization of direct evolutionary research is needed to pose an interesting question: What kind of changes are sufficiently small to be successfully traced and experimented upon during the short period of active life of a field biologist? From the older work on polymorphism (e.g. CAIN, DOWDESWELL, EHRLICH, FORD, KETTLEWELL, SHEPPARD; see FORD, 1964) already it became evident, that in field populations selection processes sometimes may happen surprisingly quickly and may thus result in striking changes, also in organisms with only one generation a year. We have similar experiences with some newly founded populations of wing dimorphic carabid species: within a few years the percentage of fullwinged specimens decreased rapidly (in a young and numerous population of *Calathus mollis erythroderus* Gemm. & Har. in the course of five years the percent macropterous ind. decreased from 80–90% to 65%; see also *Trechus obtusus* Er. in HAECK, 1971: Table 6). Hence, also under natural conditions some selection processes may happen fast enough to distinctly alter the composition of the population within the period of observation. On the other hand, NAGEL (this volume) mentions that the outward appearance of some Paussinae did not alter for 50 million years. Apparently, in evolution varying rates are possible.

In the above cases of wing dimorphic populations it does not seem very difficult to understand the speed of this process: especially in rather isolated populations the loss

of fullwinged specimens flying away will generally be higher than the gain of macropterous individuals appearing from elsewhere (see further : DEN BOER, 1970). In some of the cases discussed by FORD (1964) however, the observed selection pressure upon certain morphological features could not be understood at first sight. Selection must have worked indirectly upon such features, i.e. they must somehow have been genetically closely connected with some vital property of the individuals. Such a situation becomes especially interesting if the morphological features concerned are also decisive taxonomic characters to separate the species from related ones. Measurable changes in such characters would then be indicators of a selection process that might be a reasonable model for processes that have led to speciation among the kind of organisms concerned. An example of this was found in the number of pits on the elytra of *Pterostichus oblongopunctatus* F. (DEN BOER, 1962). This species is taxonomically separated from the closely related *P. angustatus* Dfts. (with 3 pits on each elytron in 89.8 % of 971 ind. studied, or at least with 3 pits on one elytron : 98.4 %) mainly because it has five, six or even more pits on each elytron (in 7 % of the ind. only 4 pits on one of the elytra). The number of pits is partly genetically fixed and the ratio 'low pitters' (4 or 5 pits)/'high pitters' (6 or more pits) in the populations of this forest species is changing from year to year under the apparent (direct or indirect) influence of the yearly changing moisture content of the litter during the period of larval development: 'low pitters' are relatively favoured under dry conditions and 'high pitters' under moist conditions (these correlations were provisionally confirmed by some field experiments and a breeding experiment by THIELE; more data are being studied, and more experiments are planned). In confirmation of this *P. angustatus* (an 'extreme low-pitter', see above) is living in dryer localities than *P. oblongopunctatus*, especially in places where the forest has recently been burned. Hence, the diagnostic character of the number of pits on the elytra is closely connected with habitat preference in these species (see also: MOSSAKOWSKI, this volume). The above example was not only mentioned to illustrate that also among carabid beetles interesting selection processes may sometimes happen fast enough to be studied under field conditions and to be manipulated in experiments, but also to illustrate two other points:

1. Natural selection does not operate on separate genes, but on whole individuals.

Therefore, the result of selection will always be a compromise, not only because of the obvious restrictions imposed by the starting material, but also because of the restricted number of combinations of traits that can be realized and/or will be sufficiently viable (e.g. in the above case, the combination of a high number of pits with a high tolerance of dry conditions is apparently impossible). BRANDMAYR (this volume) gives good examples of such compromises among a number of closely related carabid species. Hence, simple optimality models of evolutionary processes will almost necessarily be biologically unrealistic (see also : STEARNS, 1976).

2. Selection can only operate within restricted (local) groups of phenotypically different individuals (and not within 'gene-pools'), thus relatively favouring the survival of the gene-combinations of the best of the available individuals. However, the

above example already illustrates that under different circumstances (e.g. in years with different moisture conditions, but also in different places within the habitat of the same population) different individuals may be the 'best' ones. This means, that it can hardly be expected that natural selection will often be an unidirectional process, although we all hope to have the opportunity of studying such cases (see FORD, 1964). More generally, natural selection will be a complicated, multicausal process the direction of which will often change, because it comprises the integrated result of a number of varying factors that in each generation anew together determine the different magnitudes of the mortality and reproduction of a number of different individuals.

