



Functional types of diving beetle (Coleoptera: Hygrobiidae and Dytiscidae), as identified by comparative swimming behaviour

IGNACIO RIBERA AND GARTH N. FOSTER

Environmental Sciences Department, The Scottish Agricultural College, Auchincruive, Ayr KA6 5HW

WILLIAM V. HOLT

Institute of Zoology, Regent's Park, London NW1 4RY

Received 19 August 1996; accepted for publication 23 January 1997

The swimming behaviour of ten species of diving beetles was studied with a video image analysing system, with the aim of testing the interpretation of their size and shape as functional characters reflecting adaptations to different swimming strategies. Velocity, sinuosity of the trajectory, and the relation between the two were studied in an unobstructed aquarium and, for the four largest species, in an aquarium with vertical sticks. Species predicted to be poor swimmers had the lowest average and maximum velocities. A globular species considered to have high manoeuvrability swam in highly sinuous trajectories, and could maintain this sinuosity at a wide range of velocities. One of the larger species, considered to be adapted to high speed swimming, also swam in highly sinuous trajectories, but only at slow velocities; its swimming pattern was considered to be the product of behavioural rather than morphological constraints. For two of the largest species, there was a significant decrease in sinuosity at higher velocities, whilst another was found to have a good compromise between velocity and manoeuvrability. In the aquarium with obstacles all the species reduced their maximum velocity, while the effect on sinuosity varied between species. Although the space limitation of the aquarium and the lack of motivation could have prevented some species from reaching their maximal velocities, a good agreement was found between the predicted and the actual swimming characteristics.

© 1997 The Linnean Society of London

ADDITIONAL KEY WORDS:—shape – size – functional morphology – image analysis.

CONTENTS

Introduction	538
Material and Methods	541
Recording	541

Correspondence to Dr G. N. Foster. Email: g.foster@au.sac.ac.uk

Image processing and selection	543
Data analysis	544
Results	546
Velocity and sinuosity in the unobstructed aquarium	547
Relationship between velocity and maximum sinuosity in the unobstructed aquarium	548
Principal Component Analysis of the ten species in the unobstructed aquarium	549
Comparison between the swimming behaviour of the largest species in the two aquaria	551
Discussion	553
Acknowledgements	557
References	557

INTRODUCTION

Two basic components can be distinguished in the swimming performance of aquatic organisms: velocity (both average and maximum) and manoeuvrability (Nachtigall, 1977; Webb, 1984). Poor swimmers are expected to perform poorly in both respects, while species considered to be good swimmers should have higher velocities. Among the good swimmers, there is a possible trade-off between high manoeuvrability and comparatively lower maximum velocity, or high maximum velocity against comparatively low manoeuvrability (e.g. Nachtigall, 1977; Webb, 1984). Similar trade-offs between alternative characters are a recognized constraint in most kinds of morphological specialization, and have been studied in a wide variety of organisms and environments (e.g. Hespeneide, 1975; Forsythe, 1983; Evans & Forsythe, 1984; Norberg, 1994; Garland & Losos, 1994). Manoeuvrability can be measured by the frequency of turns and by the relationship between the velocity and the sinuosity of the trajectory. Species with good manoeuvrability are expected to be able to turn at a wider range of velocities, while species adapted to high speed swimming might be expected to decrease their turning ability, and the frequency of turns, as velocity increases.

The aim of this work was to test for selected species of diving beetles (Coleoptera, Dytiscidae and Hygrobiidae) the correspondence between actual swimming behaviour in artificial standard conditions and their theoretical performance according to their size and shape, as interpreted by Ribera & Nilsson (1995) in a more detailed study of the morphometric patterns of 77 species of aquatic Adephega. This does not constitute evidence of the fitness or adaptive value of the morphological characters in present natural populations, but it does contribute significantly to an understanding of the functional morphology of the group. The interpretation of the morphological characters was based on theoretical hydrodynamic considerations and on comparison with other groups. The measurement of the actual swimming performance of different species is the only direct way to test the correspondence between morphology and function, that is, the relation between the shape and size of a structure and its use (Lauder, 1990).

Hygrobiidae and Dytiscidae are families of predaceous aquatic Adephega that capture their prey while swimming actively. The only European species of Hygrobiidae, *Hygrobia hermanni* (Fab.), has a comparatively less developed swimming method, a 'dog paddle' (cf. Hydrophilidae and Haliplidae); using all three pairs of legs. Dytiscid adults move both hind legs simultaneously for swimming. The mid

pair of legs can also be used in small or medium-sized species, but in large dytiscids they are used only for manoeuvring, while the front legs are usually kept folded close to the ventral surface (Nachtigall, 1977). Those structural modifications of the adults of Dytiscidae that diverge from the typical form of terrestrial Adephaga are generally considered to be adaptations to swimming (e.g. Guignot, 1931–33; Gallewski, 1971; Nachtigall, 1974, 1977; Roughley, 1981; Lawrence & Newton, 1982; see Ribera & Nilsson, 1995 and references therein).

Ribera & Nilsson (1995) interpreted differences in shape and size of diving beetles as indicative of different swimming strategies and, in general, of different ways of life. Four broad morphometric types were identified among the species studied:

- (1) Large to medium size species; streamlined, wide, with the maximum width in the rear part of the body and the maximum height in the front part, with short tibia and long tarsi, considered to be adapted to high speed swimming in open waters.
- (2) Small to medium size species with spherical body and long femora, considered to be adapted to manoeuvre in stagnant waters.
- (3) Small species with a discontinuous outline, narrow body and long and slender legs, considered to be poor swimmers in running waters.
- (4) Small to medium size species, in general being streamlined, relatively deep-bodied, and with short and wide legs, considered to be adapted to crawl among dense vegetation or detritus. This group is heterogeneous and not so well delineated.

Some of the species had, however, less extreme characteristics and were not included in any particular morphometric group. It must be noted that the species were ordered with factor analysis in a continuum, without delimited boundaries between groups. However, the unavoidably subjective delimitation of species groups was useful in describing the main morphometric patterns among them. The detailed composition of the groups was less important than their general outline, and particular species could always be included or excluded without significant alterations to the results (Ribera & Nilsson, 1995).

Species of group 1 had morphological characteristics usually considered to be adaptive to high speed swimming, with well developed, hydrodynamic, dorsoventrally flattened, bodies and powerful hind legs. The thin edges of the elytra in the larger species increase resistance, but also increase horizontal stability, allowing them to brake and to turn by shifts in their angle of attack (Nachtigall, 1974).

Species of group 2 had poor horizontal stability, owing to the lack of thin edges in the elytra and the pronotum and to their more spherical shape, but they were thought to be able to turn in every direction more easily, because they experience similar drag forces whatever the angle of attack.

Species in group 3 did not have the typical adaptations to swimming well developed, though this does not necessarily imply that they are not adapted to aquatic life, nor that they are more primitive or less evolved than other species in the group. They had marked angles between the body segments, long and slender hind legs, and, in most cases, short swimming hairs.

Allocation of the species to group 4 was mainly based on the morphology of the hind legs, as the streamlined body and continuous surface were more difficult to interpret: they could be adapted to crawl at low velocity in a dense physical environment, but they could also provide an example of an 'exaptation' (*sensu* Gould

TABLE 1. Species studied.

