

D. Johan Kotze · Robert B. O'Hara

Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe

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Abstract We investigated some of the causes of ground beetle decline using atlas data from Belgium, Denmark and the Netherlands, countries in which natural environments have all but disappeared. We used ordinal regression to identify characteristics that are significantly correlated with the decline of carabid beetle species over the last 50–100 years, using a stepwise selection procedure to select the optimal model according to the Akaike Information Criterion. The results showed that large-bodied carabid populations have declined more than smaller ones, possibly because of their lower reproductive output and lower powers of dispersal. Habitat specialist populations (i.e. species with small niche breadths) have also decreased more than habitat generalist populations. Species with both long- and short-winged individuals have been less prone to decline than those that are exclusively either short-winged or long-winged. Dimorphic species may survive better in highly altered environments because long-winged individuals are good at dispersing between suitable habitats and short-winged individuals are good at surviving and reproducing in these newly colonised habitats. Finally, populations of large carabids associated with coastal, woodland or riparian habitat types were less prone to decline than populations of large carabids associated with various, open or grassland habitat types. The pattern is reversed for carabid species smaller than 8 mm in size. These results are explained in the context of habitat restoration and destruction in these highly modified western European countries.

Keywords Carabidae · Extinction risk · Western Europe · Body size · Specialisation

Introduction

Species are buffeted by a myriad of forces: human interference, interspecific interactions (such as predation, parasitism and competition), changes in the environment, and pure bad luck (Pimm 1991; Simberloff 1994; Rosenzweig 1995; Gaston and Blackburn 1995, 1996; Baur and Schmid 1996; Davies et al. 2000). How a species responds to these forces depends in large part on its own characteristics. It has been shown that extinctions are not random with respect to either geography (Myers et al. 2000; Pimm and Raven 2000; Regan et al. 2001) or phylogeny (Purvis and Hector 2000; Purvis et al. 2000) but neither of these can provide general explanations of what places an individual species at risk. It is therefore necessary to study ecological and morphological traits to understand why some species go extinct whilst others survive in the same region (see Moyle 2000).

Body size and specialisation have both received considerable attention as predictors of risk (McKinney 1997). The effect of body size depends on population size, with larger-bodied species believed to be less prone to extinction at low population sizes but more prone at high numbers compared to small bodied species (Pimm 1991; Gaston and Blackburn 1995; Moyle 2000). Specialisation is seen as being simpler in that specialist species are usually more prone to extinction than generalists at all population sizes (Pimm 1991; McKinney 1997).

The possible reasons for declines of ground beetle (Carabidae) populations in Europe have been studied before. Turin and Den Boer (1988) showed that changes in land use in the Netherlands since 1880 have changed the carabid fauna, favouring those that are able to disperse better and tolerate agricultural environments. Desender and Turin (1989) examined data from Belgium, Denmark, the Netherlands and Luxembourg and showed that in these countries carabid species decreased in range size if

D. J. Kotze (✉) · R. B. O'Hara
Department of Ecology and Systematics,
Division of Population Biology, P.O. Box 65, Viikinkaari 1,
00014 University of Helsinki, Finland
e-mail: johan.kotze@helsinki.fi
Tel.: +358-9-19157707
Fax: +358-9-19157694

R. B. O'Hara
Rolf Nevanlinna Institute, P.O. Box 4,
00014, University of Helsinki, Finland

they were specialists, at the edges of their distribution area, or were inhabitants of dry biotopes such as heathlands, dunes and poor grasslands. These studies, however, failed to investigate how the interactions (see Tracy and George 1992) between these variables influence the probabilities of carabid extinction. For example, although poorly dispersing species may be more prone to extinction than well dispersing species, it is unclear whether this is because of differences in dispersal ability or because large-bodied carabid species are usually short-winged (Lindroth 1985). They also did not investigate the influence of body size, which has been shown to be a powerful predictor of the risk of extinction (Gaston and Blackburn 1995).

The aim of this study is to test the effects of, and interactions between, eight beetle characteristics, including body size and carabid phylogeny, on the changes in carabid status in Belgium, Denmark and the Netherlands over the last 50–100 years. This is a relatively short time scale, and the changes will probably reflect reactions to recent changes in the environment due to changes in human land use. Specifically we test the following predictions:

1. Large-bodied carabids have declined more than small-bodied carabids.
2. Carabid specialists have declined more rapidly than generalists.
3. Wing dimorphic species (with both long-winged and short winged individuals in the same species) have declined less than either macropterous (long winged) or brachypterous (short winged) species.

