STEPPING PATTERNS IN ANTS

II. INFLUENCE OF BODY MORPHOLOGY

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Summary

The locomotory behaviour of 12 ant species belonging to four different genera (Formicinae: *Cataglyphis*, *Formica*, *Lasius*; Myrmicinae: *Myrmica*) was studied by filming individuals during walking on smoked-glass plates. Subsequent multivariate analyses of walking kinematics and footfall positions showed marked species-specific as well as size-dependent differences in the locomotory behaviour. The geometric properties of the footfall patterns resulting from the alternating tripod gait scale to leg dimensions in a geometric manner. At high speed, footprint distances between succeeding tripods exceed maximum leg extension, indicating that ants are 'trotting' from one tripod to the next one with intermittent aerial phases. In at least one species (*Cataglyphis bombycina*), there is evidence for quadrupedal locomotion at the highest speed. The functional relationship between stride length (s, the distance between successive footprints of the same foot) and speed (v) was best described by a curvilinear model, $s=av^b$. Exponent b ranges from 0.3 to 0.6 and reveals differences between species. Within species, exponent b is constant, whereas factor a scales to leg length. Females and males show metachronal interleg coordination patterns rather than the alternating tripod coordination pattern seen in workers of the same species.

Introduction

In walking insects, the coordination patterns of the legs reflect to a large extent the constraints imposed by body morphology. Force measurements as well as biomechanical considerations have demonstrated that the scope of spatiotemporal interleg coordination patterns is limited by stability requirements (e.g. when walking around curves and when moving uphill or downhill) as well as by the general leg morphology (*Acheta domestica*: Harris and Ghirardella, 1980; *Blatella germanica*: Franklin, 1985; *Carausius morosus*: Cruse, 1976; Jander, 1985; Dean, 1991). The effects of body size and shape on arthropod gait patterns have been analysed in spiders (*Lycosa tarentula*, *Trochosa ruricola*: Ward

and Humphreys, 1981) and in crabs (*Ocypode quadrata*: Blickhan and Full, 1987), but comparative aspects of the kinematics of insect locomotion are only beginning to be investigated (Carabidae: Evans, 1977).

In this paper, the influence of body morphology on interleg coordination and walking kinematics is examined in different ant species. In this taxon, the degree of intraspecific diversity is considerable, with respect to both morphology and behaviour. Worker castes are wingless and appear to be specialized for terrestrial locomotion. Non-worker castes, i.e. males and females, are winged, and the latter cut off their wings after mating.

The ant species investigated here display high variability in both body proportions and size. Thus, differences in locomotory performance may be traced to a variety of factors, such as mechanical constraints, scale effects and caste-specificity or species-specificity of behaviour. These factors may be examined by comparative analyses of locomotion and morphology within/between species.

As has been shown in a previous paper (Zollikofer, 1994), walking worker ants exhibit rigid temporal and geometric tripod gait patterns over a wide range of speeds and degrees of curvature. These regular patterns build up a framework for the description of locomotory variables and for comparative analyses.

First, I relate spatial interleg coordination patterns to body morphology. After an evaluation of body size effects, features that are specific for species and/or castes (workers, females, males) can be extracted.

The same procedure is applied to walking kinematics. The analysis focuses on the relationship between stride length and speed. Furthermore, the relationship between speed and curvature is traced to morphological features as well as to factors affecting stability.

Materials and methods

Both the 12 ant species used in the experiments and the methods of data acquisition are as described in a previous paper (Zollikofer, 1994). In addition, females and males of *Lasius niger* have been included in the analysis. The variables describing footfall geometry, walking kinematics and morphology are described in Table 1. Species and numbers of individuals are listed in Table 2. The footfall geometry was determined by a set of variables indicating distances between tarsal imprints. The reference configuration was the alternating tripod gait pattern (tripods L1R2L3 and R1L2R3 act in antiphase; L is the left and R is the right side and 1, 2 and 3 represent the fore-, mid- and hindlegs, respectively). Tripod size was measured by the distance between the tarsal positions of a foreleg and of the ipsilateral hindleg (ipsilateral span, $d13$). The span between successive tripods was determined by the distance between the tarsal positions of a hindleg and of the successive contralateral foreleg (contralateral span, $c31$). Stride lengths of individual legs ($s1$, $s2$ and $s3$) were defined as the distance between successive imprints of the tarsus of the respective leg. These variables were used to calculate stride length $s=(s1+s2+s3)/3$, which measures the distance travelled in a full stride (Alexander, 1977). Variables describing walking kinematics were speed (v) and stride frequency ($f=v/s$). To analyze the stability when walking around curves, curvature (c), transverse acceleration ($a_t=v^2c$), the