HYGROBIIDAE	
<i>Hygrobia hermanni</i> (Fabricius, 1775)	
DYTISCIDAE	
Copelatinae	
<i>Copelatus haemorrhoidalis</i> (Fabricius, 1787)	
Hydroporinae	
<i>Hyphydrus aubei</i> Ganglbauer, 1892	
<i>Deronectes opatrinus</i> (Germar, 1824)	
Colymbetinae	
<i>Agabus bipustulatus</i> (Linnaeus, 1767)	
<i>Colymbetes fuscus</i> (Linnaeus, 1758)	
<i>Meladema coriacea</i> Castelnau, 1834	
Dytiscinae	
<i>Eretes sticticus</i> (Linnaeus, 1767)	
<i>Graphoderus cinereus</i> (Linnaeus, 1758)	
<i>Dytiscus marginalis</i> Linnaeus, 1758	

TABLE 2. Morphometric group (Gr, numbers in brackets refer to species sharing characteristics of different groups, see Introduction), number of specimens, sex, aquarium (Aq, A empty, B with obstacles), total time swimming, number of valid tracks, and dimensions of the species studied. Values of the time and number of tracks are the average of the replicated measurements

Species	Gr	Aq.	No spec.	Sex	Total time s	No Tracks	Body length mm	Frontal area mm ²	Volume mm ³
<i>Hygrobia</i>	(2)	A	2	m/f	65.0	42	8.8	18.0	105
<i>Copelatus</i>	(1)(4)	A	2	m/f	26.6	11	6.9	6.1	28
<i>Hyphydrus</i>	2	A	2	m/f	13.3	14	4.4	6.0	17
<i>Deronectes</i>	3	A	1	f	43.3	15	5.1	3.9	13
<i>Agabus</i>	(1)	A	2	m/m	85.6	43	9.7	14.8	95
<i>Colymbetes</i>	1	A	1	f	4.2	2	13.7	29.1	264
<i>Meladema</i>	1	A	2	m/f	60.0	44	19.3	53.7	686
		B	2	m/f	54.8	42			
<i>Eretes</i>	1	A	2	m/f	48.3	25	11.9	22.6	179
		B	2	m/f	59.7	32			
<i>Graphoderus</i>	1(4)	A	2	m/f	117.9	52	11.9	26.8	211
		B	2	m/f	48.0	26			
<i>Dytiscus</i>	1	A	2	m/m	33.1	34	27.4	113.4	2069
		B	2	m/m	37.9	25			

& Vrba, 1982), i.e. a character originally evolved for high speed swimming in open waters, but found to be equally useful in a displaced activity, crawling in or pushing through vegetation or detritus.

Ten species ascribed to different morphological groups were studied—the only European species of Hygrobiidae and nine species of Dytiscidae, with sizes ranging from 4.4 to 27.4 mm (Tables 1 and 2). Species of all European subfamilies of Dytiscidae were included, except for Laccophilinae with four species in one genus in Europe. These families and subfamilies are usually considered to be monophyletic, although the detailed phylogeny of Dytiscidae is unresolved (e.g. Alarie, 1995; Beutel,

1995). A tentative phylogeny of the species studied, based on published data, is provided by Ribera & Nilsson (1995). Despite the clear relationships between morphometry and phylogeny, most characters were found to be homoplastic a number of times within the families studied (Ribera & Nilsson, 1995). This can be considered as evidence supporting the adaptive interpretation of the morphometry of the species (Lauder, 1990; Miles & Dunham, 1993; Losos & Miles, 1994).

The three species of Dytiscinae studied, plus the two largest Colymbetinae (*Meladema coriacea* Castelnau and *Colymbetes fuscus* (L.), Tables 1 and 2), were included in group 1; *Hyphydrus aubei* Ganglbauer in group 2; *Deronectes opatrinus* (Germar) in group 3; *Copelatus haemorrhoidalis* (Fab.) shared some characteristics of groups 1 and 4; *Hygobia hermanni* was considered to have a peculiar morphology, with very long and thin hind legs and a pronounced neck between the head and pronotum, although it shared some characteristics with group 2 (its globular shape and the long and thin femora); and *Agabus bipustulatus* (L.) was included in a group which had average values for the measured variables, although sharing some of the characteristics of group 1 (Ribera & Nilsson, 1995). The shape and size of the species are typical of the respective groups (Fig. 1). The position of the ten studied species in the morphological space defined by Ribera & Nilsson (1995) is shown in Figure 3B.

MATERIAL AND METHODS

Recording

All the studied specimens were collected in the Eastern Pyrenees in 1990, and were kept and fed in the laboratory for a short period (less than 48 h) before their swimming behaviour was recorded. Two specimens of each species (usually a male and a female, Table 2) from the same locality and sampling date were studied separately in an unobstructed aquarium 40 × 20 × 25 cm, with 5 cm depth of water at 15–20°C. They were left undisturbed and filmed continuously for 10 minutes in natural light using a fixed video camera above the aquarium.

The beetles usually swam close to the bottom of the aquarium, with no or few vertical movements in the water column. To renew their air supply they stopped swimming and floated up to the surface until the tip of the abdomen came in contact with the air. The dimensions of the aquarium probably prevented the larger species from reaching their maximum velocity. Beetles were not disturbed while being recorded, so the results cannot be considered representative of the maximum velocity achievable, but more an analysis of their standard swimming behaviour.

A second aquarium with nine vertical white plastic sticks of 5 mm diameter, arranged centrally in a 3 × 3 rectangle in the aquarium (8 and 5 cm between them), was used to study the possible effect of the presence of obstacles in the swimming behaviour of the larger species, Dytiscinae plus *Meladema coriacea* (Table 2). No observations were made of the smaller species as their swimming would not be obstructed by the obstacles.

For each specimen, the body length from apex of the elytra to the anterior margin of the pronotum (BL), the maximum width of the elytra (MW), and the maximum body depth (MH) were measured. The frontal area (FAR) was calculated as the area of an ellipsoid defined by the axes MW and MH; volume (VOL) was calculated

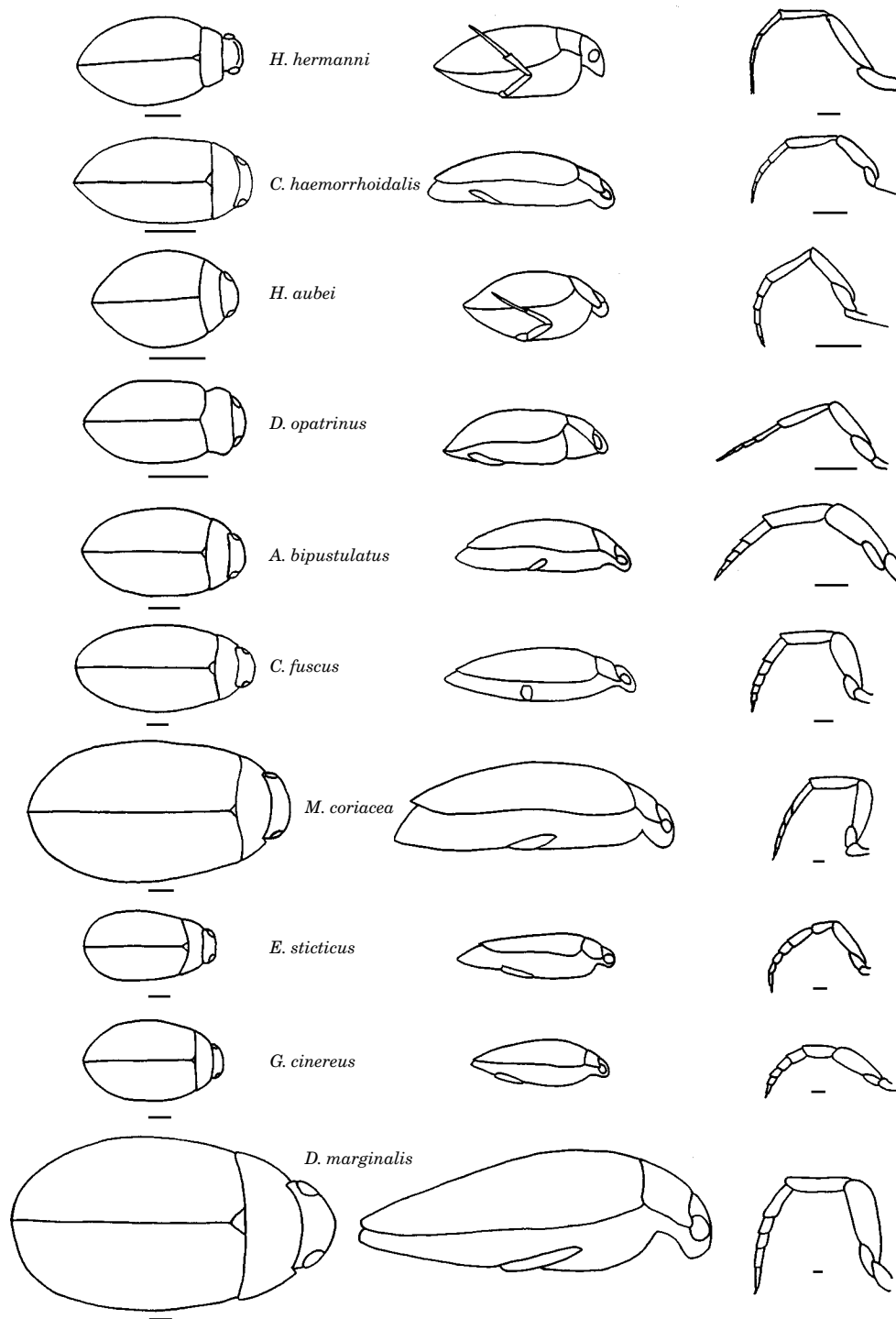


Figure 1. Outlines of the dorsal and lateral view, and the hind leg of the species studied, drawn from photographs. Scale bars of body outlines = 2 mm; of hind legs = 1 mm.

as the volume of the spheroid defined for these three measurements (Table 2). This was considered to be a rough approximation of the general oval shape of the species (Fig. 1).