The reason for postulating an advantage of wing dimorphism is that in a contemporary world with frequent and large-scale human disturbances it provides the best of two worlds. Long wings enable a beetle to disperse better (as short winged beetles have to disperse by walking), but incur a high cost in terms of building the machinery of flight, and then of using this machinery. Habitat heterogeneity has favoured the evolution of a wing dimorphism in plant hoppers, where flight-capable males locate females more frequently in sparse vegetation, whereas flightless males of the same species find females more often in contiguous vegetation (Langellotto and Denno 2001). Some beetle species have also adapted to living in variable environments, having evolved the capability of absorbing and regenerating flight muscles (Robertson 1998; Desender 2000). Indeed, the proportion of flightless individuals increases with increasing habitat persistency and time since colonisation in a number of dimorphic carabid species (Den Boer et al. 1980). For example in *Pterostichus melanarius*, a carabid introduced into Canada, long winged forms colonise new areas, and then the populations shift towards more short-winged individuals as the populations get older (Niemelä and Spence 1991, 1999).

Materials and methods

The data and statistical analyses

Data

In order to investigate factors affecting the declines in carabid beetle assemblages, we used data from comprehensive carabid atlases for Belgium (Desender 1986), Denmark (Bangsholt 1983) and the Netherlands (Turin 2000), supplemented where necessary with information from Lindroth (1985, 1986), Turin and Den Boer (1988), Desender and Turin (1989) and Turin (1990). We obtained information on the area occupied by each species within each country, whether the species is at the edge of its range in the country, degree of ecological specialisation, habitat association, environmental tolerance, body size, wing form, the tribe that the species belongs to, and the status of the species in the country (Table 1).

Range size

For our purposes, we defined range size as the area occupied by a species. This was measured towards the end of the assessment period, as the number of 10×10 km (9 km×8 km in Denmark) grid cells in which the species had been observed.

Range position

Carabids were defined as being either in the centre or edge of their range visually by using the European distribution maps in Turin (2000), and from range central-range edge classifications in the carabid atlases. A carabid species was classified as a range edge species when the edge of its European distribution was within the country investigated (see Fig. 2 in Hengeveld and Haecck 1982), otherwise it was classified as being range central in that country.

Specialisation

Beetle ecological specialisation was defined by Dufrière and Legendre (1997) as lying along a continuum from strict specialist (species with small niche breadths occurring in only one or two habitat types) to extreme generalist (species with wide niche breadths occurring in a variety of habitat types). In the atlases, this scale was split into five categories (Table 1), but speciality was treated as a continuous variable in the analyses.

Habitat association

We used six habitat classifications (Table 1). These associations were broad, with each classification potentially covering a variety of habitat types.

Environmental tolerance

We recorded whether a species could tolerate anthropogenic environments, as changes in land use are largely related to changes in human activity.

Body size

Body size was recorded as the mean length of the beetle species, in millimetres.

Table 1 Carabid characteristics used in the analyses. Status categories were measured differently in the different countries. In Belgium, range size changes (beetle status) were determined using both records of species and grid cell occupancy, while range size changes in Denmark and the Netherlands were determined using grid cell occupancy only. winged individuals)

Beetle characteristics		Environmental tolerance ^c			
Range position ^a	Specialisation (S_G)	Habitat	Body size (in mm)	Wing form	Number of tribes
Central species	Strict specialist	Habitat 1, Woodland	From 1.8 mm	Macropterous	Belgium =27
Edge species	Average specialist	Habitat 2 ^b , Many	(<i>Tachys bistriatus</i>)	Dimorphic	Denmark =26
	Average specialisation	Habitat 3, Open	to 34.6 mm	Brachypterous	The Netherlands =27
	Extreme generalist	Habitat 4, Grassland	(<i>Carabus coriaceus</i>)		
		Habitat 5, Riparian			
		Habitat 6, Coastal			
Carabid status ^d					
Belgium (n =366/379)		Denmark (n =293/314)	The Netherlands (n =374/380)	Explanation	
Code	Explanation	Code	Code	Explanation	
II	Increase in records and grids	+	I	Increase	
I	Increase in records	*	=	No change, stagnant	
S	Stagnant	=	D	Decrease in parts of the area	
D	Decrease in records	1	Dd	Definite decrease	
DD	Decrease in records and grids	2	DD	Decrease in whole area	
		3	DDD	Strong decrease in whole area	
		4	E	Possibly extinct in the country	

^aThe Range Central category includes species with an even distribution within the country in question, while the Range Edge category includes species with a marginal distribution into the country in question.

^bHabitat category 2, Many, includes species with a wide range of habitat preferences

^cThe environmental tolerance category distinguishes between beetles that cannot tolerate human environments (Natural) and those who can (Human)

^dThe *n* values represent the number of species for which status data were available / total number of carabid species in the country. Note that different status categories were available for the different countries studied

Wing form

We defined three wing forms. Macropterous species are those with only long wings, brachypterous species have short or no wings, and dimorphic species are those in which both short and long winged forms have been recorded. We assume that flight capability, and therefore dispersal ability, is a function of carabid wing form (Lövei and Sunderland 1996). Macropterous and dimorphic species are likely to be better dispersers than brachypterous species. Although this seems to be a reasonable assumption to make, some carabids with full wings do not necessarily possess functional flight muscles (Den Boer et al. 1980; Lindroth 1985, p 19; Desender 2000).

