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Wing Polymorphism and Dimorphism in Ground Beetles as Stages in an Evolutionary Process (Coleoptera: Carabidae)*

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For a number of species of the familia Carabidae, inhabiting the province of Drenthe (The Netherlands), the relationship could be studied between the capabilities to disperse and the degree of stability of the habitats occupied. The investigations were based on comparisons of the relative wing sizes of individuals captured in window traps with those of individuals caught in pitfalls. These data were supplemented by others on the reduction of flight muscles, on the reproductive state of flying ♀♀, and on the genetic background of wing dimorphism. The dispersal power of Ground Beetle species proved predominantly to be determined by natural selection, because individuals leaving the population take away genes associated with a high dispersal ability. The more stable the habitats occupied, the more natural selection will reduce relative wing size, as well as the ability to develop flight muscles. If both, stable and unstable habitats, are inhabited, the species concerned may become wing polymorphic. If next the effect of the unstable sites decreases, such a species will change into a wing dimorphic one. This disruptive selection does not only separate long-winged from short-winged populations, but also concentrates the genes influencing wing size in such a way that being «short-winged» becomes a single dominant character, long-winged individuals, consequently, being homozygotes. Both, monomorphic macropterous populations and wing dimorphic ones, will thus gradually evolve towards brachyptery, if the habitats occupied become more and more stable.

1 Introduction

The evolutionary significance of the phenomenon of wing polymorphism in Coleoptera was recognized by Darwin [1859]. He tried to explain the high numbers of flightless beetles on the isle of Madeira by supposing that winged specimens would gradually be blown into the sea and thus be eliminated by selection. More than eighty years elapsed before this particular point was taken up again, when Darlington [1943] called our attention to the high frequencies of brachypterous Carabidae on isolated islands and mountaintops. He stated that the flightless forms would be favoured there, because of a generally higher «viability». The first to take a really dynamic stand on the issue of wing polymorphism was Palmén [1944]. He showed that only the fully winged specimens of functionally dimorphic species were washed ashore at the Northern coast of the Gulf of Finland when certain meteorological conditions occurred, such as high temperatures (inducing spontaneous flight) and southeasterly or southerly winds. He concluded that the flying insects were carried out to sea by the prevailing winds, dropped to the water surface and eventually drifted ashore. There their

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accumulation would increase the chance of successful colonization as compared with dispersal by a purely anemochorous transport [see also Palmén 1971].

It was especially Lindroth [1949], who saw the study of wing polymorphism as a tool for the reconstruction of the colonization history of certain species in Fennoscandia. To be able to use this tool he had to make some assumptions:

- (1) Individuals capable of flying can usually be distinguished externally from flightless individuals;
- (2) The degree of wing development should be genetically determined (at least partly), in such a way that in all di(poly)morphic species, macropterous (fully winged) individuals are distinctly different from brachypterous ones (wings not fully developed);
- (3) All species or their ancestors were originally monomorphic macropterous (even the monomorphic brachypterous ones).

The first author of this paper was highly stimulated by the great work of Lindroth [1949] to study the consequences for population biology of the supposed differences in dispersal power between brachypterous and macropterous species of Carabidae. In spite of the scarcity of observations on flying Ground Beetles at that time, Den Boer [1970] could show that the fully winged specimens of a polymorphic population can indeed be considered to represent the «dispersal morph». The possibility of comparing the dispersal power of different species was greatly improved in 1969 with the use of window traps [Den Boer 1971; see also: Haeck 1971, and Meijer 1971, 1974]. With the help of such data, together with indirect estimates on the «turnover» of populations in the respective species, Den Boer [1977, 1979 a] was able to give a preliminary picture of the changes in the probability of survival of different species of Carabidae as a result of the cultivation of extensive natural areas. In the course of that study a closer examination of many individuals showed that, although the assumptions of Lindroth appeared to be generally right, the relationship between capability to fly and wing development is often less self-evident than was supposed by Lindroth [1949]. First of all, to be able to fly, a beetle not only needs suitable wings but also functional flight muscles. It was already known to Lindroth [1949] and further documented by Tietze [1963] that the presence of sufficiently developed wings does not necessarily coincide with usable flight muscles.

At present, evidence is accumulating that not all species of Carabidae conform to the «oogenesis flight syndrome», as it is described by Johnson [1969]. The syndrome was illustrated by Van Huizen [1977] with the case of *Amara plebeja* Gyllenhal 1810 [see also Van Huizen 1979]. By comparing the wings of individuals captured in window traps with those of individuals caught in pitfalls, it appears that in different species flying individuals often show quite different relative sizes of wings. In some cases it becomes difficult to distinguish externally the individuals that might have been capable of flying. On the other hand, it was exactly this large range of possibilities concerning flight capacities that enabled us to get some idea of the possible way in which monomorphic macropterous species can develop, via a wing polymorphic stage, into apparently wing dimorphic species, and eventually into monomorphic brachypterous ones. Therefore, as a continuation of an important part of the work of Lindroth [1949], in this paper we will present a tentative picture of this process, both by a more extensive treatment of the data [Den Boer-Daanje] which up till now were only summarized in Den Boer [1977: Tab. 3], by giving new data on some species [Van Huizen, Den Bieman, Aukema], and by discussing preliminary data on the reduction of flight muscles [Van Huizen, Den Bieman], on the reproductive state of flying females [Van Huizen] and on the genetic background of wing dimorphism [Aukema].

2 Material and methods

2.1 Investigated species of Carabidae

In this paper the following species of Carabidae will be treated (or at least mentioned):

Nebriini

Leistus rufescens (Fabricius 1775)

Leistus rufomarginatus Duftschmid 1812

Nebria brevicollis (Fabricius 1792)

Notiophilini

- Notiophilus rufipes* Curtis 1829
Notiophilus biguttatus (Fabricius 1779)

Loricerini

- Loricera pilicornis* (Fabricius 1775)

Scaritini

- Dyschirius globosus* (Herbst 1783)
Clivina fossor (Linnaeus 1758)

Trechini

- Trechus obtusus* Erichson 1837

Bembidiini

- Bembidion tetracolum* Say 1823

Pterostichini

- Pterostichus* Bonelli 1810
Pterostichus versicolor (Sturm 1824)
Pterostichus melanarius (Illiger 1798)
Pterostichus niger (Schaller 1783)
Pterostichus anthracinus (Illiger 1798)
Pterostichus oblongopunctatus (Fabricius 1787)
Pterostichus strenuus (Panzer 1797)
Calathus Bonelli 1809
Calathus piceus (Marsham 1802)
Calathus erratus Sahlberg 1827
Calathus melanocephalus (Linnaeus 1758)
Calathus mollis erythroderus Gemminger & Harold 1868
Calathus mollis mollis (Marsham 1802)
Agonum Bonelli 1809
Agonum sexpunctatum (Linnaeus 1758)
Agonum ericeti (Panzer 1809)
Agonum assimile (Paykull 1790)
Agonum dorsale (Pontoppidan 1763)

Amarini

- Amara* Bonelli 1809
Amara plebeja (Gyllenhal 1810)
Amara majuscula Chaudoir 1850
Amara ingenua (Duftschmid 1812)
Amara equestris (Duftschmid 1812)
Amara brunnea (Gyllenhal 1810)
Amara familiaris (Duftschmid 1812)
Amara lunicollis Schiödte 1837

Harpalini

- Harpalus* Latreille 1802
Harpalus rufipes (de Geer 1774)
Harpalus rufitarsis (Duftschmid 1812)
Harpalus quadripunctatus Dejean 1829
Harpalus latus (Linnaeus 1758)
Harpalus fuliginosus (Duftschmid 1812)
Anisodactylus Dejean 1829
Anisodactylus binotatus (Fabricius 1787)
Trichocellus Ganglbauer 1892
Trichocellus cognatus (Gyllenhal 1827)
Trichocellus placidus (Gyllenhal 1827)
Bradycellus Erichson 1837
Bradycellus ruficollis Stephens 1828
Bradycellus harpalinus (Serville 1821)
Bradycellus collaris (Paykull 1798)

2.2 Investigation methods

To obtain an unbiased measure of the relative size of the expanded wings of a Ground Beetle, one should exclude the allometric influence of differences in size between individuals. Den Boer-Daanje, who investigated different possibilities and did most of the necessary measurements, found that two values are adequate for that:

$$(a) \frac{\text{greatest length of postala}}{\text{greatest length of elytrum}}$$

$$(b) \frac{\text{greatest length of postala} \times \text{greatest width of postala}}{\text{greatest length of elytrum} \times \text{greatest width of elytrum}}$$

Although index (a) has a lower variance than (b) and gives reliable results [it was used by e. g. Palmén 1944], we developed some preference for (b) because in different individuals planimeter measurements of postala¹ and elytrum gave quotients that better followed the trends between the respective (b) measurements than those between the (a) measurements. Therefore, comparisons will mainly be made on the basis of index (b), which will be called «relative wing size», quantity (a) will be named «relative wing length».

By having some window traps in «strategic» positions in operation continuously from 1969, it gradually became possible for certain species to compare the relative wing size of specimens caught during the act of flying (in window traps) with that of individuals captured in pitfalls (or by hand) in the favoured habitats. Thus it could be learned what kind of individuals can be expected to fly away from the populations under study [Den Boer, Den Boer-Daanje, Van Huizen]. Such data could be checked and/or supplemented by carrying out experiments in which individual beetles are forced to show flight behaviour, if possible², and by dissecting certain individuals caught in pitfalls to study the degree of development of the flight muscles [Van Huizen, Den Bieman].