Image processing and selection

The recorded images were analysed using the Hobson Sperm Tracker® package. This system was designed for the study of the swimming behaviour of spermatozooids, but it has since been used for a wide range of different purposes (Holt, 1993; Holt & Palomo, 1996). Video images were captured at 25 Hz, the image analysis was performed in real-time and the data stored. Algorithms designed to detect moving images were applied across the series of images, assuming that in the following image the object would lie within a certain radius of their initial position, a search being carried out within the defined distance. During analysis one monitor displayed the video recording whilst a personal computer monitor displayed the number of the track and the average or instantaneous values of the variables measured.

Analysis was confined to the paths in a rectangle 35 × 15 cm in the aquarium's centre in order to avoid edge effects associated with the walls. The analysed time is therefore only a small fraction of the total swimming time of each beetle.

Three variables were considered. Velocity (VEL) was calculated by deriving a smoothed path and dividing its total length by the time of the track. The use of a smoothed path instead of the full measured path reduced irregularities and random erratic changes in the actual tracking point over the surface of the beetle (signalled by a dot in the screen), particularly in large species. The system was calibrated to give measurements in cm s^{-1} . The straightness of the path was calculated by dividing the straight line distance between the first and last point of the track by the distance along the smoothed path. The inverse of this ratio was used as a measure of sinuosity (SIN). A sinuosity of e.g. 1.2 means that the trajectory was 1.2 times longer than the straight line between the initial and the final points.

The same measure of straightness, but using the full path instead of the smoothed path, was used as a control (see below). For the statistical analysis the sinuosity was logarithmically transformed. The third variable was the time of the track (TIM), measured in tenths of seconds.

The sinuosity of the swimming path and its relation to velocity were together found to be a good indicator of the manoeuvrability of the beetle. Other measurements possible using the Hobson Sperm Tracker® output, such as the angular displacement between consecutive points in the same track, were greatly affected both by random changes of the tracking point over the surface of the beetle and by 'wobble', minor lateral movements of the beetle while swimming, even when it did not change its main trajectory.

The setting specifications of the program were adjusted to obtain a good tracking of the beetle. They affected mainly the brightness of the image, the minimum number of points in a track to be computed, and the search radius to allow a continuous tracking. The values of the settings were adjusted for each species and specimen to optimize the analysis of the image, that is, to obtain a continuous and smooth tracking. Simultaneous visualization of the tracks undergoing analysis made it possible to measure them with great accuracy. All the recorded images were analysed three times with slightly different values of the settings.

The bright image of a moving signal in an oscilloscope was used as a control to estimate the random error of the measurements. Twenty sequences of different types of movement with known characteristics were studied, and the range of the variation for each variable was considered as a measurement of the error of the system. The precision of the system was estimated at $\pm 1 \text{ cm s}^{-1}$.

There were three main difficulties in tracking the beetles: spurious tracks due to reflections from the water surface, random tracks while the beetle was floating at the surface, and irregular or discontinuous tracks due to an incomplete pursuit of the image. These tracks were easily recognized on the monitor while being measured. Independently of this visual, direct, identification of invalid tracks, four additional criteria were developed to discard spurious measurements:

- (1) Velocity less than 2 cm s^{-1} , associated either with very slow swimming or slight movements when a beetle was floating.
- (2) Sinuosity of the smoothed path larger than the sinuosity of the full path, with an allowed random variation equal to the error in the control measurements of uniform, straight movement in the oscilloscope.
- (3) Difference between both measurements of sinuosity exceeding 50%. Large discrepancies between both measures indicate a very irregular tracking of the beetle. This limit was defined according to controls and to the examination of the visually discarded tracks. Most of the tracks rejected by this criterion were already detected by some of the others, so the chosen limit of 50% was not of great relevance.
- (4) Tracks lasting less than 0.5 seconds. Being very short and irregular, these random tracks gave extreme values for different variables.

Most of the discarded tracks were excluded by more than one of these criteria, and were also detected visually during the analysis. Other criteria based on the values of other variables proved to be largely redundant. The remaining tracks were inspected to check the possible existence of obvious outliers, but it was found necessary to exclude only one further track because of an apparent inconsistency in its variables.

The total analysed swimming time (average of the three replicated measurements) ranged between 4.2 seconds in *Colymbetes fuscus* (with two tracks) and 117.9 seconds in *Graphoderus cinereus* (L.) (52 tracks), with an average of 49.7 seconds (Table 2). One of the individuals of *Deronectes* did not swim during the observation time. The images of one specimen of *Colymbetes fuscus* could not be analysed owing to poor illumination. Differences between average time per track were not significant when all species were jointly compared with ANOVA. The difference between the total analysed time and the number of tracks was not studied, because the time during which the beetle swam close to the walls of the aquarium had to be excluded from analysis.

Data analysis

Velocity, logarithm of sinuosity, and time of each track were compared between the three repeated analyses for each specimen by multiple analysis of variance. Time was included as a control measure. No significant differences were found among the three repeated measurements of each specimen, except for the first replicate of one specimen of *Eretes sticticus* (L.) and one of *Hygrobia hermanni*. The total analysed

time and the time per track of these replicates were significantly lower than in the other two replicates of the same specimen. This was an indication of a bad tracking, and these tracks were subsequently excluded from analysis.

Velocity and logarithm of sinuosity were compared with analysis of variance both between the two specimens of each species and between species, using the raw data of only one of the repeated measurements of one specimen at a time. The replicated measurements were not included in the same analysis because, although not strictly equivalent, they were not independent. No differences were found among specimens of the same species except for the average velocity in *Dytiscus marginalis* L. (3.6 and 6.4 cm s⁻¹ respectively), *Graphoderus cinereus* (5.1 and 3.7) and *Hygobia hermanni* (6.1 and 10.2).

For comparison between species the specimen was considered to be a factor nested within the species. Different analyses were repeated using different combinations of the replicated measurements of each specimen. In a preliminary series of analyses neither the volume, the frontal area or the body length had a significant effect as covariates, as there were no significant correlation between them and any of the variables studied (Table 4). They were thus not considered in subsequent analyses.

The average velocity (xVEL), average logarithm of the sinuosity (xLSIN), standard deviation of both variables (sVEL and sLSIN) and the maximum measured velocity (mVEL) were computed for each of the replicates. All variables except the maximum measured velocity were weighted by the time of the track. The values of the replicas were then averaged for each specimen without being weighted. Differences in the maximum measured velocity, and in the standard deviation of the velocity and the logarithm of the sinuosity, were studied by analysis of variance. Individual comparisons of the average value of the variables in each species were analysed with one tailed Student's *t*-test.

In studying the relationships between the velocity and the sinuosity of the path it must be recognized that each species can swim in straight trajectories at low speed, irrespective of its manoeuvrability. Therefore, the methodology proposed by Blackburn, Lawton & Perry (1992) to estimate the slope of upper bounds of triangular distributions was used instead of the linear regression between the individual values of the velocity and the sinuosity of each track. The range of the velocities of each species was divided into equal classes of 2 cm s⁻¹, and the maximum measured sinuosity was selected for each of them. If the species did not change the sinuosity of its trajectory when increasing its velocity, the correlation between the maximum sinuosity and the velocity is expected to be low, while if the species cannot follow intricate trajectories while swimming at higher velocities this correlation is expected to be larger, and the slope of the regression line negative. All replicated measurements were pooled in this analysis, because individual tracks were not totally equivalent between them and could reflect different relationships between velocity and sinuosity.

A Principal Component Analysis of the correlation matrix of xVEL, mVEL, sVEL, xLSIN, sLSIN and the slope of the regression between the maximum sinuosity and the velocity for each species (SLO) was used to summarize the relationships between the variables studied. The correlation matrix was preferred to standardize the variables with a different scale. No statistical test of significance was conducted with this procedure.