Phylogeny

As phylogeny has been used to predict extinction risk, this was included in the analysis. The known carabid phylogeny is rather sketchy (see Maddison et al. 1999), so instead we used the tribe of a species as a factor as a measure of phylogeny. This is clearly an approximation, as it does not include any information about the phylogenetic distance either within or between tribes, so is a compromise between not including phylogeny and incorporating information in the analysis that may not be reliable. From a biological perspective, genus might have been a better factor to use, as genera are relatively free of phylogenetic constraints (Harvey and Pagel 1991). However this would have had between 56 and 67 levels, and so would receive an extremely large penalty in the model selection procedure, as well as becoming confounded with other factors and interactions.

Status

Population status categories were measured differently in the different countries. In Denmark and the Netherlands, the changes in status were in range size (which was measured as the number of grid cells occupied), whereas in Belgium the changes were a combination of change in range size and abundance (measured as the number of records of the species). For our purposes, a decline in a population therefore principally means a contraction of the species' range, but may also include a reduction in abundance.

The numbers of categories also differed, from five in Belgium to seven in both Denmark and Holland (Table 1). The status categories were taken directly from the atlas authors, and although subjective, they do indicate changes in the status of the carabid species in these countries. Changes in beetle status in Belgium were determined in the time period from 1950 to 1986 (Desender 1986). It is not entirely clear over which time period the status of carabid beetles were evaluated in Denmark, but it appears to be from 1950 to 1989 (see Desender and Turin 1989; Turin 1990). In the Netherlands, beetle status was determined by evaluating three time periods; pre-1900, from 1900 to 1970, and from 1970 onwards (Turin 2000).

Analyses

The beetle population status categories have a natural order from increasing to decreasing (Table 1), i.e. they are measured on what is called an ordinal scale. The effect of the explanatory variables on status was modelled by ordinal regression (McCullagh and Nelder 1989, chapter 5). This assumes that there is an unobserved variable (here the change in status of the species), termed a latent variable, which we are trying to model. We do not observe this latent variable, but rather another variable which is a discrete version of the latent variable, but which still has a natural order (here the population status categories, Table 1). An observation of a high value on the ordinal scale implies that the latent variable is also high. For our data, the higher categories are those representing a greater decline in the species, so a higher value of the latent

variable will mean a more severe decline. Ordinal regression is a type of generalised linear model, so the covariates are entered into the model in the same way as they are for regression or ANOVA. In our analysis, we only used the main effects and first order interactions in the regression model, as higher order interactions are often aliased with lower order effects.

Variable selection is not a trivial process, especially with observational data where the covariates are correlated. We used stepwise selection of variates (McCullagh and Nelder 1989) to find an initial model that was close to optimal. At each stage in the model selection, the current model was modified by adding or subtracting single variable effect until the model could not be improved. Akaike's Information Criterion (AIC) (Akaike 1973) was used to compare models,

$$\text{AIC} = \text{Deviance} + 2 \times \text{number of parameters} \quad (1)$$

The deviance represents the fit of the model, and this is penalised for complexity of the model, as represented by the number of parameters in the model. Stepwise model selection procedures are not guaranteed to find the best model, so we explored this chosen model by dropping terms in the model, and adding terms that had not been included, until we arrived at a model that we deemed to be the best. This was carried out separately for the data from all three countries.

Results

At the time of the publications of the atlases, 379, 314 and 380 carabid species were known to be present in Belgium, Denmark and the Netherlands respectively. The status of more than 93% of these species is known (*n* values in Table 1), with the majority of species showing marked declines over the past 50–100 years. For example, 46%, 31% and 42% of the ground beetle species in Belgium, Denmark and the Netherlands, respectively, have shown some level of decline. Only about 20% of the species have shown an increase in numbers or range.

Neither environmental tolerance nor carabid phylogeny were retained in the final model for any country. This suggests that if there is any significant phylogenetic inertia then it is either in the traits that are included in the model, or is correlated with these traits. For example, species in the tribe Carabini are large-bodied (mean size ~23.4 mm) and are predominantly short-winged (between 65 and 70% per country, see country averages below). None of the species in the Carabini are extreme generalists. Pterostichini (mean size ~9.7 mm), one of the three most speciose tribes in the three countries investigated, has a higher proportion of short-winged species compared to the country averages (Belgium short-winged percentage =12%, Pterostichini short-winged percentage in Belgium =22%; Denmark =10%, Danish Pterostichini =11%; The Netherlands =11%, Dutch Pterostichini =19%). Finally, Bembidiini (body size ~4.0 mm), a small-sized species rich tribe, is mainly long-winged (between 75 and 82% per country compared to the country average of ~74%), and has very few short-winged species (below 2% per country). These traits are more useful as predictors of extinction risk than phylogenetic relatedness, as they can be generalised to other species and are also more informative in the sense that they can imply something about the mechanisms of extinction risk.