By dissecting ♀♀ that were captured in window traps, the suggestion of Lindroth [1949], which was supported by Den Boer [1971], and by Van Huizen [1977] in *Amara plebeja*, that only unfertilized females should show flight activities, could be tested more extensively on larger numbers of individuals from a greater number of species [Van Huizen].

Aukema carried out a number of breeding experiments with selected individuals of the wing dimorphic species *Calathus mollis erythroderus*. Methods and results of these experiments will be treated in separate papers. In this paper, however, we will use some of these results to test the hypothesis of Lindroth [1949] that in wing dimorphic species of Carabidae «brachypterous» would be a dominant character, the fully winged individuals, consequently, being homozygotes. – As far as possible we followed the nomenclature used by Lindroth [1974].

2.3 Presentation

In the following the frequency distributions of relative wing sizes of all species, of which more than 12 specimens taken from pitfall-catches were studied, will be presented and discussed. Generally, samples of 50 or 100 individuals were taken at random from the abundant pitfall-catches that were collected during nine years in all kinds of habitat in the neighbourhood of Wijster (Drenthe), The Netherlands [Den Boer 1977: Tab. 3]. The species studied were not selected: at that time our main purpose was to get some idea of the differences between the mean relative wing sizes of the more abundant macropterous and wing dimorphic carabid species [Den Boer-Daanje]. As far as available these data are supplemented now by the relative wing sizes of individuals captured in window traps, i. e. during the act of flying [Van Huizen]. In most species all individuals caught in window traps were studied, only in a few species [e. g. *Bradycellus harpalimus*, *Amara plebeja*, *Amara familiaris*] we had to take random samples from the abundant captures.

¹ postala = wing in further text

² Lindroth [1949], who was the first to carry out such experiments, tried to get accepted such an experimental approach of distributional problems [Lindroth 1953].

3 Results

3.1 Monomorphic macropterous species

In Tab. 1–5 we brought together the data on the relative wing sizes of the 26 macropterous species³ that were studied so far. Because in general ♂♂ and ♀♀ showed about the same relative wing sizes, the sexes are not treated separately. In each table we tried to bring together some species that are closely related taxonomically and show about the same general body shape [only Tab. 4 does not reach this level of comparability, mainly because we also had to accommodate *Notiophilus rufipes*]. As far as possible, we tried to give some indication of the actual difference that may exist between the frequency distribution of relative wing sizes of flying individuals and that of individuals caught in pitfalls by calculating the relevant chi-square value. Because in many cases this value will only be an approximation, we can best trust extreme values, i. e. chi-square values that are far from the critical one (with $p=0.05$).

3.1.1 The oogenesis flight syndrome in *Amara plebeja*

Among these 26 species, only *Amara plebeja* appears to conform completely to the oogenesis flight syndrome [Johnson 1969]: in May (nearly) all individuals have developed their flight muscles and are ready to fly; flying ♀♀ are never fertilized; with the start of reproduction (June) the flight muscles are reduced, and after reproduction they are developed again [Van Huizen 1977]. In this species the oogenesis flight syndrome is apparently connected with a change of habitat: hibernation occurs in deciduous forest and reproduction in grass vegetations. Because nearly all individuals of *A. plebeja* will fly, flying individuals show the same distribution of relative wing sizes as individuals caught in pitfalls (Tab. 1).

3.1.2 Deviations from the syndrome in *Anisodactylus binotatus*

A similar relationship between the distributions of relative wing sizes of individuals captured in window traps and of those caught in pitfalls is found in *A. binotatus* (Tab. 2). Hence, it seems that also in this species in some period(s) of the life cycle nearly all individuals will be able to fly. In spite of the low numbers of individuals studied, this can be postulated, since *A. binotatus* belongs to the five species (out of 80) with the highest catches in window traps. *A. binotatus* deviates from the oogenesis flight syndrome: a high percentage of the ♀♀ captured during flight had already copulated, in other cases the eggs were developing or even ripe. The reduction of flight muscles apparently starts, when the first eggs are ready for oviposition, i. e. have accumulated in the common oviduct. More seldom it starts in some earlier stage already. This is not only a common situation in *A. binotatus* but also in most of the species that will be discussed in the following [see also: Van Huizen 1979].

³ Up to now we were unable to reliably separate all individuals of *Bradycellus collaris* from those of *Bradycellus harpalinus*, because all characters used for identification are highly variable and overlapping. At this moment we can only trust the fully winged *harpalinus*-like individuals. Among the many thousands of such individuals caught in window traps we never saw a *collaris*-like specimen. For the present we therefore will treat the fully winged individuals of *B. harpalinus* with the monomorphic macropterous species. The fact that we are convinced that both fully winged specimens of *B. collaris* and short-winged specimens of *B. harpalinus* exist will not influence our present conclusions.

Tab. 1: Relative wing sizes of individuals of some species of the genus *Amara* Bonelli 1809 caught in pitfalls (continuous sampling) as compared with those of individuals captured in window traps (continuous sampling) [Coleoptera: Carabidae].

Relative wing size	from to	frequency										
		0.71 0.80	0.81 0.90	0.91 1.00	1.01 1.10	1.11 1.20	1.21 1.30	1.31 1.40	1.41 1.50	1.51 1.60	1.61 1.70	
<i>A. plebeja</i> (Gyllenhal 1810)												
window traps												
pitfalls												
<i>A. familiaris</i> (Duftschmidt 1812)												
window traps												
pitfalls											1	
<i>A. lunicollis</i> (Schödte 1837)												
window traps												
pitfalls ^d											1	1
<i>A. brunnea</i> Gyllenhal 1810)												
window traps												
pitfalls								1	4	4	16	
<i>A. equestris</i> (Duftschmidt 1812)												
window traps												
pitfalls			2	1	4	11	18	20	19	16	5	

^dmeasurements by Den Boer-Daanje, Van Huizen and I. Kema (practical work, Agricultura College, Groningen)

Tab. 2: Relative wing sizes of individuals of some species of the genus *Harpalus* Latreille 1802 and of *Anisadactylus binotatus* caught in pitfalls (continuous sampling) as compared with those of individuals captured in window traps (continuous sampling) [Coleoptera: Carabidae].

Relative wing size	from to	frequency										
		1.01 1.10	1.11 1.20	1.21 1.30	1.31 1.40	1.41 1.50	1.51 1.60	1.61 1.70	1.71 1.80	1.81 1.90	1.91 2.00	
<i>H. rufipes</i> (de Geer 1774)												
window traps												
pitfalls												
<i>A. binotatus</i> (Fabricius 1787)												
window traps												
pitfalls												
<i>H. rufitarsis</i> (Duftschmidt 1812)												
window traps												
pitfalls										1	1	
<i>H. fuliginosus</i> (Duftschmidt 1812)												
window traps												
pitfalls										1		
<i>H. 4-punctatus</i> (Dejean 1829)												
window traps												
pitfalls							1			3	6	
<i>H. latus</i> (Linnaeus 1758)												
window traps				1			1	2	3	2		
pitfalls		4	9	17	31	15	13	6	3	1		

1.71	1.81	1.91	2.01	2.11	2.21	2.31	2.41	2.51	2.61	2.71	2.81	2.91
1.80	1.90	2.00	2.10	2.20	2.30	2.40	2.50	2.60	2.70	2.80	2.90	3.00
			2	8	22	23	9	3	3			a
			3	5	21	12	7	2	1	1		a
2	3	2	11	20	29	38	13	8	2		1	b
			7	12	37	21	16	1				b
3	12	83	9	29	30	20	1	2	1			c
			137	153	109	61	11	1				c
22	22	15	1									
			12	4								
3				1								

^a $\chi^2 = 2.42$ (d.f. = 6) $0.90 > p > 0.80$

^b $\chi^2 = 23.60$ (d.f. = 7) $0.005 > p > 0.001$

^c $\chi^2 = 50.56$ (d.f. = 8) $p \approx 0.001$

2.01	2.11	2.21	2.31	2.41	2.51	2.61	2.71	2.81	2.91	3.01	3.11	3.21	3.31
2.10	2.20	2.30	2.40	2.50	2.60	2.70	2.80	2.90	3.00	3.10	3.20	3.30	3.40
						1	4	3	3	6			a
				2	6	4	9	10	7	5	5	1	1 ^a
			10	15	14	4							b
			3	9	8	1	2						b
2	1	1	1	1	6	2	1						c
		6	8	10	13	6	1		1				c
3	5	7	14	11	6	2	1						
7	7	8	1										
			5	2	2	2							
1													
1													

^a $\chi^2 = 9.92$ (d.f. = 5) $p \approx 0.10$

^b $\chi^2 = 1.08$ (d.f. = 3) $p \approx 0.80$

^c $\chi^2 = 4.71$ (d.f. = 5) $p \approx 0.50$

3.1.3 Other deviations from the oogenesis flight syndrome

As far as we know at the moment, in *Harpalus rufitarsis* (Tab. 2) the situation does not deviate fundamentally from that in *A. binotatus*. Possibly in this species there is a weak tendency among individuals with relatively large wings to fly more readily or more frequently than individuals with smaller wings. The same phenomenon seems to occur in *Harpalus rufipes*. Also in *Agonum dorsale*, and especially in *A. sexpunctatum* (Tab. 3), this tendency seems to be indicated. *A. dorsale* is peculiar because in this species at least some, but possibly even many individuals never develop flight muscles. This is the more interesting, since this species shows a change of habitat: reproduction in agricultural fields, and hibernation in waste sites and hedgerows. Because agricultural fields, especially the older ones, are generally bordered by waste sites or hedgerows, the habitat can often be changed by walking, however.