Table 1. *List of variables*

Body morphology

h	Mean height above ground of the centre of mass (mm)
l	Mean lateral distance of midleg from body axis (mm)
$L1, L2, L3$	Length of fore-, mid- and hindlegs (mm)
$L2'$	$L2/Th$, relative length of midleg
m	Body mass (mg)
Th	Alitrunc length (mm)

Tripod geometry

$c31$	Contralateral span (mm) (distance between a hindleg tarsal position and the contralateral foreleg tarsal position of the subsequent tripod)
$c31'$	$c31/(L1+L3)$, relative contralateral span
$d13$	Ipsilateral span (mm) (distance between hindleg and foreleg tarsal positions belonging to the same tripod)
$d13'$	$d13/(L1+L3)$, relative ipsilateral span
s	Stride length (mm) (average of the distances between successive tarsal positions of the legs belonging to a tripod)
s'	$s/(2\times L2)$, relative stride length

Kinematics

a_t	Transversal acceleration $= v^2 c$ (m s^{-2})
c	Curvature $= 1/$radius of curvature (mm^{-1})
f	Stride frequency $= v/s$ (s^{-1})
v	Speed (mm s^{-1})

mean lateral distance of the midleg from the body axis (l) and the mean height above ground of the centre of mass (h) were determined. Body dimensions used in the analyses were body mass (m), the length of the thorax (Th) and the lengths of the fore-, mid- and hindlegs (measured from the coxofemoral joint to the tarsal tip; $L1$, $L2$ and $L3$, respectively). Relative dimensions have been calculated with the aim of eliminating the effects of body size and, to this end, average and peak values of a set of variables were related to the dimensions of the legs and of the thorax. Stride length was expressed as a proportion of the length of the midlegs, $s'=s/(2\times L2)$. Spans were related to the summed lengths of the fore- and hindleg ($L1+L3$), yielding $c31'=c31/(L1+L3)$ and $d13'=d13/(L1+L3)$. The relative length of the midleg was defined as $L2'=L2/Th$.

All statistical tests were performed with the Statistical Analysis Software package SAS. For each of the above variables, an analysis of variance was executed, modelling the effects of body mass, leg length and species; after excluding the effects of body size, differences between species were tested using F-statistics (SAS procedure GLM).

Results

Body dimensions

It is reasonable to assume that leg dimensions and body mass are among the most important scaling factors of locomotion. There are considerable interspecific as well as intraspecific differences in the sample studied here. Within species, body mass varies by up to a factor of 10 (Table 2), whereas relative leg length (Table 2, $L2'$) may be regarded

Table 2. *Morphological and locomotory variables of 12 ant species*

Species	N	Size range (mg)		L2′ (%)	d13′ (%)	s′ (%)	f (s⁻¹)	c31′ (%)
		Minimum	Maximum					
Cataglyphis albicans	5	1.8	8.2	2.5	54	62	17	106
C. bicolor	6	3.1	39.6	2.7	55	66	14	111
C. bombycina	10	2.8	30.4	2.6	50	68	20	104
C. fortis	5	4.6	29.2	2.8	51	64	19	99
Formica fusca	4	4.7	6.5	2.3	55	68	17	101
F. lefrançoisi	5	3.5	36.3	2.2	57	70	20	100
F. pratensis	5	4.6	21.6	2.3	54	61	10	97
Lasius flavus	3	0.7	1.4	1.9	59	66	10	104
L. fuliginosus	3	2.4	5.1	2.3	56	57	12	100
L. niger (worker)	3	1.7	1.8	2.3	56	64	19	107
L. niger (female)	2	20.2	26.0	1.4	53	53	11	98
L. niger (male)	1	2.2	2.2	2.0	55	41	12	93
Myrmica ruginodis	4	0.5	2.8	1.6	44	63	10	93