Table 2 Generalised linear model estimates. Main factors and first order interactions are shown. See Table 1 for variable descriptions. Estimates (Values and SE values) shown have been multiplied by 10³

Factors	Belgium		Denmark		The Netherlands	
	Value (SE)	<i>t</i>	Value (SE)	<i>t</i>	Value (SE)	<i>t</i>
Main factors						
Range size	-3.7 (7.19)	-0.52	4.9 (8.05)	0.61	-13 (6.79)	-1.946
Position 2 (Edge species)			-750 (311)	-2.4	-420 (521)	-0.810
Specialisation	-320 (131)	-2.4	-190 (178)	-1.0	-6,020 (1,550)	-3.87
Habitat 2 (Many)	-1,900 (868)	-2.2	-4,100 (930)	-4.4	-1,070 (1,053)	-1.02
Habitat 3 (Open)	110 (1,340)	0.08	-6,600 (380)	-17.1	-6,020 (1,553)	-3.87
Habitat 4 (Grassland)	-1,200 (920)	-1.3	-2,800 (1,020)	-2.7	-2,900 (1,199)	-2.42
Habitat 5 (Riparian)	-390 (693)	-0.57	-27 (1,000)	-0.03	-360 (864)	-0.42
Habitat 6 (Coastal)	2,000 (940)	2.2	-300 (1,214)	-0.25	-2,130 (1,093)	-1.95
Body size	290 (147)	2.0	640 (169)	3.8	220 (190)	1.152
Wings 2 (Dimorphic)	-1,900 (690)	-2.7	-750 (949)	-0.79		
Wings 3 (Brachypterous)	720 (978)	0.75	3,000 (760)	4.0		
1st order interactions						
Range size × Body size	-4.2 (2.1)	-1.9	-6.1 (1.87)	-3.2	-4.3 (1.87)	-2.28
Range size × Specialisation			-3.4 (1.79)	-1.9		
Specialisation × Wings 2	470 (215)	2.2				
Specialisation × Wings 3	-170 (342)	-0.49				
Body size × Wings 2			350 (337)	1.0		
Body size × Wings 3			-700 (202)	-3.5		
Habitat 2 × Position 2					-1,700 (810)	-2.1
Habitat 3 × Position 2					-1,100 (1,080)	-1.0
Habitat 4 × Position 2					620 (790)	0.79
Habitat 5 × Position 2					-1,400 (790)	-1.8
Habitat 6 × Position 2					1,800 (950)	1.9
Habitat 2 × Range size			7.7 (5.16)	1.5	-1.9 (4.88)	-0.39
Habitat 3 × Range size			21 (5.60)	3.7	10.7 (6.04)	1.76
Habitat 4 × Range size			19 (7.88)	2.4	6.8 (7.06)	0.96
Habitat 5 × Range size			-8.1 (6.44)	-1.2	-5.7 (6.10)	-0.93
Habitat 6 × Range size			5.3 (11.7)	0.46	15.3 (7.31)	2.10
Habitat 2 × Body size	1,100 (280)	3.9	1,300 (300)	4.5	920 (316)	2.9
Habitat 3 × Body size	510 (410)	1.2	1,500 (210)	7.4	1,640 (466)	3.53
Habitat 4 × Body size	900 (300)	2.9	860 (330)	2.6	930 (334)	2.78
Habitat 5 × Body size	420 (260)	1.6	-100 (338)	-0.30	450 (293)	1.53
Habitat 6 × Body size	-850 (370)	-2.38	-380 (450)	-0.84	-64 (433)	-0.15

Carabid beetle range size and its interactions are difficult to interpret because grid cell occupancy (i.e. range size) was used to determine the status categories (Table 1). Indeed, any interpretations of the results may be circular because species with smaller range sizes tended to decline more, but the measurement of range size was made at the end of the period over which the assessments were made, when species that had declined would be unable to have large range sizes.

Main effects

As these are observational data (rather than a designed experiment), the main effects are informative even in the presence of an interaction, in that they show the general trend in the effects of the different factors. However, as all main effects also appear with interaction terms, their interpretation should be read with some caution.

Range position

Carabid species which had Denmark and the Netherlands at the edge of their ranges were more prone to decline than species for which these countries were more central (Table 2). For the Netherlands we also found an interaction with habitat association (Table 2).