The above remarks not only point to the kind of difficulties one may expect to meet when studying selection processes that occur under field conditions, they also indicate another phenomenon: When natural selection is not unidirectional, but follows a very tortuous route, many different kinds of genes will be preserved in the population in an increasing number of combinations (genotypes). In this way, by continually 'testing', so to speak, the members of the population against a wide variety of different combinations of environmental factors, natural selection will broaden its own base, i.e. the genetic heterogeneity of the population as it is distributed between individuals. It can be expected, that in the long run (when the environment does not change fundamentally) the influence of natural selection will thus become more and more subtle, just as the differences in many characters between the resulting individuals, i.e. in spite of an enormous genetic heterogeneity between individuals the phenotype will have a tendency to become more and more uniform (at least in many features), or to split in a few quite distinct types (polymorphism) with a not very different overall selective value. Note, that the existence of polymorphism within natural populations (which need not to be restricted to morphological features, but is especially very common – and theoretically very important – at many enzyme-producing loci, (see e.g. SCHARLOO, VAN DIJKEN, HOORN, DE JONG & THÖRIG, 1977) already shows that simple optimality models must generally be inadequate (STEARNS, 1976): apparently, in nature there are more 'solutions' for the same 'problem'. In many cases these 'different solutions' will have the significance of 'spreading the risks' that are connected with living in a heterogeneous and/or fluctuating environment over different gene-combinations, (DEN BOER, 1968), e.g. : in our example no larva of *P. oblongopunctatus* is apparently able to tolerate every humidity-value that may occur in the natural environment of the larvae, but by 'dividing' the range of tolerances between 'low-pitters' and 'high-pitters' respectively, the population can nevertheless survive under fluctuating moisture conditions. In this connection it would be very interesting to study the level of polymorphism of populations which have already lived for many generations in nearly constant environments, e.g. deep into caves (see JUBERTHIE, this volume, and WEBER, this volume).

When in the same population natural selection already preserves 'different solutions for the same problem', this may be expected to occur still more between related species living together in the same habitat (in spite of the general belief in 'competitive

Table 1. Life tactics of carabid species that occur together in the litter of oak-birch forests in Drenthe (stable habitat).

Species	breeding season ³	mean number of eggs in ovaries ⁴	larvae in	young adults in ³	length of life of adults	size class adults ⁵	active during the	feeding habits	dispersal power ⁶
1	2	3	4	5	6	7	8	9	10
<i>Pterostichus oblongo-punctatus</i> F. ¹	spring	13	summer (in the soil)	autumn	> 1 year til 3-4 y.	III	mainly night	polyphagous	(macr.?) flies only rarely
<i>Agonum assimile</i> Payk. ¹	spring	27	summer (in the soil)	autumn	> 1 year till 3-4 y.	III	night	polyphagous	(macr.?), no flying ind. so far
<i>Pterostichus strenuus</i> Panz	spring	7	spring (in the soil)	summer	> 1 year	II	night	polyphagous	dim: 23% m., flies regularly
<i>Carabus nemoralis</i> Müll.	spring	8?	summer (at the surface)	autumn	> 1 year	IV	night (and day?)	oligophagous: worms, snails, etc.	brach.
<i>Loricera pilicornis</i> F.	spring	18	? (at the surface?)	autumn?	only one year?	II	day (and night?)	oligophagous: Collemb., mites	macr., flies regularly
<i>Amara brunnea</i> Gyll.	summer	3	winter? (in the soil)	spring	> 1 year	I-II	night (and day?)	polyphagous, prefers ants?	macr., flies only rarely
<i>Carabus problematicus</i> Hbst.	late in summer	9	winter (at the surface)	June	> 1 year til 3-4 y.	IV	night	oligophagous? snails?	brach.
<i>Abax ater</i> Villers ²	spring and summer	few	eggs laid in mud cell made by ♀	spring and autumn	> 1 year developm. in two years?	IV	night	oligophagous? mainly worms?	brach.
<i>Calathus piceus</i> Mrsh. ¹	spring (old ind.) summer (juv.)	± 7	winter (summer?) (in the soil)	summer (+ few in autumn)	> 1 year till 2 y.	III	night	polyphagous?	dim: 93% m., flies only rarely
<i>Notiophilus biguttatus</i> F.	spring and autumn	± 4	mainly summer (at the surface)	late in spring and in autumn	> 1 year?	I-II	day	oligophagous: Collemb.	dim.: 79% m., flies infrequently