A final comparison of the velocity and sinuosity of the largest species between the two aquaria (unobstructed and with obstacles) was performed with analysis of

TABLE 3. Average value per species of the studied variables. Aq: aquarium (A empty, B with obstacles); xVEL: average velocity, cm s^{-1} ; mVEL: maximum measured velocity, cm s^{-1} ; sVEL: standard deviation of the velocity; xlSIN: average logarithm of the sinuosity; xSIN': antilogarithm of xlSIN; slSIN: standard deviation of the logarithm of the sinuosity

Species	Aq.	xVEL	mVEL	sVEL	xlSIN	xSIN'	slSIN
<i>Hygrobia</i>	A	8.17	12.50	1.73	0.016	1.038	0.024
<i>Copelatus</i>	A	4.41	6.67	0.92	0.008	1.019	0.009
<i>Hyphydrus</i>	A	6.87	11.17	2.26	0.138	1.373	0.157
<i>Deronectes</i>	A	3.45	7.00	1.12	0.007	1.015	0.012
<i>Agabus</i>	A	5.07	8.00	1.07	0.014	1.033	0.020
<i>Colymbetes</i>	A	8.84	11.33	1.65	0.067	1.168	0.028
<i>Meladema</i>	A	10.28	16.33	2.23	0.015	1.036	0.023
	B	8.83	14.33	2.22	0.028	1.066	0.039
<i>Eretes</i>	A	4.37	8.50	1.34	0.271	1.865	0.256
	B	3.42	6.67	1.20	0.325	2.114	0.259
<i>Graphoderus</i>	A	4.42	8.67	1.21	0.015	1.035	0.020
	B	4.69	6.83	0.97	0.027	1.064	0.028
<i>Dytiscus</i>	A	5.03	8.17	1.35	0.017	1.040	0.032
	B	3.87	6.50	0.87	0.088	1.225	0.086

variance of the raw data. A Principal Component Analysis of the same variables used in the general comparison between species was done to compare the general swimming behaviour of the species in the two aquaria.

The two individuals of each species were considered separately in all analyses except for the relation between sinuosity and velocity, in which all the individual tracks of the two specimens were pooled, and the Principal Component Analysis, in which the average values per species were used.

RESULTS

Velocity and sinuosity in the unobstructed aquarium

The analysis of variance of the raw tracks, taking one replicate of each specimen at a time, gave significant differences for both the velocity and the logarithm of the sinuosity ($P < 0.05$). The analysis was repeated for different combinations of the three measured replicates of each specimen, and the results were found to be consistent.

The lower velocity was found in *Deronectes* (3.45 cm s^{-1}), and the highest in *Meladema* (10.28 cm s^{-1}) (Table 3). *Eretes*, *Graphoderus*, *Copelatus*, *Dytiscus* and *Agabus* had similar average velocities, with a significant increase in *Hyphydrus*, *Hygrobia*, *Colymbetes* and *Meladema*. When compared with individual one tailed Student's *t*, differences among two adjacent species were not significant, but differences were immediately significant between species from different general groups. The largest cut-point was between the group formed by *Deronectes* to *Agabus* and that formed by *Colymbetes* and *Meladema*, with *Hyphydrus* and *Hygrobia* having intermediate values, although more close to the group with a higher velocity.

The logarithm of the sinuosity was lower in a group formed by *Copelatus* and *Deronectes*; it had slightly higher values in *Agabus*, *Graphoderus*, *Meladema*, *Dytiscus* and

TABLE 4. Correlations between the studied variables in the empty aquarium. Values for each of the specimens were considered separately except for the slope of the regression line between the maximum sinuosity and the velocity (SLO). xVEL, average velocity; sVEL, standard deviation of the velocity; mVEL, maximum measured velocity; xlSIN: average logarithm of the sinuosity; slSIN: standard deviation of the logarithm of the sinuosity; VOL: volume; FAR: frontal area; BL: body length. Significant correlations ($P < 0.05$) are marked by asterisks

	xVEL	mVEL	sVEL	xlSIN	slSIN	VOL	FAR	BL
xVEL	1							
mVEL	0.92*	1						
sVEL	0.75*	0.87*	1					
xlSIN	-0.18	-0.17	-0.02	1				
slSIN	-0.18	-0.11	0.10	0.96*	1			
VOL	0.00	-0.00	0.01	-0.17	-0.18	1		
FAR	0.09	0.09	0.06	-0.17	-0.18	0.99*	1	
BL	0.16	0.16	0.05	-0.14	-0.18	0.93*	0.97*	1
SLO	0.27	0.17	0.13	-0.86*	-0.83*	0.07	0.04	-0.04

Hygrobia; *Colymbetes* had an intermediate value; and two species, *Hyphydrus* and *Eretes*, had much higher values than the rest (Table 3). Differences between the three groups were highly significant, irrespective of the inclusion of *Colymbetes* among the species with intermediate or high sinuosity ($P < 0.05$).

Differences in the maximum measured velocity and the standard deviation of the velocity, when all species were jointly compared with ANOVA, were significant at a $P < 0.1$ level ($P = 0.078$ and $P = 0.083$ respectively). Differences in the standard deviation of the logarithm of the sinuosity between species were also significant ($P < 0.05$).

The groups distinguished on the basis of mean velocity could also be distinguished by their maximal velocities. The maximal velocity was low in *Copelatus* and *Deronectes* (around 7 cm s^{-1}); had intermediate values in *Agabus*, *Dytiscus*, *Eretes* and *Graphoderus*; was higher in *Hygrobia*, *Hyphydrus* and *Colymbetes*, and the highest value, 16.33 cm s^{-1} , was found in *Meladema* (Table 3). Mean and maximal velocities were highly correlated (Table 4). Again, Student's t comparisons between individual species were highly significant when species from different general groups were compared, and differences between the three main groups were all significant ($P < 0.05$).

Three groups of species could be distinguished according to their values for the standard deviation of the velocity, with significant differences between them ($P < 0.05$): *Copelatus*, *Agabus* and *Deronectes* had the lower standard deviations; *Graphoderus*, *Dytiscus*, *Eretes* and *Colymbetes* had intermediate values; and *Meladema* and *Hyphydrus* had the highest standard deviations (Table 3). *Hygrobia* had an intermediate value between *Colymbetes* and *Meladema*, and might be included in any of the three groups without changing the significance of the comparison.

The standard deviation of the sinuosity was highly correlated with the average sinuosity (Table 4). The same groups were distinguished, but the only change was the clear inclusion of *Colymbetes* (with only two tracks) in the intermediate group (Table 3). Differences among the three groups were highly significant when compared by a one tailed t -test ($P < 0.05$).

TABLE 5. Relation between velocity and sinuosity. Aq: aquarium (A empty, B with obstacles); n: number of intervals of velocity (see text); r: correlation between maximum sinuosity in the interval and velocity; *P*: significance; SLO: slope of the regression line between the maximum sinuosity and the velocity

Species	Aq.	n	r	<i>P</i>	SLO
<i>Hygrobia</i>	A	8	-0.56	0.13	-0.01
<i>Copelatus</i>	A	4	-0.30	0.71	-0.02
<i>Hyphydrus</i>	A	6	0.04	0.94	0.02
<i>Deronectes</i>	A	4	-0.78	0.22	-0.03
<i>Agabus</i>	A	5	-0.24	0.70	-0.01
<i>Colymbetes</i>	A	3	-0.89	0.30	-0.04
<i>Meladema</i>	A	8	-0.42	0.30	-0.01
	B	9	-0.30	0.43	-0.02
<i>Eretes</i>	A	6	-0.65	0.17	-1.41
	B	5	-0.65	0.23	-1.62
<i>Graphoderus</i>	A	5	-0.91	0.03	-0.02
	B	5	-0.97	0.01	-0.05
<i>Dytiscus</i>	A	6	-0.97	0.00	-0.07
	B	4	-0.89	0.10	-0.71

Relationship between velocity and maximum sinuosity in the unobstructed aquarium

The correlation between the maximum measured sinuosity in the 2 cm s^{-1} intervals of velocity and the average velocity of the interval was negative for all the species except *Hyphydrus*, although it was significant at only $P < 0.05$ in *Dytiscus* and *Graphoderus* (Table 5 and Fig. 2). Some correlations, although non significant, were high (e.g. in *Colymbetes*, *Deronectes* and *Eretes*). In some species the low correlation owed to the value of a single interval, and this always had a lower sinuosity than expected (e.g. the first class of *Agabus* or *Copelatus*, Fig. 2).