Specialisation

There are more specialist carabid species than generalist ones, decreasing from 30–35% strict specialist species in the three countries to between 8–10% extreme generalist species (Fig. 1A). In general, specialist carabid species were more prone to decline than generalist species (negative values in Table 2).

Habitat association

There were differences between responses of beetles associated with different habitat types, and habitat association

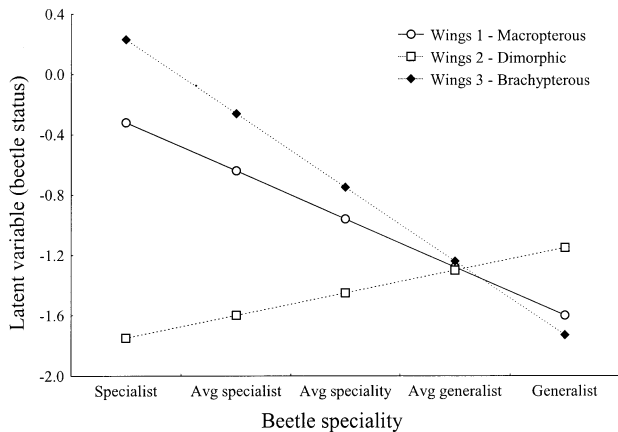
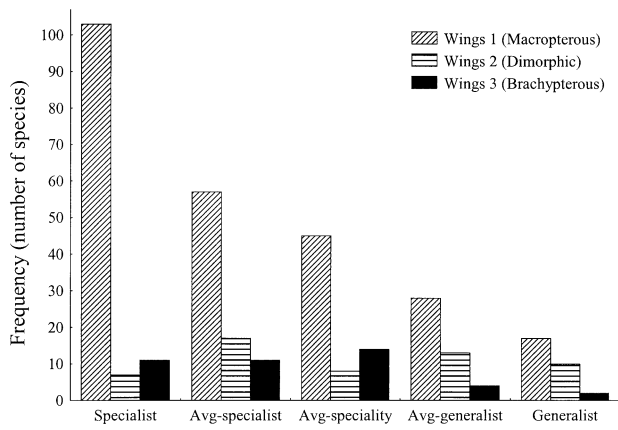


Fig. 1A, B Carabid specialisation-wing form interaction in Belgium. **A** The frequency distribution of wing form within each specialisation category. **B** The interaction is plotted against the regression latent variable (beetle status). A larger latent variable value translates into a greater risk of decline

interacted with carabid beetle body size in all three countries investigated (Table 2); this is discussed further below.

Body size

In all three countries, larger beetles were significantly more prone to decline than smaller ones (Table 2). Most carabids are small, with more than 90% of all species between 1.8 and 14 mm in size. Because of this highly right skewed body size distribution (Fig. 2A), the patterns observed pertain mainly to small and medium sized beetles. The small number of large species means that their patterns should be treated cautiously, as the regression is dominated by the large number of small species.

Wing form

Overall, dimorphic species were less prone to decline than either macropterous or brachypterous species (Table 2).

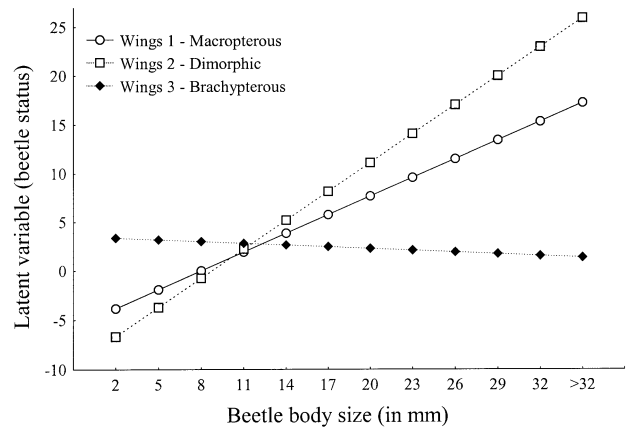
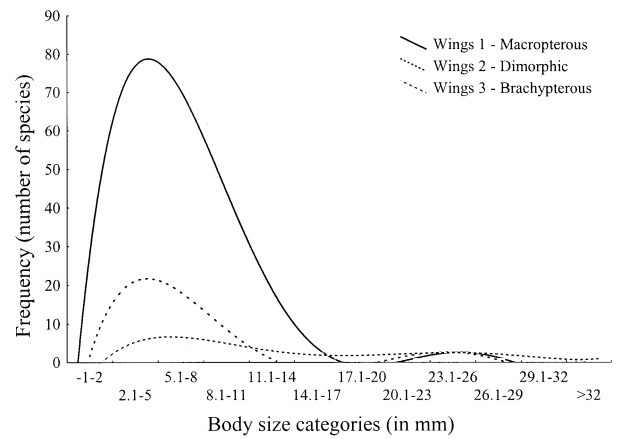


Fig. 2A, B Carabid body size-wing form interaction in Denmark. **A** The frequency distribution of beetle wing form within beetle size categories. **B** The interaction is plotted against the regression latent variable (beetle status)

Dimorphic species make up 14–17% of the three species pools, whereas macropterous species make up 73–74% (brachypterous species are between 10 and 12% of the three species pools) (Fig. 2A).