<i>Notiophilus rufipes</i> Curt.	autumn, winter, spring	± 4?	? (at the surface)	?	? > 1 year?	I-II	day	oligophagous? (Collemb.?)	macr., no flying ind. so far
<i>Nebria brevicollis</i> F. ¹	late in autumn	19	winter (at the surface)	spring (aestivation)	only one year	III	night	polyphagous prefers Collemb.?	macr., flies only rarely
<i>Leistus rufomarginatus</i> Dfts.	late in autumn	13	winter (at the surface)	spring (aestivation)	only one year?	II-III	night	oligophagous : Collemb., mites	macr.(?), no flying ind. so far
<i>Trichocellus placidus</i> Gyll.	autumn, winter, spring	?	?	summer	?	I	day (and night?)	?	macr., flies frequently

¹ see also: DEN BOER, this volume

² see also: BRANDMAYR, this volume

³ see also: PAARMANN, this volume

⁴ from VAN DIJK (this volume) it will be evident that the number of eggs in the ovaries does not give reliable information about the number of eggs laid; in each species this relation should be carefully investigated. These numbers are only given here to show that they do not indicate any trend, neither in favour, nor in contradiction of the theories of r- and K-selection, and we expect that better information would not give a significant difference between the species of Table 1 and those of Table 2 in this respect.

⁵ size-classes: I. < 5 mm
 II. 5-8½ mm
 III. 9-12½ mm
 IV. > 12½ mm

⁶ abbreviations: (macr. ?) = although the wings are larger than the elytra there is some doubt about the possibility of using them for flying (see also: VAN HUIZEN, this volume).

dim: 23% m. = wing dimorphic (or polymorphic) with 23% of the individuals studied with fully developed wings.

macr. = macropterous, i.e. wings always fully developed. brach. = brachypterous, i.e. no individuals with functional wings.

flies only rarely = in the course of 5-8 years sampling with window-traps only one or two specimens were caught during flying.

flies (very) regularly = each year a few (sometimes more) specimens are caught in window-traps.

flies (very) frequently = each year during the whole flight (migration?) period specimens (sometimes even many) are caught in window traps.

Table 2. Life tactics of carabid species that occur together at the surface of recently abandoned agricultural fields in Drenthe (unstable habitat).

Species	breeding season ³	mean number of eggs in ovaries ⁴	larvae in	young adults in ³	length of life of adults	size class adults ⁵	active during the	feeding habits	dispersal power ⁶
1	2	3	4	5	6	7	8	9	10
<i>Amara plebeja</i> Gyll. ¹	spring	10	summer (in the soil)	August-Sept.	> 1 year	II	day	phytophagous	macr., all ind. fly 2x a year!
<i>Amara aenea</i> de Geer	spring	?	summer (in the soil)	autumn	> 1 year	II	day	mainly phytophagous	macr., flies very frequently
<i>Amara familiaris</i> Dfts.	spring	8	summer (in the soil)	late in summer	> 1 year	II	day	mainly phytophagous?	macr., flies very frequently
<i>Amara lunicollis</i> Schiödte	spring-summer	5	summer (in the soil)	summer-autumn	> 1 year	II	day	polyphagous	macr., flies regularly
<i>Anisodactylus binotatus</i> F.	spring	5	summer (in the soil)	late in summer	> 1 year	III	day + night?	polyphagous	macr., flies very regularly
<i>Loricera pilicornis</i> F.	spring	18	? (at the surface?)	autumn?	only 1 year?	II	day (+ night?)	oligophagous: Collemb., mites	macr., flies regularly
<i>Pterostichus coerulescens</i> L.	spring	12 ²	summer (in the soil)	autumn	> 1 year till 3-4 y.	III	day	polyphagous	(macr.?) flies only rarely
<i>Bembidion lampros</i> Hbst.	spring	5 ⁷	?	autumn	?	I	day	oligophagous: mainly eggs	dim: 17% m. does not fly frequently
<i>Carabus cancellatus</i> Illig.	spring	?	summer (at the surface)	autumn	> 1 year	IV!	day	oligophagous: snails, worms	brach.
<i>Harpalus aeneus</i> F. ⁸	spring + summer	?	mainly summer (in the soil)	summer + autumn	> 1 year till 3-4 y.	III	day	phytophagous?	macr., flies regularly
<i>Harpalus pubescens</i> Müll.	late in summer	5	summer? (in the soil)	summer, also late in autumn	> 1 year	IV	night	very polyphagous	macr., flies very regularly