A very convincing difference between the distributions of relative wing sizes of individuals captured in window traps and of individuals caught in pitfalls is found in *Amara familiaris* (Tab. 1). It is evident that in this species, individuals with larger wings are captured more often during the act of flying than individuals with smaller wings. Still in another respect *A. familiaris* clearly deviates from *A. plebeja*: the flying period nearly completely overlaps in time with the breeding period. A high percentage of ♀♀ has already copulated when flying (often with developing or even ripe eggs). Nevertheless also in this species during the greater part of the period in which some individuals deposit eggs, the flight muscles will be reduced to be rebuilt again when reproduction is terminated.

3.1.4 Dimorphism of flight muscles in *Amara lunicollis*

Also in *Amara lunicollis* individuals with larger relative wing size are captured in window traps highly significantly more than individuals with smaller wings (Tab. 1). In our area *A. lunicollis* is a very abundant species in many kinds of grass stands [Den Boer 1977: Tab. 3], especially in heath and peat moor. Den Boer [1971: 129] wondered already why this species with apparently normally developed wings is not caught in high numbers in our window traps. Van Huizen [1979] solved this problem: only about 16% of the individuals caught in pitfalls will develop functional flight muscles during some period(s) of the life cycle (before and/or after reproduction); most individuals will never dispose of flight muscles, however! This is a very interesting phenomenon, because many populations of *A. lunicollis* are living now in habitats that only during the last hundred years (say) have become remarkably stable⁴: dense grass stands [especially *Molinia*] in desiccating peat bog and in formerly wet heath areas that have suffered a considerable lowering of the water table [see also: Den Boer 1977: 67]. We could further show that individuals with flight muscles during some period(s) of the life cycle have significantly larger wings than individuals without: $\chi^2 = 20.11$; d.f. = 6; $0.01 > p > 0.001$ [Van Huizen].

The disappearance of the capability to develop flight muscles is thus distinctly connected with (or followed by) a reduction of wing size, and this sufficiently explains the data presented in Tab. 1.

It is obvious now to suppose that the species discussed in 3.1.3. are in an earlier stage of the same process. This is the more likely because all these species are mainly, but not exclusively [see Den Boer 1977: Tab. 4], occupying unstable habitats. Hence, only some out of many populations

⁴ «Unstable» means that at least in one season during the main period of observation (9 years) survival was impossible in the habitat or in any case reproduction could not occur. When during one or more decennia reproduction could be realized each year (although to a variable extent) the habitat is called «stable» [see further: Den Boer 1977: 33].

Tab. 3: Relative wing sizes of individuals of some species of the genera *Agonum* Bonelli 1809 and *Pterostichus* Bonelli 1809 caught in pitfalls (continuous sampling) or by hand as compared with those of individuals captured in window traps (continuous sampling). [Coleoptera: Carabidae].

Relative wing size	from to	frequency																			
		0.61 0.70	0.71 0.80	0.81 0.90	0.91 1.00	1.01 1.10	1.11 1.20	1.21 1.30	1.31 1.40	1.41 1.50	1.51 1.60	1.61 1.70	1.71 1.80	1.81 1.90	1.91 2.00	2.01 2.10	2.11 2.20	2.21 2.30	2.31 2.40	2.41 2.50	2.51 2.60
<i>A. dorsale</i> (Pontoppidan 1763)																					
window traps															2	3	1	2			
pitfalls												2	7	6	2	6	2		1		
hand-catches												1	3	6	10	5		1			
<i>A. sexpunctatum</i> (Linnaeus 1758)																					
window traps																		1	2	2	
pitfalls									1	1		3	3	8	8	4	4	5	1	1	
<i>P. versicolor</i> (Sturm 1824)																					
window traps													1	3							
pitfalls					1	1	7	16	19	24	18	11	2		1						
<i>A. assimile</i> (Paykull 1790)																					
window traps																					
pitfalls					2	7	21	24	29	11	5		1								
<i>P. oblongopunctatus</i> (Fabricius 1787)																					
window traps											1										
pitfalls			1	3	8	8	8	27	24	14	3	4									
<i>P. niger</i> (Schaller 1783)																					
window traps																					
pitfalls			1	4	6	11	10	22	18	9	9	6	3	1							

will have a relatively low chance of extinction. This means, that only in some (out of many) sites the frequency of individuals being unable to fly away from the population will increase [see further Den Boer 1970, 1977, 1979 a].

3.1.5 The special case of *Loricera pilicornis*

With only one exception, *Loricera pilicornis* (Tab. 4), all other species treated in Tab. 1 to 4 are only caught incidentally⁵, or even not at all (up to now) in window traps. Tietze [1963] already mentioned that he merely saw specimens of *L. pilicornis* in which the flight muscles were fully developed [but he only studied 10 individuals]. Although so far we did not study many individuals from pitfall catches either, we found already that 5 out of 13 specimens, caught during the height of the breeding season, in another than our traditional study area around Wijster [catches of M. Nelemans], showed reduced flight muscles.

On the other hand, we found individuals with fully developed flight muscles both in any part of the reproduction period and outside of it; this is confirmed by the captures in the window traps: both virgin females, fertilized ♀♀ in all stages of reproduction, and ♀♀ after the reproductive phase. Hence, *L. pilicornis* is a good example of a «nomadic» species [Den Boer 1977: 7.6.3.]: Although mainly living in stable habitats, it shows a high level of flight activities throughout the whole life cycle (at least in many places), by which both the individuals and the eggs deposited will be spread out over a large area. Such a behaviour may have the significance of «spreading the risk of extinction» over many individuals (both larvae and adults) which live under very different conditions [Den Boer 1968]. Thus, it should be most effective when large and more or less continuous areas can be inhabited. In accordance with this picture, we did not find any difference between the frequency distributions of relative wing sizes in individuals captured by window traps and in those caught by pitfalls (Tab. 4).

3.1.6 Macropterous species of stable habitats

The remaining species in Tab. 1–4 are mainly living in stable habitats [Den Boer 1977: Tab. 7]. In some of these species, such as *Harpalus fuliginosus*, *Harpalus quadripunctatus* (Tab. 2), *Leisurus rufomarginatus*, *Notiophilus rufipes* and *Nebria brevicollis* (Tab. 4), the low catches in window traps are not sufficiently understood at the moment, because the respective frequency distributions of relative wing sizes do not deviate very much from those of comparable flying species. We know already that many individuals of *N. brevicollis* never develop flight muscles. Thus, we can offer the hypothesis that these species (or at least some of them) show the stage in the reduction of flight capacities following that of *A. lunicollis* (3.1.4): There is already a low frequency of individuals which develop flight muscles in some period(s) of the life cycle, but in which the reduction of wing sizes is still retarded.

One could suggest that this situation might result from a close connection with stable habitats that is still developing in intensity. Thus, *H. fuliginosus* is found in spatially rather dynamical, mosaically structured vegetations in the heath, and the other four species are living in light and rather dry forest where they generally prefer the borders [see also: Lindroth 1945, Den Boer 1977: Appendix A.].

⁵ All individuals of *Harpalus latus* captured in window traps (Table 2), apart from a single specimen caught in 1977 [Van Huizen 1979], were collected in 1979 when some window traps were erected in the middle of a very dense population of this species. Although interesting we think this situation to be rather exceptional.

Species such as *Amara brunnea*, *Amara equestris* (Tab. 1) and *Leistus rufescens* (Tab. 4) could then be considered to have reached a still more advanced stage of the reduction of wing sizes; i.e. they might already be on the road to brachyptery. A similar case seems to occur in *Pterostichus niger* (Tab. 3), but for a quite different reason. *P. niger* is the most eurytopic species in our area [den Boer 1977: 70, Tab. 4 + 7]. Since its individuals are also rather big (16–21 mm), and can thus walk rather large distances, dispersing by flight can hardly be very profitable, not even in the long run. A reduction of dispersal power, as it is found in the last four species, will eventually lead to a kind of brachyptery, as it is shown by *Agonum ericeti* (with relative wing sizes around 0.65).

3.1.7 Some species with apparently too small wings to fly

This, however, meets with the curious situation that some species of small relative wing size do nevertheless show some flight activities, i.e. a few specimens with remarkably small wings are captured in window traps. This occurs in *H. latus* (Tab. 2), *Pterostichus versicolor* and *Pterostichus oblongopunctatus* (Tab. 3).

In *Agonum assimile*, it was observed by Neudecker that such an individual was able to undertake short hopping flights over a few centimeters [Thiele 1977: 292, 293, Fig. 149].

Under special conditions (e.g. starting from a protruding object) such a hopping individual can be imagined to become a flying, or at least a floating one. Hence, in spite of the fact that up to now not a single individual of *A. assimile* was captured in a window trap (Tab. 3), we have good reasons to consider the above flight behaviour of *A. assimile* also to be a model for that of the other three species. Although such a flight behaviour will not enable the individual to actively direct its flight to some stimulus, the ability to disperse passively (like the seeds of e.g. *Acer*) will possibly have been preserved. We can not exclude the possibility that these species are thus escaping from the general selective trend towards brachyptery that was suggested to occur in species occupying stable habitats (3.1.6). However, we prefer to present another hypothesis. If we assume that the ability to build-reduce-rebuild functional flight muscles is somehow genetically determined with an incomplete and/or decreasing dominance structure, an increasing tendency of some Ground Beetles species to occupy more and more stable habitats will set going a directional selective process against this ability [many flying individuals will select themselves away from these habitats], which – after a slow start – can be expected to run fairly fast. This is illustrated by *A. lunicollis* (3.1.4).