N, number of test individuals; $L2'$, relative midleg length; $d13'$, relative span between hindleg and foreleg swinging in phase; s', relative stride length; f, stride frequency; $c31'$, relative span between hindleg and consecutive foreleg; average values are given for $L2'$, $d13'$, s' and f; maximal values for $c31'$.

as constant. Log–linear regression of midleg length ($L2$) *versus* body mass (m) yields the following equations, depending upon the relative leg length ($L2'$).
Cataglyphis species ($L2'>2.4$):

$$\log L2 = (1.27 \pm 0.05) + \log m(0.326 \pm 0.02); \ (r=0.94; \ P<0.01),$$

other species ($L2'<2.4$):

$$\log L2 = (0.86 \pm 0.05) + \log m(0.338 \pm 0.03); \ (r=0.89; \ P<0.01).$$

The exponents (approximating 0.33) indicate a cubic relationship between body mass and leg length, suggesting that the locomotory apparatus scales to body mass as any other linear dimension. The long-legged *Cataglyphis* group, however, displays a higher scaling factor than the remaining species (comparison of intercepts, F-test, $P<0.05$).

Locomotory performance related to morphology

If related to body dimensions, the values of the variables characterizing the locomotory performance appear to be quite uniform within species. However, between-species comparisons reveal common traits of locomotory behaviour as well as species-specific features (Table 2).

For leg length, tripods turn out to be of a similar size in most species (Table 2, $d13'$). Significantly higher values were found only in *L. flavus* (analysis of variance, F-test, $P<0.05$). Mean stride length expressed as a proportion of leg length is similar in most species. Significantly lower values were found in females and males of *L. niger* (Table 2, s'; F-test, $P<0.05$). In contrast to stride length and tripod size, stride frequency reveals marked interspecific differences. High mean frequencies are found in *C. bombycina*, *C. fortis*, *F. lefrançoisi* and *L. niger* (Table 2, f).

In most species, the actual maximum values of the contralateral spans (Table 2, $c31'$) exceed the expected morphological limits given by the sum of the actual leg lengths ($L1+L3$). Thus, when running at high speed, ants are 'trotting' from one tripod to the next one, which would involve complete loss of ground contact during certain phases of the stepping cycle. Direct observation of aerial phases was not possible, since the resolution of the video apparatus was insufficiently high to show when all the legs were off the ground. However, ants running in a channel and filmed in close-up from the side did not attain 'trotting' speed.

Specific stepping patterns

In both females and males of *Lasius niger*, phase interrelationships between the legs were found to deviate from the usual pattern of tripod coordination. Frame-by-frame analysis of the video records revealed that forward locomotion in a straight line is characterized by an undulating movement of the body axis. Moreover, in females the hindlegs are dragged rather than used to exert propelling forces.

In *Cataglyphis bombycina*, the tripod pattern (L1R2L3, R1L2R3, etc.) is reduced, at the fastest speed, to a diagonal quadrupedal pattern (R2L3, L2R3, etc.), with only occasional use of the front pair of legs. A close analysis of the video sequences and the corresponding tarsal imprints revealed that foreleg contact diminishes with increasing speed, gradually leading to a complete lift-off of the forelegs. Distances between tarsal imprints during this quadrupedal gait indicate that there are aerial phases between the stance phases of the dipods.

Relationship between stride length, speed and body size

As stated earlier, mean stride frequency varies considerably between species, whereas mean stride length is proportional to the leg dimensions. Thus, any individual may display a specific combination of stride frequency (f) and stride length (s) to attain a given speed (v), depending on its leg dimensions and species-specific variables.

The analysis of these interdependencies is confined to the relationship between s and v (f is given by v/s), and is described by a log–linear regression model:

$$\log s = a + b \log v. \tag{1}$$

Within each species, the individuals were grouped into size classes according to their midleg length. The resulting s/v functions were compared between and within species (Table 3). Within a given species, the regression equations mainly differ by proportionality factors (intercepts a), whereas the exponents (slopes b) are similar. Increasing leg length causes an upward parallel shift of the regression lines. The between-species comparison of similar size classes reveals differences in both slopes and intercepts, suggesting species-specificity of these factors.