<i>Amara apricaria</i> Payk.	late in summer	?	spring, winter (in the soil)	early in summer	> 1 year	II	night?	polyphagous	macr., flies very regularly
<i>Calathus fuscipes</i> Goeze	autumn	?	winter (in the soil?)	June	> 1 year	III	night	polyphagous	dim: 0.85% m. no flying ind.
<i>Pterostichus vulgaris</i> L.	autumn	?	winter (in the soil)	late in summer	> 1 year	IV	night	polyphagous	dim: 2% m. no flying ind. so far
<i>Notiophilus aquaticus</i> L.	during the whole year!	±4?	? (at the surface)	spring, summer + autumn	? > 1 year?	I-II	day	oligophagous? ; Collemb.?	dim: 1.2% m. no flying ind. so far
<i>Bradycellus harpalinus</i> Payk.	autumn, winter, spring	5	?	late in summer	> 1 year	I	day (night?)	phytophagous	dim: 78% m. flies in very high numbers (thousands)

¹ see also: VAN HUIZEN (1977)

² see also: VAN DIJK (1979), and this volume

³, ⁴, ⁵, ⁶ as Table I

⁷ from MITCHELL (1963)

⁸ data from SCHJØTZ-CHRISTENSEN (1965)

exclusion', within a restricted area – like Drenthe – related species are more often than not coexisting; see e.g. WILLIAMS, 1964; for carabids, see also THIELE, 1977). A good example is given by NAGEL (this volume), who shows that Paussinae developed two quite different solutions to solve the problem 'How to live with ants?', the 'Trutztyp' and the 'Symphilentyp'. Therefore, it seems not very probable that only special assemblages of traits will co-evolve, and will thus always be found together as 'optimal strategies', as is predicted in theories of r- and K-selection (compare e.g. BAUER, 1971, with BAUER, this volume). This latter approach, which has already been criticized sufficiently by STEARNS (1976), is based on a number of biologically unrealistic assumptions, by which these ideas in fact cannot be tested. The only thing one can do with it, is – and this is rather in fashion at the moment – selecting examples that more or less seem to be 'r-strategists' or 'K-strategists' respectively. But one cannot make science by carefully selecting examples that seem to confirm some idea, as long as one does not also logically exclude the possibility of collecting counter-examples. To illustrate the latter point I wrote down what I know at the moment about the 'life tactics' (STEARNS, 1976) of the carabid beetles that generally live together in rather high numbers. Table 1 shows the species from the oak-birch forests of Drenthe (a stable habitat that should favour 'K-strategists'). Table 2 shows the species from very recently abandoned agricultural fields in Drenthe (an unstable habitat that should favour 'r-strategists').

Although much of the data in these tables (especially those in column 3) are only provisional, a comparison clearly suggests that among carabid species no special combination of traits has co-evolved to enable (or even 'maximize') survival in either a stable or an unstable habitat. All kinds of annual reproductive rhythms (compare PAARMANN, this volume) are apparently possible in both stable and unstable habitats. Actual differences between these two groups of carabid species are apparently not found among life-history traits (columns 2–6), but among other features: forest species are generally night-active, whereas most species from unstable habitats (but also of other open sites) are day-active (column 8); some carabid species from unstable habitats (only when these are associated with agricultural fields, or other man-made sites) are more or less phytophagous (column 9); most species from unstable habitats have high powers of dispersal, whereas the dispersal power of most forest species is low (column 10); (see also VAN HUIZEN, this volume). Only the latter trait is directly connected with the degree of stability of the habitat (see DEN BOER, 1977), but is – interestingly enough – not joined to a higher or lower reproductive power (column 3),* and/or a shorter or longer adult life (column 6), as predicted by theorists on r- and K-selection (STEARNS, 1976). It is also apparent in this respect that many 'solutions for the same problem' (survival in a certain kind of habitat) are possible.

* Although these data cannot be trusted (see VAN DIJK, this volume), they at least indicate that a species such as *Agonum assimile* (Table 1) will not always lay low numbers of eggs, whereas species like *Anisodactylus binotatus*, *Bembidion lampros*, *Harpalus pubescens*, *Bradycellus harpalinus* (Table 2) will not lay very high numbers of eggs.