As soon as the frequency of the individuals that are still able to develop flight muscles has become low (a few percent, say), however, the speed of this selective process can be expected to slow down substantially by which each further lowering of this frequency will take a progressively higher number of generations [for further reading on this topic, see e.g. Dobzhansky (1970): under «genetic load»]. During this prolonged stage the reduction of relative wing sizes can progress [in 3.2 we will see that the reduction of wing sizes can go on uninterruptedly until very low values are reached]. In this way, in large samples of such a species a few specimens can be expected that dispose of the combination of functional flight muscles and small wings.

Under favourable conditions, such a specimen can apparently be captured in a window trap. In the cases of *P. versicolor* and *P. oblongopunctatus*, conditions are indeed favourable, as far as they belong to the five most abundant species of Carabidae of our study area [Den Boer 1977: Tab. 3]. Moreover, Van Huizen [1979] could show that among 200 individuals of *P. versicolor*, caught in pitfalls during the suitable period, only two specimens disposed of functional flight muscles [relative wing sizes as among captures in window traps: Tab. 3]. Such a low frequency highly supports the above hypothesis! The much lower abundance of *A. assimile* is a sufficient explanation for the lack of window trap catches of this species up to now (Tab. 3). Also *H. latus* (Tab. 2) seems to fit this pattern (see footnote to 3.1.5).

Tab. 4: Relative wing sizes of individuals of *Loricera pilicornis*, *Notiophilus rufipes*, and some species of the tribus Nebriini caught in pitfalls (continuous sampling) as compared with those of individuals captured in window traps (continuous sampling). [Coleoptera: Carabidae].

Relative wing size	from to	frequency										
		1.01 1.10	1.11 1.20	1.21 1.30	1.31 1.40	1.41 1.50	1.51 1.60	1.61 1.70	1.71 1.80	1.81 1.90	1.91 2.00	2.01 2.10
<i>Loricera pilicornis</i> (Fabricius 1775)												
window traps												
pitfalls												
<i>Leistus rufomarginatus</i> (Duftschmidt 1812)												
window traps												
pitfalls										2		4
<i>Notiophilus rufipes</i> (Curtis 1829)												
window traps												
pitfalls									3	1	1	12
<i>Nebria brevicollis</i> (Fabricius 1792)												
window traps												1
pitfalls									3	3	17	32
<i>Leistus rufescens</i> (Fabricius 1775)												
window traps												
pitfalls			6	2	8	8	6	1	4	1		1

Tab 5: Relative wing sizes of individuals of some species of the genera *Bradycellus* Erichson 1837, and *Trichocellus* Ganglbauer 1892, caught in pitfalls (continuous sampling) as compared with those of individuals captured in window traps (continuous) [Coleoptera: Carabidae].

Relative wing size	from to	frequency										
		1.31 1.40	1.41 1.50	1.51 1.60	1.61 1.70	1.71 1.80	1.81 1.90	1.91 2.00	2.01 2.10	2.11 2.20	2.21 2.30	2.31 2.40
<i>B. harpalinus</i> (Serville 1821)												
window traps												
pitfalls												
<i>B. ruficollis</i> (Stephens 1828)												
window traps								3	3	3	10	8
pitfalls		1		1	1	1	1	14	17	24	14	14
<i>T. congnatus</i> (Gyllenhal 1827)												
window traps									1		2	3
pitfalls									1	6	10	11
<i>T. placidus</i> (Gyllenhal 1827)												
window traps									3	1	1	2
pitfalls						3	3	9	10	6	12	5

2.11	2.21	2.31	2.41	2.51	2.61	2.71	2.81	2.91	3.01	3.11	3.21		
2.20	2.30	2.40	2.50	2.60	2.70	2.80	2.90	3.00	3.10	3.20	3.30		
				1	2	5	5	3	1	1			a
				1	2	2	4	3	1	1			a
25	19	15	12	14	6	1	1				1		
12	14	16	14	11	7	5	3	1					
1													
21	14	9	1										

^a $\chi^2 = 0.986$ (d.f. = 5) $0.99 > p > 0.95$

														frequency
2.41	2.51	2.61	2.71	2.81	2.91	3.01	3.11	3.21	3.31	3.41	3.51	3.61	3.71	
2.50	2.60	2.70	2.80	2.90	3.00	3.10	3.20	3.30	3.40	3.50	3.60	3.70	3.80	
		1	6	6	7	24	25	12	20	11	2	1	1	a
1	1	1	4	3	6	8	6	8	4	1			1	a
5	4		1											b
10	2		1											b
2	7	2	2											c
8	4	7	3											c
2	4	2	2	1										d
2														d

^a $\chi^2 = 13.81$ (d.f. = 9) $0.20 > p > 0.10$

^b $\chi^2 = 14.39$ (d.f. = 7) $0.10 > p > 0.05$

^c $\chi^2 = 9.98$ (d.f. = 7) $p \approx 0.20$

^d $\chi^2 = 34.24$ (d.f. = 8) $p < 0.001$

3.1.8 Winter breeders

The species presented in Tab. 5 will be treated separately here, because in our area they reproduce in winter: (Oct.) November up to and including April. *Bradycellus harpalinus* is a special case (see below). The other species inhabit old heath and peat moor [*Bradycellus ruficollis* and *Trichocellus cognatus*], or moist deciduous forest [*Trichocellus placidus*; see also Den Boer 1977: Appendix A]. Although these habitats are permanent, especially in winter breeding conditions are highly unpredictable, however, and in some winters (e.g. 1962/63 and 1978/79) at the more exposed sites reproduction may even be completely impossible. Hence, for winter breeders, these permanent habitats are unstable (compare footnote to 3.1.4), and accordingly we find that flight activities occur frequently [Den Boer 1977]. As in *B. ruficollis* and *T. cognatus*, the distributions of relative wing sizes of individuals captured in window traps do not differ significantly from those of individuals caught in pitfalls (Tab. 5); the degree of instability of winter conditions in heath and peat moor will generally be fairly high.

The causing factors of this instability are not, however, frequent (often yearly) changes in the structural properties of the habitat, as in many spring breeders, but extreme weather conditions. In this respect, winter breeding Ground Beetle species are in a situation that resembles the conditions that have been studied and described (and tested in simulation models) by Thompson et al. [1976] for the Western tent caterpillar [*Malacosoma californicum pluviale* Stehr & Cook 1968 of the Saanich Peninsula, British Columbia]: Accordingly, there exists a permanent habitat (deciduous trees), but highly unpredictable (and often very unfavourable) weather conditions during critical phases of the life cycle.

It is very interesting that *T. placidus* – [although showing the same frequency distribution of relative wing sizes among flying individuals as *T. cognatus* (to which it is taxonomically closely related)] – has already reached a remarkable shift towards lower relative wing sizes among individuals trapped in pitfalls. Extreme weather conditions are apparently sufficiently leveled down by litter and humus layers to make many deciduous forests also reasonably stable in winter. Hence, with a quite different life cycle, *T. placidus* seems to have attained a stage in the reduction of dispersal power that is comparable with that of *A. lunicollis* (3.1.4).

B. harpalinus is peculiar, because in late summer it shows mass flights [Den Boer 1977: Tab. 3], the significance of which is not yet completely understood. During these flight periods, they feed on the seeds of grasses, and can thus easily be swept from grass stands along road sides and at other waste sites. As in our area reproduction mainly occurs in grass vegetations in the heath or at the boundary heath-agricultural fields, there should also be some kind of return flight in autumn. We have indications that this occurs indeed. Further studies on this species are still in progress.

Many ♀♀ of the species mentioned in Tab. 5 appeared to have already copulated before they started flight activities.

3.2. Wing polymorphic and dimorphic species

In our area, the number of wing polymorphic and/or dimorphic Ground Beetle species that can be studied satisfactorily along the above lines, is much lower than that of suitable monomorphic macropterous species. As far as polymorphic species are concerned, this most probably results from wing polymorphism apparently being only a transitional stage, that comparatively easily will change into dimorphism [see also: Lindroth 1949: 339–341]. Nevertheless, there will appear to be some more wing polymorphic species of Carabidae in our area than the three presented in Tab. 6. Most wing dimorphic species in our area have only a very low frequency of macropterous individuals: [Den Boer 1977: Tab. 3]. Among the few exceptions to this, up to now three species have been studied closely enough (together with one of the wing polymorphic

species). They even allow to compare populations of the same species from different kinds of habitat. In spite of the low number of species studied so far, we are convinced that the resulting picture will appear to be a general one for wing polymorphic and dimorphic Ground Beetle species, the more so, because the comparisons within the species illustrate the actual occurrence of the processes that were assumed to support our conclusions.

3.2.1 Wing polymorphic species

In this respect, the frequency distributions of relative wing sizes must be compared in individuals of *Pterostichus strenuus* trapped in pitfalls (Tab. 6) with those of e.g. *A. familiaris* or *A. lunicollis* (Tab. 1), and likewise in *Clivina fossor* (Tab. 6) with those of *B. harpalinus* (Tab. 5). This shows that in wing polymorphic species the frequency distributions mainly deviate, because also very low relative wing sizes are realized. In a number of the macropterous species such an asymmetrical elongation of the frequency distributions to the left is already indicated in e.g. *A. familiaris* (Tab. 1), *H. rufitarsis* (Tab. 2), *P. oblongopunctatus* (Tab. 3).