In *Meladema* and *Hygrobia* the pattern was not defined, although the correlation was negative and relatively high (Table 5). In both species the maximum values of sinuosity were low (around 1.5, Fig. 2). In *Hyphydrus* there was clearly no correlation, and maximum values of sinuosity were around 8. The maximum measured sinuosity was in *Eretes*, with some values higher than 30, that is, the path was more than 30 times longer than the straight distance between its starting and ending points. In these tracks the beetle almost completed a full circle in a short distance. However, this sinuosity was found only at the lowest velocities ($2\text{--}3 \text{ cm s}^{-1}$). When the beetle swam at a higher velocity, the sinuosity rapidly decreased to lower values. By contrast, *Hyphydrus* maintained high values of sinuosity at higher velocities: in the interval between 10 and 12 cm s^{-1} it reached a sinuosity up to 7.7, while *Eretes*, in the same interval, only reached a maximum value of 3.1 (Fig. 2).

The slope of the regression line between velocity and maximum sinuosity (SLO) could be interpreted as a measure of the decline of the maximum measured sinuosity as velocity increased. The steepest slope was that of *Eretes* (Table 5), which showed a dramatic decrease in sinuosity from 33 to less than 7 when velocity increased only 2 cm s^{-1} (Fig. 2). *Dytiscus*, despite its low average velocity, also had a relatively steep slope (Table 5).

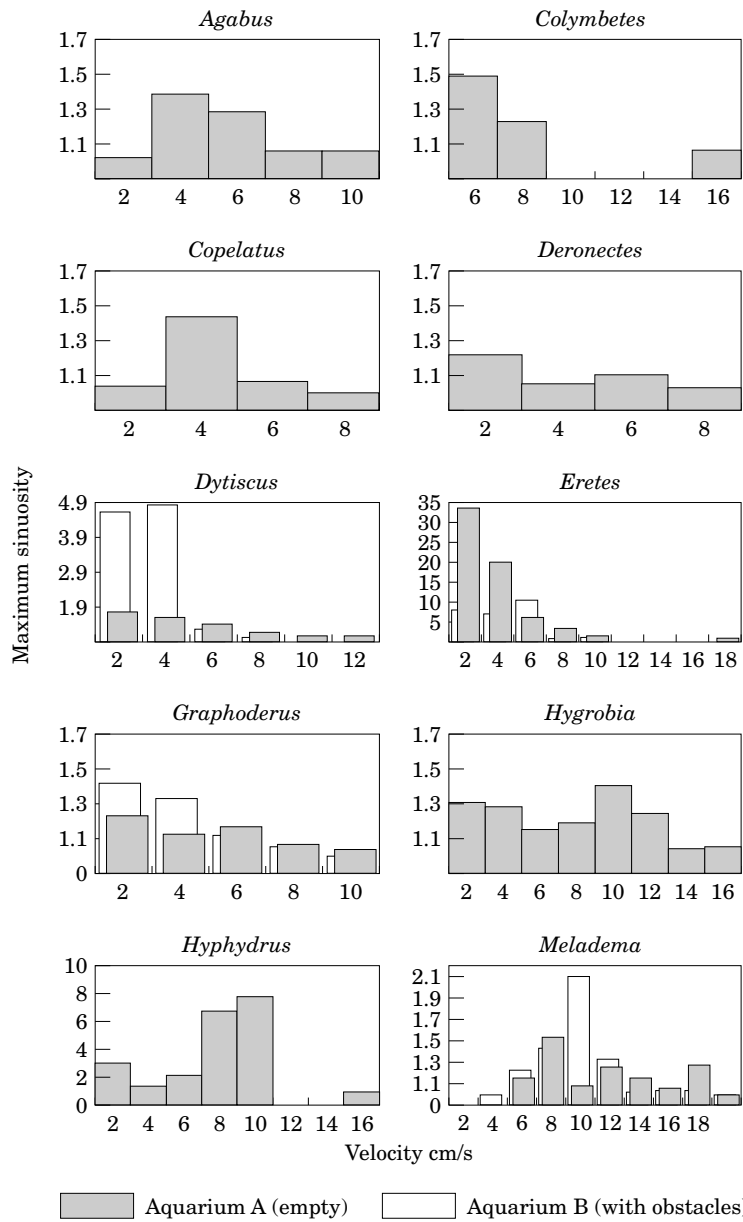


Figure 2. Maximum sinuosity in 2 cm s^{-1} intervals of velocity. See Table 3 for the correlation and the slopes of the regression lines.

Principal Component Analysis of the ten species in the unobstructed aquarium

The two first axes of the Principal Component Analysis of the average values per species of xVEL, mVEL, sVEL, xISIN, sISIN and SLO explained 49.1 and 44.7 per cent of the total variance respectively. The first axis was strongly and positively correlated with both measures of sinuosity, and negatively correlated with the slope of the regression between sinuosity and velocity. It had very low correlations with

TABLE 6. Correlation between the variables and the axis in the PCA comparing the average values per species in the empty aquarium. xVEL: average velocity, cm s^{-1} ; mVEL: maximum measured velocity, cm s^{-1} ; sVEL: standard deviation of the velocity; xlSIN: average logarithm of the sinuosity; slSIN: standard deviation of the logarithm of the sinuosity; SLO: slope of the regression line between the maximum sinuosity and the velocity

Variable	PC1	PC2
xVEL	-0.16	0.95
mVEL	-0.05	0.98
sVEL	0.14	0.95
xlSIN	0.99	0.06
slSIN	0.98	0.06
SLO	-0.92	0.19

the measures of velocity. The second was strongly positively correlated with all three measurements of velocity, and had very low correlation with the other variables (Table 6).

The main groups defined by the previous analysis of individual variables could be equally recognised in the plot of the scores of the species (Fig. 3A). *Copelatus* and *Deronectes* had the lowest scores for axis 2, and also very low values for axis 1. They were the slowest species, with a reduced manoeuvrability. *Meladema* was mainly characterized by its high velocity, and had the highest score for axis 2. On the contrary, *Eretes* had a medium score for axis 2, but an extreme score for axis 1, owing to its very high average sinuosity. Its low score for axis 2 was due to its relatively low velocity and the steep slope of the regression between maximum sinuosity and velocity (Table 5). *Hyphydrus* had the second highest score for both axes, due to its high average sinuosity in addition to its relatively high average velocity, and the low slope of the regression between maximum sinuosity and velocity. *Hygrobia* and *Colymbetes* were grouped together, with relatively high scores for axis 1, although *Colymbetes* had a larger value for this axis. *Dytiscus*, *Graphoderus* and *Agabus* were also clustered close to the origin, though with negative values for both axes, *Agabus* being the worst swimmer of the three (Fig. 3A).

The dispersion of the species in the first two axes of the morphological space defined by Ribera & Nilsson (1995) is plotted in Figure 3B (the order of the axes has been changed to facilitate a direct comparison with Fig. 3A). Factors 1 and 2 were considered to reflect the trade-off between velocity and manoeuvrability, with species considered to be adapted to high speed swimming in the negative extreme of factor 1, and species considered to have a good manoeuvrability in the positive extreme of factor 2. When compared with the first and second axes of the PCA (Fig. 3A), the most striking difference is the position of *Eretes*, which swam in highly sinuous trajectories despite being considered a species adapted to fast swimming according to its morphology. However, it could maintain this high sinuosity only at low velocities, as seen above.

In addition to a positive score for factor 1, *D. opatrinus* and other species included in group 3 had low values for a third factor mainly related with the shape of the hind legs, long and thin in the species considered to be poor swimmers (Ribera & Nilsson, 1995).