A synopsis of these results is given in Fig. 1A. Locomotory performance is characterized by stride length at a Froude number of 1, i.e. at speed:

$$v = (\boldsymbol{g}h)^{1/2}, \tag{2}$$

where v is the maximum speed attainable with the 'inverted pendulum' mechanism of walking, $\boldsymbol{g}$ is the gravitational constant and h is the radius of the inverted pendulum (Alexander, 1977). Stride length attained at $v=(\boldsymbol{g}h)^{1/2}$ has been plotted against the height

Table 3. *Coefficients of log–linear functions log$v$=a+blogs, relating speed to stride length*

Species	Midleg length $L2$ (mm)	N	r^2	a	s_a	b	s_b
Cataglyphis albicans	3.5–4.5	292	0.66	−0.13	0.07	0.41	0.02
	5.5–6.5	322	0.62	0.10	0.02	0.49	0.02
C. bicolor	4.5–6.5	444	0.53	0.45	0.67	0.34	0.02
	6.5–8.5	289	0.58	0.35	0.10	0.41	0.02
	10.5–12.5	202	0.36	0.96	0.16	0.34	0.03
C. bombycina	5.5–6.5	269	0.67	−1.03	0.13	0.60	0.03
	6.5–8.5	943	0.69	−0.72	0.06	0.57	0.01
	8.5–10.5	216	0.64	−0.26	0.14	0.53	0.03
C. fortis	5.5–6.5	99	0.42	−0.16	0.25	0.43	0.05
	6.5–8.5	269	0.68	−0.62	0.12	0.55	0.02
	8.5–10.5	147	0.71	−0.40	0.15	0.54	0.03
Formica fusca	3.5–5.5	538	0.75	−0.81	0.06	0.56	0.01
F. lefrançoisi	3.5–4.5	230	0.54	−0.65	0.14	0.51	0.03
	4.5–5.5	298	0.77	−0.60	0.08	0.51	0.02
F. pratensis	3.5–4.5	251	0.54	0.06	0.10	0.40	0.02
	4.5–5.5	172	0.85	−0.47	0.08	0.54	0.02
	5.5–7.5	374	0.56	0.92	0.05	0.26	0.01
Lasius flavus	1.5–2.5	462	0.63	−0.45	0.05	0.44	0.02
L. fuliginosus	3.5–4.5	389	0.56	−0.21	0.02	0.43	0.02
	4.5–5.5	213	0.45	−0.07	0.12	0.40	0.03
L. niger (worker)	2.5–3.5	450	0.70	−0.61	0.06	0.45	0.01
L. niger (female)	4.5–5.5	239	0.11	0.60	0.17	0.24	0.04
L. niger (male)	3.5–4.5	84	0.06	0.06	0.40	(0.29)	0.17
Myrmica ruginodis	0.5–1.5	205	0.32	−0.18	0.10	0.29	0.03
	2.5–3.5	541	0.50	0.11	0.05	0.33	0.01

Individuals were assigned to size classes according to midleg length $L2$ (mm).

Functions are characterized by the number of data points (N), the square of the correlation coefficient (r^2), the intercept (a) and slope (b) and their respective standard errors (s_a, s_b); slope values are significantly different from zero (*t*-test, $P<0.01$), except those for *L. niger* males.

of the centre of mass above ground (h). For species consisting of more than one size class, data fit the regression lines with roughly similar slopes (0.8–1.0). Thus, stride length at a Froude number of 1 appears to scale in a dynamically similar way, as defined by Alexander (1977), to h for most species. This effect corresponds to the upward parallel shift of the s/v regression lines with increasing leg length.