One gets the impression that in wing polymorphic species two processes do affect relative wing size: On the one hand, there is a distinct tendency towards a reduction of relative wing size, which can even lead to very low values as in *P. strenuus*. On the other hand, there is also an apparent tendency to preserve at least part of the individuals with relatively large wings, and especially such individuals do show – as could be expected – flight activities (Tab. 6). One could imagine such a dualism to occur, if there were also a distinct and lasting dualism in the choice of habitat of wing polymorphic Ground Beetle species: Certain populations are supposed to inhabit stable habitats, whereas others would occupy unstable sites, and the latter in such a way that fully winged individuals from these unstable populations will regularly invade populations in stable habitats. Such a situation is perfectly realized in the case of *P. strenuus*, is all but certain in the case of *C. fossor* [see Den Boer 1977: Appendix A], and is at least probable for the so far only little studied *Bembidion tetracolum* [see: Lindroth 1945].

Under more or less natural conditions, *P. strenuus* inhabits moist deciduous forest in generally sparse populations [Den Boer 1977], and also temporarily occupies certain kinds of artificial, moist grass vegetations. It is often caught there in pitfalls in higher numbers than in the more traditional forest sites. To give an example: From 1972 to 1978 in a pasture were caught: 61, 91, 38, 13, 29, 12 and 6 specimens resp. [Den Boer 1977: 168]. As compared with forest populations, the frequency of individuals with relatively large wings is very high in these temporary ones (Tab. 6). Den Boer [1970: 4.2, Fig. 3] already showed that fully winged «migrants» of *P. strenuus* can be found in many different places. Hence, such «stragglers» can be expected also to have a good chance to penetrate some of the forest populations, and thus to contribute to preserving of the wing polymorphic feature of this species. It seems not very probable that also fully winged specimens from more stable habitats will play an important part in this exchange: Den Bieman dissected 107 ind. of *P. strenuus* from such places (among which about 17% fully winged) and did not find a single specimen with functional flight muscles.

In *C. fossor* a similar situation is found: sparse populations in stable, heath-like sites [Den Boer 1977: 153], and often more dense, but unstable populations in agricultural fields [an example: From 1973 to 1978, in a just abandoned cornfield were caught: 45, 16, 3, 4, 2 and 0 specimens respectively]. Fully winged individuals of this species are flying readily (Tab. 6). Also *B. tetracolum* seems to fit this pattern: sparse populations in light deciduous forest, and denser populations in different kinds of disturbed sites with a weedy vegetation: Den Boer [1977: 145]. From Tab. 6 one gets the impression that in *B. tetracolum* intermediate wing sizes are either selected against or are produced only incidentally; in any case the species is close to becoming a wing dimorphic one.

morphic with an only very low frequency of macropterous individuals (Tab. 7). From Lindroth [1949] it becomes clear that *C. erratus* could only settle down in southern Finland postglacially. Also at present, it is still living there close to the Northern boundaries of its distributional area [Lindroth 1949: 376, Fig. 35], i.e. possibly under not very stable conditions in general.

C. erratus will have been an already older inhabitant in our area when it, presumably from a start at some 3000 years ago, could occupy both rather stable habitats [heath areas that were not very intensively grazed by sheep] and unstable habitats [dry heath areas that were repeatedly overgrazed by sheep and thus became sand-covered]. About hundred years ago, sheep farming on the heath gradually stopped. At the same time, the sand-covered areas were either planted with conifers or became more naturally fixed again by vegetation [Den Boer 1977: 8.1]. Hence, though somewhat speculative, of course, we can postulate that in the recent past in our study area *C. erratus* will have been a wing polymorphic species, which especially during the last hundred years (say) was driven by natural selection into a wing dimorphic stage with a decreasing frequency of macropterous individuals.

In southern Finland, an earlier stage in the reduction of dispersal power would thus have been preserved, possibly by the regular invasions of fully winged individuals showing anemohydrochorous dispersal over the Gulf of Finland [Palmén 1944]. The extensive areas of «wandering dunes» at the south-eastern coast of the Baltic, very unstable habitats, might be a permanent source of such individuals.

3.2.3 The origin of wing dimorphism

When in a wing polymorphic species, the frequency of intermediate wing sizes is decreasing, either because the chance of them to be produced is somehow diminishing, or because they are more directly selected against, the polymorphic species will become a wing dimorphic one by some kind of disruptive selection [see e.g. Thoday 1972; see also 3.2.1: *B. tetracolum*]. In our case, the most probable cause of such a disruptive selection to occur will be a decreasing gene exchange between populations living in stable habitats and those inhabiting more unstable sites. As in most cases, an exchange of genes between populations will nearly completely depend on the extent to which flight activities occur [Den Boer 1977, 1979 a], especially a decline of the number and/or sizes of populations in unstable habitats will start and accelerate such a disruptive selection. If the sources of flying individuals continue to decrease, a directional selection will gradually drive the populations remaining in stable habitats towards brachyptery or at least towards a very low frequency of macropterous individuals (see also 3.2.8).

The three species presented in Tab. 8 are the only wing dimorphic species in which the latter process has not yet progressed very far, whereas also abundant pitfall catches were available for study [see: Den Boer 1977: Tab. 3; Van Dijk 1978]. It is interesting now to note that each of these species tells us a different story that nevertheless fits the above picture.

3.2.4 *Notiophilus biguttatus*

This species of forests (both deciduous and coniferous) shows some preference for the dryer and lighter parts. According to our experiences it is temporarily favoured by local disturbances of the forest, such as storm damage, felling of trees, etc. which leaves the structure of the litter about unchanged but brings more light to the forest floor. During our long-term pitfall samplings this hypothesis was experimentally supported when in December 1963 a coppice-forest was cut down where we had already sampled during two years: in 1964 6 times more individuals of *N. biguttatus* were caught there than before, after which – when the trees were rapidly growing out – the numbers gradually declined again [Den Boer 1977: 162, site AM]. Conspicuously high

Tab. 7: Relative wing lengths of individuals of *Calathus erratus* Sahlberg 1827 in pitfall samples from Wijster (Drenthe, The Netherlands) as compared with those of individuals from Finland, both from population samples and from material drifted ashore at the coast of the Gulf of Finland. [Coleoptera: Carabidae].

Relative wing length	from to	frequencies															
		0.01 0.10	0.11 0.20	0.21 0.30	0.31 0.40	0.41 0.50	0.51 0.60	0.61 0.70	0.71 0.80	0.81 0.90	0.91 1.00	1.01 1.10	1.11 1.20	1.21 1.30	1.31 1.40	1.41 1.50	
Biological Station, Wijster pitfalls					10	61				1	(2)	(2)	(1)				b
Finland [PALMÉN 1944] ^a pitfalls					3	26	32	11	15	12	23	136	142	63	1		
washed ashore														↓	↓		

figures estimated from Fig. 10 (p. 146) in Palmén [1944]

^b because around Wijster fully winged specimens are very rare in this species (0.2 %) some macropterous ind. had to be selected from our collections and added to this samples; these figure are placed in brackets [measurements of Van Huizen].

numbers of *N. biguttatus* were also caught in the experimental fields of the Biological Station, Wijster, after having taken away the pines from a mixed birch-pine forest, as well as after having felled a small pine forest [Den Boer 1977: 162, sites BS and BR].

As in our area large surfaces are covered with coniferous plantations in which such «disturbances» occur repeatedly, of course, on the whole *N. biguttatus* can easily dispose of both stable and unstable habitats, and will thus keep up a high frequency of macropterous individuals. But also the dispersal power of this species would readily be altered by natural selection if major changes in the spatial structure of our area would result in a preponderance of stable habitats. This is indicated by both a higher frequency of brachypterous individuals and smaller relative wing sizes among the macropterous ones in populations inhabiting old forest, as compared with the situation in populations of young forest: Tab. 8. Also in this species the frequency of individuals with functional flight muscles seems to be low [Den Bieman; Van Huizen: 4 among 180 ind.]. Note, that the single specimen with an intermediate wing size (Tab. 8) correctly connects this species with the more polymorphic ones (Tab. 6).

3.2.5 *Calathus piceus*

This species of deciduous forest shows some preference for the borders. It is an amphiatlantic species that obviously settled down in our area comparatively recently. This is concluded from the following data: Before 1860, *C. piceus* was never collected in Western Germany [Horion 1941]. Lindroth [1945] saw some more recently collected specimens from S-Sweden, Denmark and the surroundings of Hamburg, which were all macropterous. Hence, in the areas east and north-east of Drenthe *C. piceus* is a new colonizer. From the faunistic collections of the Museum of Natural History, Leiden [coll. Everts] could be derived, that in the western (45% of 42 ind. macropterous) and central (30–40% of 67 ind. macropterous) parts of the Netherlands *C. piceus* must be an already older inhabitant. In our area (Drenthe), however, we find 93% of the individuals to be macropterous.

For a colonizing species, the relative wing sizes of the macropterous individuals seem to be remarkably low (Tab. 8), however. Also the fact, that during many years of window trap sampling close to a very dense population of this species [BO, see: Den Boer 1977: 149] only a single specimen could be captured (Tab. 8), does not point to a high dispersal power. We therefore suppose, that after a prolonged period of occupying stable habitats in the western and central parts of the Netherlands the relative wing sizes were already reduced to some extent.