This does not mean, however, that we do not sometimes meet with examples that seem to confirm the ideas behind r- and K-selection. A good example is found in PAARMANN (1966): *P. angustatus* (living in unstable habitats, see above) on average produces about twice as many eggs as *P. oblongopunctatus* (living in stable habitats, see above); see also THIELE (1977, p. 132). I am quite sure, however, that it will be possible to find counter-examples (see above). This example only tells us that *P. angustatus* produces more eggs than *P. oblongopunctatus*, but not that *P. angustatus* necessarily has been 'r-selected', i.e. the work of PAARMANN (1966) is important independent of these – untestable – theories.

Each of us in his own field of study has already discovered that it is impossible to evade the hard work of rigorous empiricism (compare e.g. MOLS, this volume). There is especially no easy way to develop general insights about the diversity of nature. From the foregoing it will be evident that even the construction of general mathematical models in most cases will not bring us closer to that goal. This does not imply that such models cannot be very useful to order and test our thoughts, or the thoughts of others, concerning nature. To test nature itself however, we will have to study, compare and manipulate populations (see e.g. THIELE, this volume; LEYK, this volume). Populations are composed of individuals (see DEN BOER, this volume), we will therefore have to know the properties of these individuals, and to study how they use this equipment to react to the environment, in an attempt to begin to understand population processes. On this reason autecologists, who study the same kind of animals from different aspects, need each other. To be able to quantify these processes we will also have to take into account the variability of these properties and reactions within populations (see e.g. VAN DIJK, this volume), and here population biologists will have to invoke the help of autecologists and biomathematicians.

We therefore hope that this symposium will be the start of the kind of cooperation that will help us more than the construction of simple 'optimality models' to understand the processes that govern the diversity of at least one group of organisms. The review by THIELE (1977) made it evident that for this purpose carabid beetles are very suitable material.

REFERENCES

- BAUER, TH.: Zur Biologie von *Asaphidion flavipes* L. (Col., Carabidae). Ent. Z. **81**: 154–164 (1971).
- DEN BOER, P. J.: Fluctuations in morph frequency in catches of the ground beetle *Pterostichus oblongopunctatus* F. and its ecological significance (1962). Can be obtained from the library of the Biol. Station, Wijster.
- DEN BOER, P. J.: Spreading of risk and stabilization of animal numbers. Act. Biotheor. (Leiden) **18**: 165–194 (1968).
- DEN BOER, P. J.: On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae). Oecologia (Berl.) **4**: 1–28 (1970).

- DEN BOER, P. J.: Dispersal power and survival. Carabids in a cultivated countryside. *Miscell. Papers, Landb. Hogeschool, Wageningen* **14** Veenman & Zn. (1977).
- FORD, E. B.: *Ecological genetics*. Methuen & Co. Ltd. London, 1964.
- HAECK, J.: The immigration and settlement of carabids in the new IJsselmeerpolders. *Miscell. Papers, Landb. Hogeschool Wageningen* **8**: 33–52. Veenman & Zn., (1971).
- MITCHELL, B.: Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). 1. Life cycles and feeding behaviour. *J. An. Ecol.*, **32**: 289–299 (1963).
- PAARMANN, W.: Vergleichende Untersuchungen über die Bindung zweier Carabidenarten (*Pterostichus angustatus* Dfts, und *Pterostichus oblongopunctatus* F.) an ihre verschiedenen Lebensräume. *Z. wiss. Zool.* **174**: 83–176 (1966).
- SCHARLOO, W., F. R. VAN DIJKEN, A. J. W. HOORN, G. DE JONG & G. E. W. THÖRIG: Functional aspects of genetic variation. In F.B. CHRISTIANSEN & T. FENCHEL (eds.): *Measuring selection in natural populations*. Springer Verlag, Heidelberg, 1977.
- SCHJØTZ-CHRISTENSEN, B.: Piology and population studies of Carabidae of the Corynephorum. *Natura Jutlandica* **11**: 1–173 (1965).
- STEARNS, C.: Life-history tactics: a review of the ideas. *Quart. Review Biol.* **51**: 3–47 (1976).
- THIELE, H. U.: *Carabid beetles in their environments*. Springer Verlag, Heidelberg, 1977.
- VAN DIJK, TH, S.: On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coerulescens* L. (Coleoptera, Carabidae). *Oecologia (Berl.)* **40**: 63–80 (1979).
- VAN HUIZEN, T. H. P.: The significance of flight activity in the life cycle of *Amara plebeja* Gyll. (Coleoptera, Carabidae). *Oecologia (Berl.)* **29**: 27–41 (1977).
- WILLIAMS, C. B.: *Patterns in the balance of nature*. Academic Press London, 1964.