Interactions

There was no consistent pattern of the interactions between factors in the different countries. This may partly be a statistical phenomenon, the interactions may not have been strong enough to have been included in the model, or it might be real, reflecting differences between the carabid beetle populations in the countries.

Body size, specialisation, wing form

In Belgium, brachypterous and macropterous specialists were more prone to decline than generalists, while dimorphic specialists were less prone to decline than dimorphic generalists. Overall, dimorphic species were

Table 3 Generalised linear model results. (AIC Akaike’s information criterion; LR Likelihood Ratio Test). Models: Belgium: Extinction ~ Range size + Specialisation + Habitat + Body size + Wings + Range size×Body size + Habitat×Body size + Specialisation×Wings. Denmark: Extinction ~ Body size + Wings + Range Position + Range size + Specialisation + Habitat + Body size×Wings + Range size×Specialisation + Range size×Body size + Habitat×Body size + Habitat×Range size. The Netherlands: Extinction ~ Body Size + Range Size + Habitat + Range Position + Body Size×Range Size + Body Size×Habitat + Range Size×Habitat + Habitat×Range Position

Country and factor	df	AIC	LR	χ^2 probability
Belgium				
(none)		833.79		
Specialisation × Wings	2	835.09	5.29	0.0007
Range size × Body size	1	835.55	3.76	0.0526
Habitat × Body size	5	845.03	21.23	0.0710
Denmark				
(none)		763.93		
Body size × Wings	2	764.82	4.89	0.0866
Range size × Specialisation	1	765.64	3.71	0.0541
Range Position	1	767.93	5.86	0.0155
Range size × Body size	1	769.94	8.01	0.0047
Habitat × Body size	5	775.49	23.76	0.0002
Habitat × Range size	5	777.69	21.56	0.0006
The Netherlands				
(none)		919.04		
Range Size×Habitat	5	921.08	12.04	0.0342
Body Size×Range Size	1	922.25	5.21	0.0225
Body Size×Habitat	5	924.17	15.13	0.0098
Habitat × Range Position	5	927.43	18.39	0.0025

less prone to decline than either macropterous or brachypterous species, except for extreme generalist species, where dimorphic species were more at risk (Tables 2, 3, Fig. 1B). In Denmark, small dimorphic and macropterous species were less prone to decline than large species, and have also been less prone than small brachypterous carabids. The pattern is reversed for large species (Tables 2, 3, Fig. 2B).

Habitat interactions

We found significant interactions between carabid habitat association and body size in all three countries (Tables 2, 3). Carabids larger than 11 mm in size were less prone to decline when associated with coastal, riparian or woodland habitat, and more prone to decline when associated with open, many or grassland habitat types (Fig. 3). The pattern is reversed for carabids smaller than 8 mm in size. In the Netherlands, carabid habitat association also interacted significantly with whether the country occurs centrally or marginally in the species’ range. For example, carabids for which the Netherlands is at the edge of their range were at a lower risk if they were associated with riparian, many, open or woodland habitat types. Carabids associated with coastal habitat types were more likely to decline if they were at the edge of their range in the Netherlands (Table 2).