Only more recently *C. piceus* possibly extended its distributional area to Drenthe, as shown by the high percentage of macropterous individuals there. The fact that we could not find convincing differences between the frequency distributions of relative wing sizes of individuals from old forests and those of individuals from young forests (Tab. 8) also suggest that most populations in Drenthe are comparatively young.

Den Bieman studied the behaviour of *C. piceus* at the edge of the forest. First of all he found, that in all stages of the life cycle many individually marked beetles will get out of the forest while moving around (they were recaptured along fences that were placed at 5, 10, 15 and 20 m from the edge of forest BO [Den Boer 1977]. The relative wing sizes of 97 specimens trapped outside the forest showed the same distribution as those of 182 individuals caught inside ($\chi^2 = 4.39$, d.f. = 7, $p \approx 0.70$). One is inclined to conclude from this that leaving the forest occurs unintentionally, i.e. the beetles cannot avoid it [compare Baars 1979: concerning the entering of *Molinia*-stands by some species of heath]. As they are found to be able to orientate towards a forest silhouette they can return to the forest again. However, among the individuals trapped outside the forest, the frequency of specimens with functional flight muscles (37 among 97 ind.) was significantly higher than among those caught inside (17 among 182 ind.): $\chi^2 = 33.65$ (d.f. = 1).

$p \ll 0.001$). Hence, individuals with functional flight muscles either tend more to leave the forest than individuals without, or tend less to return to it. At the moment we are inclined to favour the latter hypothesis. In contrast to the situation in *A. lucicollis* (3.1.4) in *C. piceus* individuals without and those with functional flight muscles do show about similar distributions of relative wing sizes ($\chi^2 = 8.32$; d.f. = 6, $p \approx 0.20$). Functional flight muscles can be found in adults in any stage of the life cycle, though most frequently among young adults at the start of reproduction (or just before) in July-August. Even among hibernated adults [while reproducing for a second

Tab. 8: Relative wing sizes of individuals of some wing dimorphic Ground Beetle species caught in pitfalls (continuous sampling) as compared with those of individuals captured in window traps (continuous sampling) [Coleoptera Carabidae].

Relative wing size	from	0.01	0.11	0.21	0.31	0.41	-----	0.91	-----	1.31	1.41	1.51		
	to	0.10	0.20	0.30	0.40	0.50	-----	1.00	-----	1.40	1.50	1.60		
<i>Notiophilus biguttatus</i> Fabricius 1779														
window traps														
pitfalls: young birch forest ^f						9								
pitfalls: mainly old forest						41							1	
<i>Calathus mollis erythroderus</i> Gemminger & Harold 1868														
window traps														
pitfalls: pasture ♂♂ g						25								
pitfalls: pasture ♀♀ g						23		2						
<i>Calathus piceus</i> Marsham 1892														
window traps														
pitfalls: old forest													1	1
pitfalls: young birch forest													1	3
pitfalls: young birch forest ^f						6	2						3	4

1.61	1.71	1.81	1.91	2.01	2.11	2.21	2.31	2.41	2.51	2.61	2.71	2.81	2.91	3.01	3.11	3.21	3.31	
1.70	1.80	1.90	2.00	2.10	2.20	2.30	2.40	2.50	2.60	2.70	2.80	2.90	3.00	3.10	3.20	3.30	3.40	
												1	2	1				a
				2	1	4	3	6	10	13	12	6	4	1	2			a
	1	1			2	6	17	17	24	11	11	6			1			a
					1	3	2	3	2									b
		1	1	1	3	7	11	18	18	20	5	5	1					b
			1	1	7	7	16	21	16	5	3		1					b
				1														
	3	10	6	3	1													c
	8	21	20	9	5	5												d
	20	37	43	40	23	8	4											e

^f measurements of Den Bieman
^g measurements made by M. Oudewesselink as practical work (Agricultural College, Groningen).
the brachypterous specimens were measured by Aukema.
^a $\chi^2 = 56.37$ (d.f. = 12) $p \ll 0.001$
^b $\chi^2 = 15.01$ (d.f. = 8) $0.10 > p > 0.05$ (only macropterous ind.)
only macropterous ind.:
^c compared with ^d: $\chi^2 = 2.48$ (d.f. = 7), $p \approx 0.92$ [Den Boer-Daanje]
^d compared with ^e: $\chi^2 = 9.39$ (d.f. = 7), $p \approx 0.50$
^c + ^d compared with ^e: $\chi^2 = 13.00$ (d.f. = 7) $0.05 < p < 0.10$

time in spring, see also Den Boer 1979 b] a few specimens with functional flight muscles can still be found, so that one is inclined to suppose that some individuals will keep their flight muscles during the whole of their adult life. By performing some flight experiments Den Bieman could show that at least part of the individuals with functional flight muscles can be stimulated to fly (relative wing sizes: 1.91, 2.02, 2.06, 2.63).

Hence, in *C. piceus* dispersal seems to be an important population phenomenon, though it could not yet be shown that this also implies a high dispersal power. On the one hand, this dispersal will inevitably result from the preference of *C. piceus* to inhabit the borders of forest, on the other hand the behaviour of individuals with functional flight muscles does especially point towards a more directional dispersal process. The latter phenomenon may be another indication that also in Drenthe *C. piceus* is still a colonizing species, i.e. a species in which dispersal is a quantitatively important or even predominant process, that will often involve a raised degree of instability of the populations concerned. Note, that such instability of populations need not necessarily imply instability of the favoured habitat, as was assumed by Southwood [1962]; compare e.g. the Western tent caterpillar [Wellington et al. 1975].

3.2.6 *Calathus mollis erythroderus*

Shortly before 1972, this species must have settled down in Drenthe as a new colonizer: in spite of sampling carabids from 1959 onwards in many different sites [Den Boer 1977] not until 1973 we could establish the presence of *C. m. erythroderus* in our area: Van Dijk (1978). In all cases observed by us *C. m. erythroderus* settled down in one of the few populations of *Calathus melanocephalus* that occupy unstable sites in our area: recently abandoned agricultural fields. The exact taxonomic status of these mixed populations (degree of interbreeding between these very closely related species) is studied now by Aukema.

In Drenthe, *C. m. erythroderus* is a wing dimorphic species with only 10–25% of the individuals short-winged. It reproduces in September–Oktober, and when breeding the flight muscles are autolysed. Flight activities occur before breeding, in July–August. As walking activities are low in this period (the same as in the related *C. melanocephalus*), so far we could only dissect low numbers of pre-reproducing adults caught in pitfalls. We could nevertheless make plausible that during this period functional flight muscles are generally built up [Aukema]: in at least 37% of these individuals they were already developed. In this respect, *C. m. erythroderus* seems to resemble *A. plebeja* in conforming to the oogenesis flight syndrome (3.1.1); this conformity is not complete, however: among 11 specimens captured in window traps (Table 8) a single female had already copulated and started the development of eggs. As could be expected for a colonizing species (see also 3.2.7), we have indications that the populations of *C. m. erythroderus* are unstable in our area and will disappear again after a number of years from sites that seem to be still suitable for reproduction (this is studied further).

3.2.7 On the genetical background of wing dimorphism

Many of the conclusions of Lindroth [1949] were based on the assumption that in wing dimorphic Ground Beetle species «short-winged» would be a single, dominant character, «long-winged» individuals, consequently, being simple homozygotes. This assumption was supported by a breeding experiment with *Pterostichus anthracinus* [Lindroth 1946], which produced 25 specimens from a single short × short cross: 18 short-winged and 7 long-winged individuals. An about similar result was reached by Jackson [1928] from extensive breeding experiments with the weevil *Sitona hispidulus* (Fabricius 1776). Although in many dimorphic species of

Carabidae, this assumption of Lindroth [1949] was in concordance with the distributional patterns of the wing forms, we thought it necessary to study this critically in other members of that family.

This point was taken up by Aukema in *C. m. erythroderus*: from six crosses between most probably heterozygous, short-winged parents, respectively 34, 30, 28, 18, 30 and 34 F₁-individuals were obtained. None of these progenies did deviate significantly from the expectation 75% short-winged/25% long-winged. Taken together, 44 F₁-individuals (25.3%) among 174 were long-winged ($\chi^2 = 0.0077$; $0.95 > p > 0.90$); males and females gave about similar results. More about these experiments will be published separately. Hence, we could strongly support the above assumption of Lindroth [1949].

As the numbers of brachypterous individuals from the crossings of Jackson [1928] were somewhat higher than theoretically expected (312 short-winged ind. instead of 291, among 473, which is narrowly significant at $p = 0.05$), Darlington [1943] concluded that brachypterous individuals of a wing dimorphic (carabid) species should have a higher «viability» than macropterous ones. From the crossings of Aukema short-winged specimens hatched in exactly the theoretically expected numbers, however, so that a supposed «higher viability» of brachypterous individuals does at least not become apparent during any stage of the development from egg to adult under optimal conditions. Therefore, as long as no better data about a «higher viability» of short-winged individuals are available, we keep our conclusions parsimoniously by assuming with Darwin [1859] and Lindroth [1949] that in many wing poly(di)morphic populations long-winged individuals will only be selected against significantly, if it can be shown (or at least made plausible) that some (or many) of them will fly away (see: Introduction). Such a selection will be especially effective, of course, if the populations concerned are fairly stable and inhabiting more or less isolated sites. Under such conditions other processes that prevent macropterous individuals from flying away, e. g., loss of the capability to build flight muscles, will be favoured, too. In the foregoing sections we tacitly accepted this assumption (see further section 4).