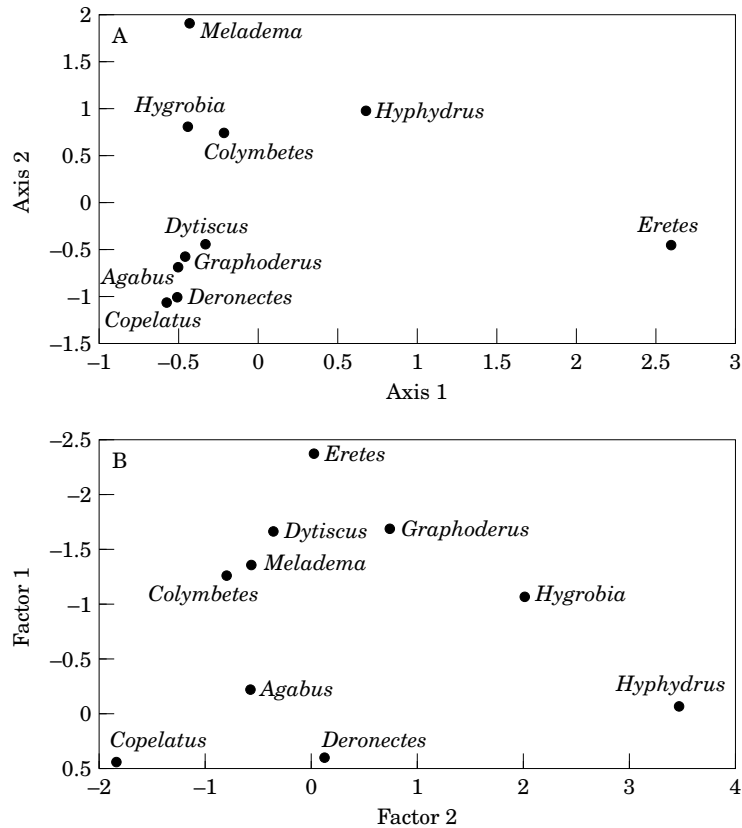


Figure 3. A, scores of the species in the two first axes of the PCA analysing their swimming behaviour in the empty aquarium. B, scores of the species in the two first axes of the morphological space defined by Ribera & Nilsson (1995) (see text).

Comparison between the swimming behaviour of the largest species in the two aquaria

Differences in velocity of the largest species between the two aquaria, using the raw data of only one measured replicate at a time, were significant ($P < 0.05$), velocity in the aquarium with obstacles being lower than in the unobstructed aquarium. There were, however, no significant differences in the logarithm of the sinuosity.

The greatest change in the relation between velocity and maximum sinuosity was found in *Dytiscus*, which had much higher maximum sinuosity in the aquarium with obstacles (Fig. 2), with a much steeper slope of the regression line (Table 5). *Eretes* greatly decreased the maximum sinuosity in the lowest interval, but increased it at higher velocities. *Graphoderus* increased its maximum sinuosity at low velocities, but decreased it at higher values. The regression line in this species was still highly significant, and the slope did not change appreciably. In *Meladema* the effect was not clear, with maximum values similar in both aquaria except for the intermediate values of velocity, in which the sinuosity in the aquarium with obstacles was much higher (Fig. 2).

The two first axes of the Principal Component Analysis of the average values in

TABLE 7. Correlation between the variables and the axis in the PCA comparing the swimming characteristics of the largest species in the two aquariums. xVEL: average velocity, cm s^{-1} ; mVEL: maximum measured velocity, cm s^{-1} ; sVEL: standard deviation of the velocity; xLSIN: average logarithm of the sinuosity; sLSIN: standard deviation of the logarithm of the sinuosity; SLO: slope of the regression line between the maximum sinuosity and the velocity

Variable	PC1	PC2
xVEL	-0.32	0.94
mVEL	-0.22	0.97
sVEL	-0.09	0.98
xLSIN	0.98	-0.19
sLSIN	0.98	0.17
SLO	-0.96	0.26

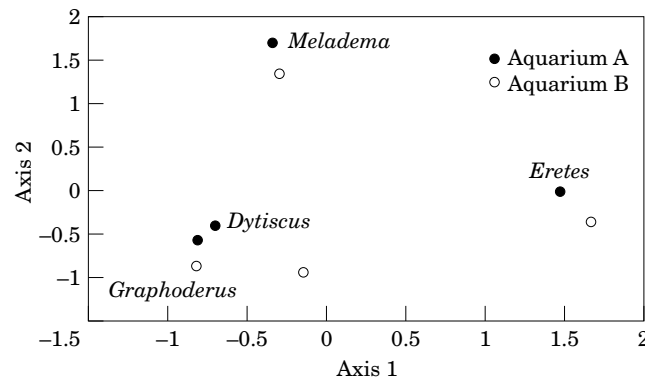


Figure 4. Scores of the species in the two first axes of the PCA comparing their swimming behaviour in the two aquaria.

each aquarium of xVEL, mVEL, sVEL, xLSIN, sLSIN and SLO explained respectively 69.6 and 29.2 per cent of the total variance. The correlations of the variables with the axis were very similar to those of the analysis of the whole set of species in the unobstructed aquarium (Table 7). The general distribution of the species was also the same found in the previous analysis, with *Eretes* and *Meladema* in the positive extreme of axes 1 and 2 respectively (Fig. 4); and *Graphoderus* and *Dytiscus* close to the origin.

Differences between the two aquaria, measured as the Euclidean distance between the scores of the two axes, were largest on *Dytiscus* (0.77), with decreasing values in *Eretes* (0.40) and *Meladema* (0.37), and smallest in *Graphoderus* (0.31).

The effect of the obstacles was clear in the scores of axis 2, all four species having lower values in the aquarium with obstacles, indicating a general decrease both in average and maximum velocity. The most pronounced effect was in *Dytiscus*, the

largest species, and in *Eretes*. All the species had lower average velocities in the aquarium with obstacles except *Graphoderus*, which had a slightly lower average velocity in the unobstructed aquarium (Table 3). The effect in the decrease of the maximum observed velocity was more general, being lower in the aquarium with obstacles for all the species. The effect on the standard deviation of the velocity was also uniform, decreasing in all species, although in *Eretes* and *Meladema* decreased only slightly, while in *Dytiscus* and *Graphoderus* the difference was much more pronounced (Table 3).

The effect of the obstacles in the first axis was not uniform: while *Meladema* and *Graphoderus* had very similar scores, *Dytiscus* and *Eretes* increased its value markedly. All the species increased their sinuosity in the aquarium with obstacles, although the largest difference was observed in *Dytiscus* and *Eretes* (Table 3). The slope of the regression between maximum sinuosity and velocity was also more negative in all the species, with *Dytiscus* and *Eretes* having again the largest difference (Tables 3 and 5).

DISCUSSION

Significant results were found for all the characteristics measured, despite some obvious methodological limitations of the study. The small number of specimens is a general drawback in the study of functional morphology (Wainwright, 1994), and for other organisms it has been shown that both the environmental conditions and the physiological state of the individuals can alter their swimming behaviour (e.g. Charoy & Clement, 1993; Charoy, 1995, or Vanduren & Videler, 1995). However, the fact that the differences between individuals of the same species were in general not significant could be indicative of the homogeneity of the swimming patterns of the species studied. Only three species had significant differences between individuals, and for only one variable, which did not however change the general interpretation of their swimming behaviour.

The lack of motivation to achieve maximum performances can be a problem in studying the correlation between morphology and performance (Losos & Miles, 1994). However, the relationship between maximum sinuosity and velocity demonstrated that in at least two large species, *Dytiscus* and *Graphoderus*, some trade-off in their manoeuvrability could be detected, with a significant decrease in the maximum sinuosity at the highest measured velocities. Daily changes in the level of activity might also condition the performances of some species, which were all recorded during the day.

The lack of significant correlation between any of the measurements of body size and maximum velocity is most likely to be the consequence of both the space limitation of the aquarium, which prevented large species from developing their maximum performance, and the lack of motivation. According to Nachtigall (1977) the 'average highest velocity' of *D. marginalis* was 40 cm s^{-1} , of *A. bipustulatus* 20 cm s^{-1} , and of *Hyphydrus ovatus* (L.) (a close relative of *H. aubei*, with a similar size and shape) 11 cm s^{-1} . In our study, differences between average and maximum velocity were not large, and maximum velocities of the largest species did not reach values close to their maximum performance. However, in small species such as *H. aubei* the maximum velocities measured were close to the maximum reported for *H. ovatus* in Nachtigall (1977). This might be a consequence of differences in the relative size of

the aquarium, the smaller species being able to develop higher relative velocities, but also to a positive allometry in the energetic cost of swimming. In aquatic diving beetles gravity is of small, if any, importance, owing to their buoyancy (Guignot, 1931–33; Nachtigall, 1977). Moreover, it has been suggested that some species can control buoyancy by changes in the volume of the air chamber or other air reservoirs within the abdomen (Hicks & Larson, 1991). Body inertia is also small, due to their low density in relation to water. Drag forces are thus the main factors to be considered in the energetic balance, and they are exclusively determined by the frontal area and the resistance coefficients (Nachtigall, 1974, 1977). In a selection of nine beetles, drag forces were found to be proportional to the third power of the body length (Nachtigall, 1977). In contrast, muscle force is proportional to the cross section of muscles, and hence roughly to the second power of the body length. This means that the energy cost of swimming increases with a positive allometry with respect to body length, and then it is more favourable for small species, which can swim almost continuously—and closer to their maximum speed—without substantially altering their energetic balance. Large species, however, swim slowly and often rest, but can dramatically increase velocity if necessary. According to Nachtigall (1974), average velocity of *Dytiscus marginalis* was in the same range of the velocities reported here, but it could reach up to 100 cm s^{-1} when pursuing prey or chasing a mate. At velocities of 5 cm s^{-1} , *Acilius sulcatus* L. (another large dytiscid, considered to have extreme characters of group 1 by Ribera & Nilsson, 1995) uses only about 1% of its available energy for thrust (Nachtigall, 1974).