To facilitate comparisons of the locomotor behaviour of ants with a wider range of animals, mean speed and mean stride length of each individual were transformed to dimensionless numbers (Alexander, 1977):

$$\hat{v} = v/(\boldsymbol{g}h)^{1/2}, \tag{3}$$

$$\hat{s} = s/h. \tag{4}$$

Equation 3 relates speed (v) to speed at a Froude number of 1 (see equation 2). As stated above, stride length (s) at a Froude number of 1 scales in a geometric manner to h
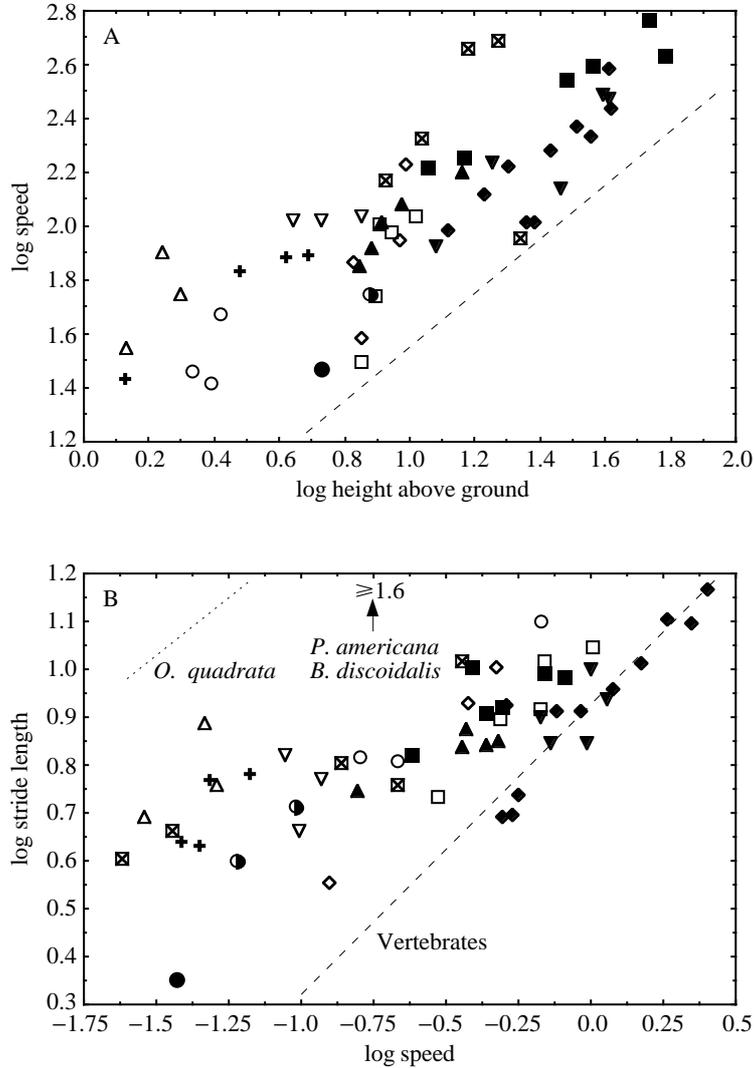
Fig. 1. Locomotory behaviour of ants related to morphology. (A) Double logarithmic plot of stride length s (mm) attained at speed $v=(gh)^{1/2}$ (at a Froude number of 1) *versus h* (mm), where h is the mean height above ground of the centre of mass and g is the acceleration due to gravity. Within species, the individuals appear to be spread along characteristic regression lines with similar slope (the dashed line has a slope of 1.00 for comparison). (B) Double logarithmic plot of dimensionless stride length ($\hat{s}=s/h$) *versus* dimensionless speed [$\hat{v}=v/(gh)^{1/2}$]. Each data point represents mean values of $\hat{s}$ and $\hat{v}$ for one ant. The individuals appear to be spread along species-specific regression lines; ▲, *Cataglyphis albicans*; ■, *C. bicolor*; ◆, *C. bombycina*; ▼, *C. fortis*; ◇, *Formica fusca*; □, *F. lefrançoisi*; ⊠, *F. pratensis*; △, *Lasius flavus*; ▽, *L. fuliginosus*; ○, ◑, ●, *L. niger* worker, female and male, respectively; +, *Myrmica ruginodis*. The dashed line ($\hat{s}=2.3\hat{v}^{0.6}$) characterizes locomotion of a variety of vertebrates (man, horse, kangaroo, ostrich; Alexander, 1977); the dotted line indicates sideways-walking at low speeds in the ghost crab *Ocypode quadrata* (calculated after Blickhan and Full, 1987); the arrow indicates estimated values of $\log\hat{s}\geqslant1.6$ at $\log\hat{v}=-0.75$ for cockroaches (*Periplaneta americana*, Delcomyn, 1971; *Blaberus discoidalis*, Full and Tu, 1990).