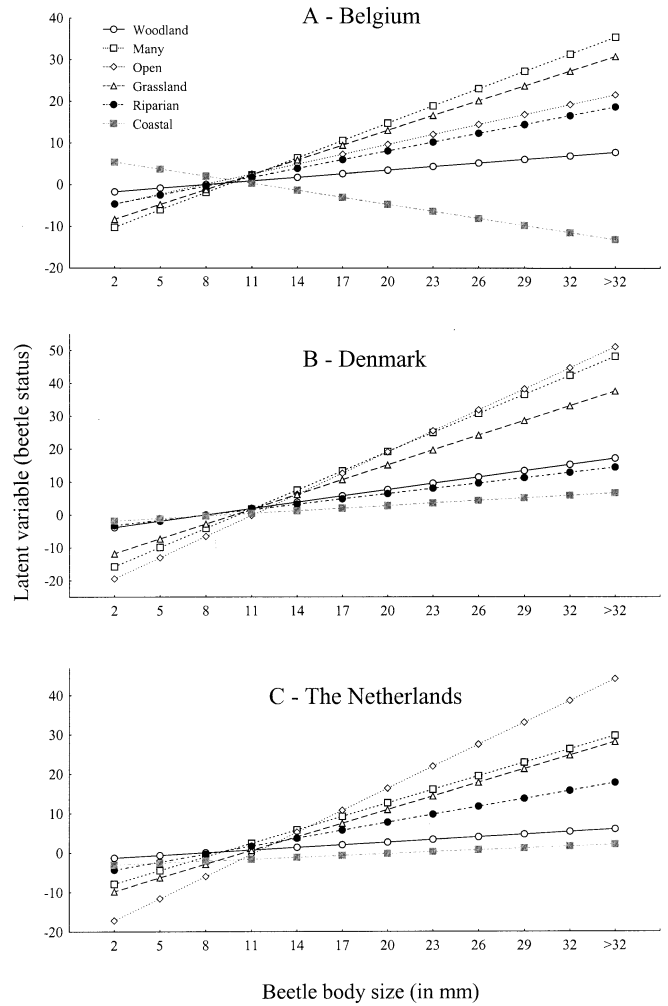


Fig. 3 Carabid beetle habitat association-body size interactions in Belgium (A), Denmark (B) and the Netherlands (C)

Discussion

As hypothesised, populations of large-bodied, specialist and short-winged carabid species tended to decrease more significantly than small-bodied, generalist and dimorphic species. Furthermore, large carabid species associated with coastal, woodland and riparian habitat types declined less than large species associated with many, open or grassland habitat types. This pattern is reversed for species smaller than 8 mm in size. The influences of these beetle characteristics on one another, and on the status of carabids are discussed below.

Carabid body size

Our results are consistent with the common notion that large-bodied species are more prone to decline than small-bodied species (Table 1 in McKinney 1997). Body size per se is not what usually places a species at risk, but rather the various life history traits and ecological

characteristics associated with it (Gaston 1994; Davies et al. 2000). For example, larger species usually have smaller populations, larger home range requirements, and relatively lower reproductive rates than smaller species (Simberloff 1994). Populations of large-bodied species tend to fluctuate less (Pimm et al. 1988; Pimm 1991; Lawton 1995), and so are able to remain longer at lower densities in a constant environment. However, when the environment changes, they respond less rapidly, and so may be at a greater risk of extinction (Beissinger 2000). Small-bodied carabid species will tend to be more responsive to environmental changes, and this elasticity will be advantageous in a landscape like Western Europe that is frequently changing (Turin and Peters 1986; Turin and Den Boer 1988; Desender and Turin 1989; Anonymus 2000).

But why do larger carabid species show a lower rate of population increase than smaller species? As with other organisms, egg numbers tend to decrease as body mass increases (Grüm 1984; Lövei and Sunderland 1996; Huk and Kühne 2000), although findings vary considerably (Thiele 1977). However larval mortality is considered to be the key factor for adult fluctuations (Den Boer 1986). Carabid larvae are soil bound and less mobile than adults (Lindroth 1992; Turin 2000), so soil conditions are important in determining adult population size. Large-bodied carabids usually have longer life cycles, and in particular longer larval periods, so their larvae will be more sensitive to soil disturbances than larvae of small-bodied species (Blake et al. 1994).

Carabid specialisation

Our habitat specialisation results indicate that most populations of specialist species have decreased, while generalist species tended to increase. Anthropogenic alteration and the abilities of different carabids to tolerate agricultural practices seem to be an important explanation for this pattern (Thiele 1977; Turin and Den Boer 1988; Desender and Turin 1989). Specialist carabid beetles are almost always only present in old, large and unfragmented habitat (Vermeulen et al. 1997; Assmann 1999; Niemelä 2001). This habitat has all but disappeared from western Europe (Turin and Den Boer 1988; Desender and Turin 1989), so the specialists have little suitable habitat for them to disperse to (Burel 1989), and consequently are stuck there.

Specialisation is often associated with extinction-prone species traits (Table 1 in McKinney 1997). Specialist species occupy narrow niches and therefore tend to be locally rare and geographically restricted (McKinney 1997; but see Brändle et al. 2000). Here, carabid specialisation is loosely defined in terms of niche breadth, and specialists are restricted geographically as compared to generalists. Specialists also tend to suffer as they have larger bodies on average (in the three countries studied, average sizes are between 8.0 and 8.2 mm for strict specialist species, and between 7.6 and 7.8 mm for

extreme generalist species), and have long wings (Fig. 1A) both characteristics that are correlated with a greater decline (Table 2).

A final point is that strict specialists of all habitat types may already have disappeared before record keeping began (see Lawton and May 1995), and the classification of strict specialists used here probably do not include very strict specialists, which had already gone extinct.