Results were in general consistent with Ribera & Nilsson's (1995) interpretation of the morphometry of the species. *Deronectes opatrinus* and *Copelatus haemorrhoidalis* were the poorest swimmers, with a relatively more rectangular and narrow shape, and the maximum width and height in a more central position. In the morphological space described by Ribera & Nilsson (1995) poor swimmers had extreme negative scores for the third ordination axis, with long and slender hind legs, and a narrow body. Differences between both species refer mainly to the depth of the body, more flattened in *C. haemorrhoidalis* (with an extreme negative score for factor 2, Fig. 3B), the length of the femora, relatively shorter in *C. haemorrhoidalis*, and the body outline (continuous in *C. haemorrhoidalis*, and with marked angles between pronotum and elytra in *D. opatrinus*, Fig. 1). Considering that *Deronectes* was one of the smallest species, and that in consequence both the limitations of the size of the aquarium and the energetic cost of swimming were of less importance, the maximum measured velocity is likely to be much closer to its actual maximum velocity than in larger species. It was also the only species for which one of the specimens did not swim at all in the aquarium unless forced to do so, and then only with short trajectories close to the substratum. *Deronectes opatrinus* occurs in streams and small rivers, usually in pools or in areas with low water flow. The poor performance of *Copelatus* was also expected, as it is considered a species adapted to crawl among dense vegetation (Ribera, Isart & Régil, 1995b; Ribera & Nilsson, 1995).

Hyphydrus aubei clearly matched the prediction of good manoeuvrability. In the morphological space described by Ribera & Nilsson (1995) it had an extreme positive score for factor 2, with a globular shape, almost spherical, and long femora (Fig. 3B). It was the only species that could maintain a sinuous trajectory at relatively high speeds, and its average sinuosity was also high. Its high average velocity can be the consequence of the low energy cost of swimming in small species, and probably the maximum measured velocity, 11.17 cm s^{-1} , was close to the actual

maximum performance of the species (11 cm s^{-1} in *H. ovatus*, as seen above). Moreover, although the morphology of *Hyphydrus* was interpreted as a specialization in manoeuvrability, it has some of the typical adaptations of the group well developed, such as a continuous outline or long swimming hairs; in consequence, it was supposed to retain a better general performance in comparison with the less modified species of the group 3 (Ribera & Nilsson, 1995).

The swimming behaviour of *Eretes sticticus* was distinguished by its high average sinuosity, whereas its average and maximum velocities were similar to those of other species. However, the relation between velocity and sinuosity showed that the actual manoeuvrability of *Eretes* was not much better than in other species, and the sinuosity was largely limited to the trajectories with the lower velocities. In the aquarium with obstacles, the pattern of extreme sinuous movement at low velocities but more straight paths at higher velocities found in the unobstructed aquarium changed, with an increase in the average sinuosity and a steeper slope of the regression line between maximum sinuosity and velocity, despite the relative decrease in the maximum sinuosity at the lowest velocity. These results suggest that the sinuosity in the swimming pattern of this species is more a product of a behavioural influence than the result of a morphological adaptation to manoeuvrability, although its longer tarsi relative to other species of Dytiscinae could bear some mechanical advantage in manoeuvring at low velocities (Ribera & Nilsson, 1995). This can be considered an example of the distorting effect than behaviour or ecology can have in the predicted performance according to theoretical biomechanical considerations. Morphology can be considered as a framework that imposes biomechanical constraints associated with the phyletic inheritance of the species, but within this framework there is still the possibility of some flexibility in performance, through the filters of the behaviour and the ecology (Reilly & Wainwright, 1994; Ricklefs & Miles, 1994). *Eretes sticticus* is a typical inhabitant of temporary, small water bodies, in which it can develop very quickly, and migrate when the pond dries up (Kingsley, 1985). It is a very active beetle, with a good colonizing ability, and it is one of the few dytiscids than can be easily seen swimming actively in open waters (unpublished observations).

Hygrobia hermanni is another species with a peculiar morphology and life habits. The larvae exclusively eat Tubificidae, and the adults live in small ponds, usually with turbid water and silt bottoms (Balfour-Browne, 1922; Ribera, Isart & Régil, 1995a). Its average and maximum velocities were relatively high, and although its average sinuosity was low, it could maintain sinuous trajectories over a wide range of velocities. This could be expected owing to its globular shape and long and thin legs (with a relatively high score for factor 2, Fig. 3B). Having a less developed swimming method was not found to be disadvantageous in what refers to its average velocity, although the maximum measured velocities cannot be considered as the actual measure of its maximal performance.

Hygrobia hermanni frequently coexists with *Eretes sticticus* and *Hyphydrus aubei* in small ponds with a clay substratum and turbid water (Ribera *et al.*, 1995a, b). Although detailed studies in natural environments are necessary to draw any conclusions, it seems likely than the patterns in the swimming behaviour of these species may be related to the cloudiness of the water and to their predatory behaviour. *Hyphydrus aubei* is also found in ponds, channels or ditches with step edges, a kind of microhabitat in which other globular species of group 2 regularly occur (Ribera *et al.*, 1995b, Ribera & Nilsson, 1995).

Meladema coriacea was the species with the highest average and maximum velocities,

and, together with *Colymbetes*, were the only species for which no velocities lower than 4 cm s^{-1} were measured in the unobstructed aquarium (Fig. 2). Both species had typical morphologies of group 1, with negative scores for factor 1 in Figure 3B. *Colymbetes* had the second highest average velocity, but its maximum velocity was lower than that of *Hygobia*. Although non-significant (probably due to the low number of values), the relation between velocity and maximum sinuosity suggested that the manoeuvring performance of *Colymbetes* is poor. The low number of measured tracks in this species, and the fact that only one specimen could be analysed, has to be taken into account in evaluating its results. In *Meladema coriacea* the change of swimming behaviour in the aquarium with obstacles was an observed decrease in maximum and average velocity, with only a slight increase in sinuosity, despite being the second largest species. It is the largest European species of the subfamily Colymbetinae, and is found usually in small pools or in the shores of small streams (Ribera & Nilsson, 1995). Results of this study suggest that it could be considered to compromise between manoeuvrability and high speed performance. In contrast, *Colymbetes fuscus* lives in stagnant water, usually filled with vegetation, including artificial habitats such as watering places or small reservoirs (Ribera *et al.*, 1995b).

Dytiscus marginalis and *Graphoderus cinereus* performed poorly both in terms of average velocity and manoeuvrability, despite being considered among the good swimmers according to their morphology (with negative scores for factor 1 in Fig. 3B). When placed in an aquarium with obstacles, *Dytiscus* and *Graphoderus* decreased their velocity, but while *Dytiscus* also increased its sinuosity, *Graphoderus* maintained a similar swimming pattern. This can be due to the difference in the size of both species relative to the distance between the sticks, being *Dytiscus* more than twice longer than *Graphoderus*. The species of *Dytiscus* are among the largest of the family, and, according to Nachtigall (1977), they represent the limit to dynamic possibilities. Both the results of this study and unpublished observations suggest that the usual swimming behaviour of these beetles is of a very slow and steady velocity, with only occasional bursts of high speed. Although *Dytiscus marginalis* prefers relatively deep, open waters (with an optimum depth of 60 cm in the Pyrenees, Ribera *et al.* 1995b), it can be found regularly in small and shallow ponds at high altitudes, in which it is likely that it could not reach high velocities. *Graphoderus cinereus* is usually found in fens or ponds with a dense vegetation of reed and other macrophytes, and in comparison with other species of Dytiscinae, its morphology had some similarities with the species of group 4, considered to be adapted to crawl among dense vegetation or detritus (a more central position of the maximum width and depth of the body, Ribera & Nilsson, 1995). Its poor performance is consistent with this interpretation, although the spatial limitation of the aquarium prevent any conclusion about its actual maximum velocity.