3.2.8 Wing dimorphic species with a very low frequency of macropterous individuals

In 3.2.3 we discussed how by some kind of disruptive selection a wing polymorphic species can be transformed into a wing dimorphic one. Such a process will especially take place, if the frequency of individuals flying away from unstable populations and arriving in more stable ones, is decreasing. The decrease of such individuals will not only be favoured by the direct disappearance (reclamation) or the becoming stable (lowering of the water table, regulation of brooks and rivers, fixation of blowing sands) of unstable natural habitats, but also by the drastic reduction and splitting up of more stable, suitable sites, by which the chance of dispersing individuals to settle down in any of the remaining stable populations will generally significantly be lowered. If we may conclude from 3.2.7 that in the long run in most (or even all) wing dimorphic carabid species «long-winged» will become a recessive character, together with the above processes this might have already driven many wing dimorphic species towards a very low frequency of fully winged individuals, i. e. a frequency that is mainly prevented from becoming zero by a low, but continuous production of recessives.

Among 26 wing dimorphic Ground Beetle species [Den Boer 1977: Tab. 3] 12 show a frequency of macropterous individuals that is below 3%. With only two exceptions, they nearly exclusively occupy stable habitats [Den Boer 1977: Tab. 4.] Among those 12 species, which are monomorphic brachypterous in our area, at least four are wing dimorphic with a very low frequency of fully winged specimens in other parts of their distributional range. On the other hand, only nine of the wing dimorphic species [Den Boer 1977: Tab. 3] have more than 20% of the in-

dividuals long-winged. Accordingly, the recessiveness of «long-winged» could actually be proved in *C. m. erythroderus* (3.2.7). Thus, most species fit (at least in some way) the general pattern described (3.2.1, 3.2.4, 3.2.5; Tab. 6, 8).

Among wing dimorphic species of Carabidae, it apparently is a very common (if not general) phenomenon, that «short-winged» is a dominant character. Contrary, long-winged individuals are recessive homozygotes. One of the basal assumptions of Lindroth [1949] could thus be supported after thirty years.

4 Conclusions and discussion

The data presented in this paper give strong evidence in favour of the hypothesis that in Carabidae the dispersal power of species is predominantly determined by natural selection. This evidence mainly originates from the fact that the necessary gene flow is here obvious: Individuals which fly away from the population are taking away genes associated with a high dispersal ability. This flow of genes is very distinct: At least during their first reproductive season, the expectancy of life of adult beetles staying in the population is very high in many species [Baars 1979, Den Boer 1979b, Van Dijk 1979]. Also, the chance of an egg to develop into an adult is apparently similar for both short-winged and long-winged individuals, at least in the case of *C. m. erythroderus* under optimal conditions (3.2.7). The chance of an individual, however, which flies away from a population to reach another site suitable for survival and reproduction will often be low. This is above all because most Ground Beetles are weak flyers, their direction of flight being highly influenced by wind [Lindroth 1949: 579, Den Boer 1970]. This means, that in most cases the number of individuals flying away from a completely or largely macropterous population will be higher than that flying in from elsewhere. This will be the more evident, of course, if isolated sites are inhabited by the starting-population. The evolutionary significance of such an unambiguously directed flow of what we call genes today, has already been recognized by Darwin [1859]. This also means, however, that a sufficient dispersal power will only be maintained by a Ground Beetle species, if new populations (in which predominantly – or even exclusively – genes favouring high dispersal abilities will be produced) can be founded regularly, i.e. if at least part of the populations is only shortlived, for instance because they occupy unstable habitats. Or the other way round, as soon as most populations do survive longer than usual, for instance because many habitats have become more stable (or many of the unstable habitats have disappeared), selection against features favouring a high dispersal power will become inevitable [Den Boer 1977].

In Fig. 1, data on the relative wing sizes of the more interesting species are arranged in such a way that these species are suggested to represent successive stages of the evolutionary process that can be imagined to result from an increasing intensity and/or an increasing period of operation of the above selective forces.

At the upper left, *A. plebeja* is pictured as a kind of null-case for this evolutionary process: Each year the populations disappear from the unstable reproduction habitats (3.1.1). As this occurs by flying, any selection that favours a lowering of dispersal abilities will be prevented (Tab. 1). This is also likely in *A. binotatus* (3.1.2; Tab. 2), though possibly less extremely so, whereas it will undoubtedly apply to the winter breeder *B. harpalinus* with its mass flights, and perhaps even to *B. ruficollis* and *T. cognatus* (3.1.8; Tab. 5). All these Ground Beetle species, together with a number of others belong to what is called «migratory insects» by many entomologists [e.g. Southwood 1962, Johnson 1969, Dingle 1972, Den Boer 1979a].

H. rufitarsis (3.1.3; Tab. 2) might represent such species in which a first sign of weak selection against a high dispersal power becomes apparent, in this case – just as in *A. 6-punctatum* (Tab. 3) – because a few populations obviously continue to stay in more stable sites [Den Boer, 1977:

138, 157]. Whether or not some individuals of these species have already lost the ability to develop flight muscles, as it was found to occur in *A. dorsale* (3.1.3), remains to be investigated. A better documented case of this first selection stage is found in *A. familiaris*, a species which shows a high level of flight activities [Den Boer 1977: Tab. 3] and predominantly lives in unstable habitats, but nevertheless already shows a significant reduction of relative wing size (Tab. 1). Therefore, this species distinctly illustrates that some reduction of wing size can occur rather easily, most probably because wing size is determined by a number of genes: In different combinations, they may additively have the effect of a smaller or greater reduction of wing size. This hypothesis of a polygenic determination not only makes clear that some reduction of wing size may readily follow an uninterrupted stay and reproduction during a number of generations in some sites, but it shows also that such a reduction will proceed if these conditions become more general and/or prolonged. This is convincingly shown to apply in *A. lunicollis* (3.1.4), and it seems to give the only plausible explanation for the continued reduction of wing sizes in the species that are arranged in Fig. 1 below *A. lunicollis*, and which predominantly inhabit more or less stable habitats (3.1.6, 3.1.7).

We also need this hypothesis to understand how wing polymorphic species may originate: If species in a stage such as *A. familiaris* or *A. lunicollis* arrive in a situation in which not only

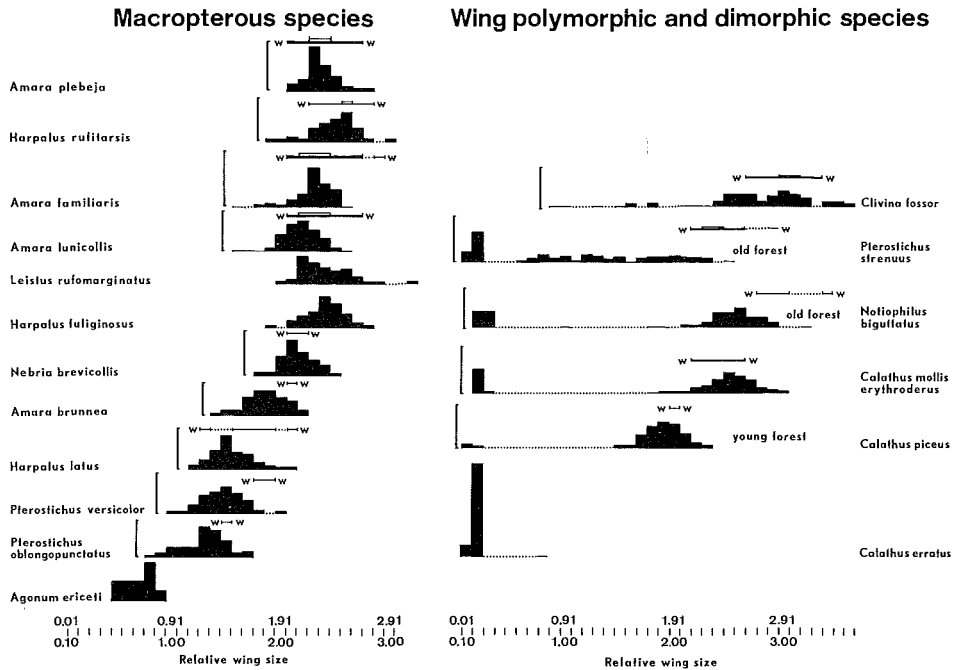


Fig. 1: Proportional frequency distributions of relative wing sizes in samples of Ground Beetles caught in pitfalls [in section 3 these species were discussed; in Tables 1–8 the actual numbers of individuals caught are presented], Above each distribution the range of relative wing sizes of individuals captured in window traps is indicated between two types «w» [actual numbers in the Tables 1–8]. The species are arranged in such a way that from the top downwards [and to the right] this figure about pictures the kind of processes that is thought to run if species of unstable habitats also increasingly change over to occupy more stable sites. The species presented are supposed to be in different stages of these processes [Coleoptera: Carabidae].

many populations can be maintained in stable habitats, but also regularly and successfully can reproduce in unstable sites, both the reduction of wing sizes will proceed (stable habitats) and the production of individuals with large wings and high dispersal abilities will continue (unstable habitats). As long as fully winged individuals also sufficiently settle down in the more stable populations, a very broad range of relative wing sizes may be maintained, as it is actually found to occur in *P. strenuus* and *C. fossor* (Tab. 6; 3.2.1 and right part of Fig. 1).