Carabid wing form and dispersal ability

Wing-dimorphic species have decreased less than either long-winged or short-winged species, as predicted. Long-winged individuals of some dimorphic species are able to disperse better from unfavourable habitat, and having found a more suitable patch, may be able to histolyse (reabsorb) their wing muscles and use the resources for reproduction, the so called oogenesis-flight syndrome (Roff 1990; Desender 2000). Wing muscle histolysis may then be used to provide resources that can be directed to reproduction, and so be the reason why egg production and survival ability have been found to be higher in some dispersing (i.e. long winged), as compared to non-dispersing (short-winged) individuals (Den Boer 1990). Short winged individuals do not need to commit as many resources to the development of dispersal features (wings and wing muscles) and dispersal, so presumably they can start reproduction earlier (as has been shown for Gerrids, Spence 1989). If the beetles do not have to disperse, then this could give short winged forms an overall reproductive advantage and may explain why the proportion of short-winged individuals is higher in more stable habitats (Den Boer 1970; Haeck 1971; Thiele 1977, p. 293; Desender 1989; Niemelä and Spence 1991).

In a landscape of deteriorating habitat quality, selection favours a greater migration propensity (Heino and Hanski 2001), so species with a greater ability to disperse will be less affected by the landscape changes. For dimorphic carabids, the proportion of long-winged individuals increases in deteriorating landscapes (Niemelä and Spence 1991), so the effects of local extinctions brought about by habitat fragmentation and isolation are more easily overcome through a greater dispersal rate.

If dimorphic species have an advantage, an interesting question remains; why are there so few dimorphic carabid species in these countries? There are two possible reasons for this. First, dimorphism could only be a transient form during the course of evolutionary change (Den Boer et al. 1980), and it is possible that carabids as a group have been evolving from fully winged species towards flightlessness, via a wing dimorphic phase (Roff 1986; Lövei and Sunderland 1996). Second, only some of those species that survived the Ice Ages south of the Alps and the Pyrenees were subsequently able to recolonise north-western Europe (Hengeveld and Haeck 1982). In particular, species with greater mobility (long-winged species) and greater spatial adaptability may have been favoured

in the climatically variable area of north-western Europe (Hengeveld and Haeck 1982).

Landscape changes in western Europe

Both the quantity and quality of carabid habitats have changed in western Europe in the last century (Turin and Den Boer 1988; Desender and Turin 1989; Anonymous 2000, p. 57). For example, although the total area of forest has increased in all three countries since 1961 (Desender and Turin 1989; Assmann 1999; FAO 2002), this has largely been a result of a switch from deciduous to coniferous forests (Turin and Den Boer 1988). This will have had different effects on different species, i.e. the composition of woodland carabid assemblages will have changed (Thiele 1977), but the overall effect on large woodland carabid species seems to be positive (Fig. 3).

In all three countries, large carabids associated with water (i.e. coastal and riparian) habitats tended to be less prone to decline than large carabids associated with other habitat types. This is a general pattern, so is almost certainly not due to a change in the size of the coastal and riparian areas (and hence not due to land reclamation in the Netherlands). An improvement in the quality of riparian and freshwater environments due to restoration efforts (Anonymous 2000) is certainly a likely explanation. The result for coastal beetles is more surprising, as coastal areas have undergone extensive alteration (see Anonymous 2000, p 73), so for example only a few natural dune areas have survived the process of expansion for tourism in Belgium (Desender et al. 1991). One possible explanation for the status quo in coastal carabids is that this environment has been a centre for human activity for millennia (Anonymous 2000), so that strict coastal habitat carabids may have disappeared before the last century.

Interestingly, carabids associated with coastal, riparian or woodland habitat types have changed less in status across all body sizes compared to carabids associated with open, many or grassland habitat types (Fig. 3). Conversely, large beetles associated with open, marshy or grassland habitats (i.e. including many agricultural habitats) have tended to suffer the largest declines (see also Desender and Turin 1989; De Vries 1996). This is probably due to changes in agricultural practices, in particular intensification of the use of pesticides and fertilisers, combined with the longer life cycles of larger species (see above), and the concomitant reduction in diversity (Janzen 1986; Turin and Peters 1986; Desender and Turin 1989; Huusela-Veistola 1996, to name but a few examples). Only a small number of generalist, highly dispersing carabids appear to have gained from this (Thiele 1977; Turin and Den Boer 1988; Niemelä 2001).

Conclusions

In general, specialist carabids of large body size, and of either short-winged or long-winged wing forms have decreased significantly over the past 50–100 years in Belgium, Denmark and the Netherlands. These, however, are statistical generalisations and should be treated cautiously as our understanding of the basic life histories of carabid beetles is incomplete, so the causal mechanisms cannot be elucidated with any certainty (Vepsäläinen and Spence 2000). We should also not forget the importance of external causal mechanisms (McKinney 1997). Although climate has been shown to be mainly responsible for the rise and decline of carabid species in the Netherlands (Hengeveld 1985), humans are currently having such a significant effect on the environment that even the species best ‘equipped for survival’ are at risk.

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