In studying the relationships between morphology and swimming behaviour the habitat can be considered a template imposing a general constraint on the available strategies (e.g. a size limitation as water velocity increases, Bournaud, Richoux & Usseglio-Polatera, 1992; Ribera & Nilsson, 1995), but at the same time allowing the development of trade-offs that canalize the morphological adaptation to particular strategies and life habits (Southwood, 1988). These morphological trade-offs can result in a different use of the same habitat, as is the case of the species swimming freely in open waters and those dwelling among the vegetation in the edges. The understanding of the ecological and functional morphology of diving beetles requires the consideration of the constraints that the habitat impose, and the special use that

the species made of the habitat, in addition to the basic knowledge of the constraints posed by morphology. But this basic knowledge is still indispensable, and a prerequisite for any intent of determining performance and fitness in natural conditions.

ACKNOWLEDGEMENTS

We thank Anders Nilsson, Peter C. Wainwright, and an anonymous referee their useful comments to the original manuscript. The analysis of the swimming behaviour with the Hobson Sperm Tracker® (Hobson Tracking Systems Ltd, Sheffield) was made possible by a short stay of IR in the Institute of Zoology (London) in 1993. The videos were recorded while IR held a post-graduate grant in the Centro de Investigación y Desarrollo de Barcelona (Consejo Superior de Investigaciones Científicas). The Scottish Agricultural College receives financial support from the Scottish Office Agriculture, Environment and Fisheries Department.

REFERENCES

- Alarie Y.** 1995. Primary setae and pores on the legs, the last abdominal segment, and the urogomphi of larvae of Nearctic Colymbetinae (Coleoptera: Adephaga: Dytiscidae) with an analysis of their phylogenetic relationships. *Canadian Entomologist* **127**: 913–943.
- Balfour-Browne F.** 1922. The life-history of the water beetle *Pelobius tardus* Herbst. *Proceedings of the Zoological Society of London* **1922**: 79–97.
- Beutel RG.** 1995. The Adephaga (Coleoptera): phylogeny and evolutionary history. In: Pakaluk J, Slipinski SA, eds. *Biology, phylogeny, and classification of Coleoptera. Papers celebrating the 80th birthday of Roy A. Crowson*. Warsaw: Muzeum i Instytut Zoologii PAN, 173–217.
- Blackburn TM, Lawton JH, Perry JN.** 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. *Oikos* **65**: 107–112.
- Bournaud M, Richoux P, Usseglio-Polatera P.** 1992. An approach to the synthesis of qualitative ecological information from aquatic Coleoptera communities. *Regulated Rivers: Research and Management* **7**: 165–180.
- Charoy C.** 1995. Modification of the swimming behaviour of *Brachionus calyciflorus* (Pallas) according to food environment and individual nutritive state. *Hydrobiologia* **313**: 197–204.
- Charoy C, Clement P.** 1993. Foraging behavior of *Brachionus calyciflorus* (Pallas) – variations in the swimming path according to presence or absence of algal food (*Chlorella*). *Hydrobiologia* **255**: 95–100.
- Evans MEG, Forsythe TG.** 1984. A comparison of adaptations to running, pushing and burrowing in some adult Coleoptera: especially Carabidae. *Journal of Zoology, London* **202**: 513–534.
- Forsythe TG.** 1983. Locomotion in ground beetles (Coleoptera Carabidae): an interpretation of leg structure in functional terms. *Journal of Zoology, London* **200**: 493–507.
- Garland Jr. T, Losos JB.** 1994. Ecological morphology of locomotor performance in Squamate reptiles. In: Wainwright PC, Reilly SM, eds. *Ecological morphology. Integrative organismal biology*. Chicago: The University of Chicago Press, 240–302.
- Gould SJ, Vrba ES.** 1982. Exaptation – a missing term in the science of form. *Paleobiology* **8**: 4–15.
- Galewski K.** 1971. A study on morphobiotic adaptations of European species of the Dytiscidae (Coleoptera). *Polskie Pismo Entomologiczne* **41**: 4874–702.
- Guignot F.** 1931–33. *Les Hydrocanthares de France*. Toulouse: Miscellanea Entomologica.
- Haspenheide HA.** 1975. Prey characteristics and predator niche width. In: Cody ML, Diamond JN, eds. *Ecology and evolution of communities*. Cambridge: Harvard University Press, 158–180.
- Hicks B, Larson DJ.** 1991. The rectum as a hydrostatic organ in the predaceous diving beetle genus *Ilybius* Erichson (Coleoptera: Dytiscidae). *Coleopterist's Bulletin* **45**: 274–278.
- Holt WV.** 1993. Sperm assessment by computer. *Microscopy and Analysis, January*: 21.
- Holt WV, Palomo MJ.** 1996. Optimization of a continuous real-time computerized semen analysis

- system for ram sperm motility assessment, and evaluation of four methods of semen preparation. *Reproduction, Fertility and Development* **8**: 219–230.
- Kingsley KJ. 1985.** *Eretes sticticus* (L.) (Coleoptera, Dytiscidae) life history observations and an account of a remarkable event of synchronous emigration from a temporary dessert pond. *Coleopterist's Bulletin* **39**: 7–10.
- Lawrence JF, Newton AF. 1982.** Evolution and classification of beetles. *Annual Review of Ecology and Systematics* **13**: 261–290.
- Lauder GV. 1990.** Functional morphology and systematics: studying functional patterns in an historical context. *Annual Review of Ecology and Systematics* **21**: 317–340.
- Losos JB, Miles DB. 1994.** Adaptation, constraint, and the comparative method: phylogenetic issues and methods. In: Wainwright PC, Reilly SM, eds. *Ecological morphology. Integrative organismal biology*. Chicago: The University of Chicago Press, 60–98.
- Miles DB, Dunham AE. 1993.** Historical perspectives in ecology and evolutionary biology: The use of phylogenetic comparative analysis. *Annual Review of Ecology and Systematics* **24**: 587–619.
- Nachtigall W. 1974.** Locomotion: mechanics and hydrodynamics of swimming in aquatic insects. In: Rockstein M, ed. *The physiology of Insecta, Vol. 3 (2nd edition.)*. New York: Academic Press, 381–432.
- Nachtigall W. 1977.** Swimming mechanics and energetics of locomotion of variously sized water-beetles Dytiscidae, body length 2 to 35 mm. In: Pedley TJ, ed. *Scale effects in animal locomotion*. London: Academic Press, 269–283.
- Norberg U. 1994.** Wing design, flight performance, and habitat use in bats. In: Wainwright PC, Reilly SM, eds. *Ecological morphology. Integrative organismal biology*. Chicago: The University of Chicago Press, 205–239.
- Reilly SM, Wainwright PC. 1994.** Conclusion: ecological morphology and the power of integration. In: Wainwright PC, Reilly SM, eds. *Ecological morphology. Integrative organismal biology*. Chicago: The University of Chicago Press, 339–354.
- Ribera I, Isart J, Régil JA. 1995a.** Autoecología de algunas especies de Hydradephaga (Coleoptera) de los Pirineos. I. Gyrinidae, Haliplidae, Noteridae e Hygrobiidae. *Zoologica Baetica* **6**: 33–58.
- Ribera I, Isart J, Régil JA. 1995b.** Autoecología de algunas especies de Hydradephaga (Coleoptera) de los Pirineos. II. Dytiscidae. *Zoologica Baetica* **6**: 59–104.
- Ribera I, Nilsson AN. 1995.** Morphometric patterns among diving beetles (Coleoptera: Noteridae, Hygrobiidae, and Dytiscidae). *Canadian Journal of Zoology* **73**: 2343–2360.
- Ricklefs RE, Miles DB. 1994.** Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright PC, Reilly SM, eds. *Ecological morphology. Integrative organismal biology*. Chicago: The University of Chicago Press, 13–41.
- Roughley RE. 1981.** Trachypachidae and Hydradephaga (Coleoptera): a monophyletic unit?. *Pan-Pacific Entomology* **57**: 273–285.
- Southwood TRE. 1988.** Tactics, strategies and templets. *Oikos* **53**: 3–18.
- Vanduren LA, Videler JJ. 1995.** Swimming behavior of developmental stages of the calanoid copepod *Temora longicornis* at different food concentrations. *Marine Ecology* **126**: 153–161.
- Wainwright PC. 1994.** Functional morphology as a tool in ecological research. In: Wainwright PC, Reilly SM, eds. *Ecological morphology. Integrative organismal biology*. Chicago: The University of Chicago Press, 41–59.
- Webb PW. 1984.** Form and function in fish swimming. *Scientific American* **251**: 58–68.