In 3.2.3 we already explained how such a polymorphic species can become a wing dimorphic one, if the input of genes, associated with large wings and a high dispersal power, into the more stable populations, decreases. In such a situation, a disruptive selection will start [Mather 1955, Thoday 1972] which gradually separates the fully winged populations in unstable habitats from the populations with reduced wing sizes in the more stable sites. As this disruptive selection is based on a decrease of exchange between stable and unstable populations, it will either result from a decline — or becoming more stable — of the unstable populations, or from a drastic reduction of the area inhabited by — or a becoming unstable of — stable populations, or from both. In all cases the most probable outcome will be that in the long run one of the groups will disappear (*N. biguttatus* (3.2.4) may be an exception). In our cultivated countryside this will often be the group occupying unstable sites (see: 3.2.8), though in *C. mollis erythroderus* (3.2.6) and possibly also in *C. piceus* (3.2.5) it seems to have been the other group; in *C. piceus* the process of reduction of dispersal power perhaps has just started anew, at least in Drenthe (3.2.5). Especially if the two groups of such a dimorphic species have also become geographically separated there is a chance that two species will arise, a macropterous or nearly macropterous species inhabiting unstable sites and a brachypterous or nearly brachypterous one (see 3.2.8) occupying more stable habitats. Such a process may have been the origin of *C. melanocephalus* (in Drenthe: 0.23% of ind. fully winged; stable sites) and *C. mollis* (still macropterous in many parts of its range, especially *C. mollis mollis* of the unstable sea-dunes). In *C.m. erythroderus* [3.2.6 and Lindroth 1949: 368–370] this process is apparently started anew.

The above disruptive selection apparently also has the effect of concentrating the polygenes determining wing size in such a way that in a true wing dimorphic species an individual will either be long-winged or short-winged. The segregation of this genetic difference becomes so complete that in crossings these characters divide according to simple Mendelian ratios with «short-winged» dominant (3.2.7). Such an origin of a distinct polymorphism from disruptive selection was already suggested by Mather [1955]; see also: Thoday [1972]. Our data on carabid beetles are especially interesting because we could apparently trace different stages of this process in natural populations, in the case of *C. erratus* (3.2.2) even the two extremes within the same species.

It is not quite clear how firmly the capability to develop flight muscles is connected with larger wings. In *A. lunicollis*, some connection is evident (3.1.4), but only part of the individuals with large wings develop flight muscles. In most species pictured in Fig. 1, the individuals captured in window traps have large wings as compared with the majority of individuals caught in pitfalls. This induces the conclusion that among individuals with relatively large wings the ability to develop flight muscles will usually occur more frequently than among individuals with smaller wings. However, especially among the macropterous species such a connection apparently is not a very deterministic one.

It seems plausible to assume, that during the process of disruptive selection which gives rise to wing dimorphic species, at least initially also the capability to develop flight muscles will become associated with the «super-gene» that determines «long-winged». So far, functional flight muscles proved to occur only among the fully winged individuals of dimorphic species, but in many cases only in a few ind. (e.g. in *N. biguttatus*: 3.2.4). Apparently, the ability to develop flight muscles, which seems to be still a more or less general feature of the long-winged individuals of *C.m. erythroderus* (3.2.6), can be lost again for the greater part among the macropterous individuals of other dimorphic species. In *C. piceus*, this process has already progressed well:

19% of 279 macropterous individuals had functional flight muscles [Den Bieman]. These, however, showed a kind of behaviour that seems to be significant to lead to flight activities (3.2.5), so that in our area dispersal may still be important in this species. The fact that in *C. piceus* the frequency distribution of relative wing sizes of macropterous individuals is the same for specimens with and without flight muscles (3.2.5) may mean that this variance mainly results from differences in the expression of the supposed «super-gene» for «long-winged». The same might apply to *C. m. erythroderus*. Accordingly, in both species the distributions concerned do not deviate importantly from a normal one.

If in wing dimorphic species the ability to develop flight muscles would indeed be associated with the «super-gene» for «long-winged», it might be supposed to be a recessive character. This is supported by the fact that also among some macropterous species – especially *P. versicolor* (3.1.7) – several indications point into the same direction. Hence, in some groups of macropterous species also genes favouring large wings may have a tendency to be (or become) recessive. In neglecting the systematic position of the species pictured in Fig. 1, an evolutionary process can approximately be reconstructed that will have occurred several times among Ground beetles, and which via a wing polymorphic stage or not, will have led to brachypterous or nearly brachypterous species. Whenever Ground Beetle species, inhabiting unstable sites, in an increasing degree also occupy more stable habitats, such a process will have become almost inevitable. As long as suitable stable habitats were more or less uninterruptedly available over extensive areas, this process will hardly have endangered the survival of the kind of Ground beetles concerned. The lowered dispersal power namely will still have been sufficient to (re)populate sites where the species became extinct. In many cases it will moreover have stimulated speciation. It may thus have been one of the causes for development of the high number of species of Carabidae [Thiele 1977]. Besides, in different stages of this process, there still will have been a way back towards an increase of dispersal power. Possible examples are *C. piceus* (3.2.5) and *C. m. erythroderus* [Lindroth 1949: 308–310; Fig. 28].

Also *P. strenuus* (3.2.1) may have changed from a wing dimorphic into a wing polymorphic species, when man took away most of his stable (forest) habitats, and in many places replaced them by unstable, but also suitable pastures and meadows. Even some wing dimorphic species with a low or even very low frequency of fully winged specimens were still able to found populations with a high percentage of macropterous individuals in the new IJsselmeerpolders [Den Boer 1970: *Trechus obtusus*, *Pterostichus melanarius*, *Dyschirius globosus*, *Calathus melanocephalus*].

However, if these extensive, stable areas disappear for the greater part, whereas the remaining habitats are cut up in small pieces, as it occurred in many places by the activities of man, this will result in an accelerated extinction of the majority of the brachypterous and nearly brachypterous species inhabiting these remnants of natural habitat. This topic is treated extensively in Den Boer [1977, 1979 a]. We may only hope that some of the species of unstable habitats will thus extend their distributional area, as it occurred already in *Amara ingenua* and *Amara majuscula* [Lindroth 1949, 1972; Den Boer 1962], and in the long run possibly evolve into new species. We think that in the past comparable large-scale processes already occurred several times [Den Boer, 1977, 1979 a]. It was a great merit of Lindroth [1949] that he tried to reconstruct one of these processes, the postglacial colonization of Fennoscandia by Ground Beetles. We could show in this paper that his assumptions were sufficiently justified, though also in this case, nature appeared to be more complicated than was supposed initially.

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Bei einigen Carabidae-Species aus der Niederländischen Provinz Drenthe wird die relative Flügelgröße von Individuen, die in Fensterfallen gefangen wurden, mit derjenigen anderer Individuen verglichen, die aus Bodenfallen stammen. Es zeigen sich Beziehungen zwischen der Flugfähigkeit dieser Tiere und der ökologischen Stabilität der von ihnen bevorzugten Lebensräume. Befunde über die Rückbildung der Flugmuskulatur, den Reifungszustand der Ovarien fliegender Weibchen und die genetischen Grundlagen des Flügel-dimorphismus zeigen, daß die Ausbreitungsfähigkeit der untersuchten Carabidae-Species vorwiegend durch natürliche Auslese bestimmt wird. Davonfliegende Individuen tragen Gene für hohe Ausbreitungsfähigkeit aus der Population heraus. Je stabiler die bewohnten Lebensräume sind, desto stärker wird die Flügelgröße und die Fähigkeit, Flugmuskeln aufzubauen, durch die natürliche Auslese reduziert. Wenn eine Art stabile und instabile Lebensräume bewohnt, kann sie einen Flügelpolymorphismus entwickeln, der sich wieder zum Flügel-dimorphismus ändert, wenn die Bedeutung der instabilen Habitate zurückgeht. Diese disruptive Auslese trennt nicht nur langflügelige und kurzflügelige Populationen voneinander; auch die die Flügelgröße bestimmenden Gene werden derart gesondert, daß «kurzflügelig» eine einfache dominierende Eigenheit wird und langflügelige Individuen demnach nur homozygot sein können. Sowohl makroptere als auch flügel-dimorphe Populationen entwickeln sich immer wieder allmählich zu brachypteren, wenn die bewohnten Lebensorte zunehmend stabil werden.

Rechenberg, I.: **Evolutionsstrategie.** – problemata. Verlag: frommann – holzboog. Preis: DM 28,-. Der Autor stellt eine Strategie vor, die eine optimale Imitation der Evolution für technische Mechanismen zum Ziel hat. Somit wendet sich die Monographie primär an den Ingenieur. – Die verbale Beschreibung des Evolutionsvorganges durch den Biologen ist für die technische Übertragung unzureichend. Der Techniker benötigt ein Programm technisch realisierbarer Befehle auf mathematischer Basis. Hierzu wählt Rechenberg aus der Vielzahl von Evolutionsfaktoren das Mutations-Selektionsprinzip aus. So diskutiert er zunächst eine vereinfachte technische Nachahmung und dann Strategien höherer Nachahmungsstufen der biologischen Evolution. Im Theorieteil zeigt er die Konvergenz des Mutation-Selektionsverfahrens, deren Fortschrittgeschwindigkeit anhand eines Korridor- und Kugelmodells und vergleicht sie mit der Gradientenstrategie. – Umgekehrt erfährt der Biologe ein mathematisches Modell, das ihm als Ansatz für die quantitative Durchdringung des Evolutionsgeschehens dienen kann. Die Erkenntnis, daß der natürlichen Selektion eine physikalisch begründbare Wertsteuerung zugrunde liegt, macht deutlich, daß es auch eine systeminhärente Strategie der Optimierung geben muß.

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