within species (Fig. 1A). Hence, equation 4 merges the intraspecific $\hat{s}/\hat{v}$ relationships into a single line, without affecting the slope (*b*) of the original *s*/*v* relationship. A plot of the individual mean values of $\hat{s}$ against $\hat{v}$ (Fig. 1B) shows that, for each species, the data fit regression lines with slopes similar to those described in Table 3. Species can be characterized by their relative position in the graphs (Fig. 1A,B). In dynamically similar situations, *Cataglyphis bombycina* (Fig. 1, ◆) generally walks with a lower stride length (and thus at higher stride frequency) than, for example, *Formica pratensis* (Fig. 1, ⊠). Comparative data from other arthropods (Delcomyn, 1971; Blickhan and Full, 1987; Full and Tu, 1990) and from vertebrates (Alexander, 1977) will be discussed below.

Relationship between speed, curvature and morphology

An ant walking along a path with a curvature *c* will lose stability if its longitudinal speed exceeds a certain limit, v_{max}. The transverse acceleration a_t at v_{max} is given by:

$$a_t = v_{max}^2 c. \tag{5}$$

If we assume that a tarsus acts as a lateral strut on the centrifugal side of the curve, with lateral distance *l* and vertical distance *h* to the centre of mass, then, relative to that tarsal position, gravitation elicits a moment *mgl*, while the transverse acceleration elicits a moment $ma_t h$. At equilibrium $a_t h = gl$. Hence:
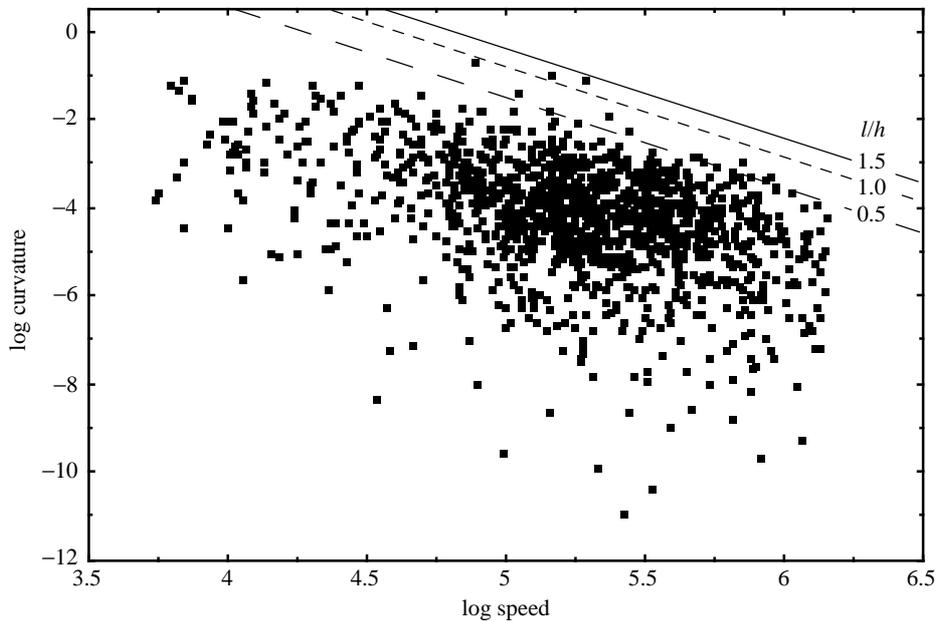
$$v_{max}^2 = (\boldsymbol{g}/c)(l/h). \tag{6}$$

Fig. 2. Curvature *c* (mm^{-1}) *versus* speed *v* (mm s^{-1}) in *Cataglyphis bombycina* (10 individuals); lines indicate critical values for *v* and *c* at given ratios of *l*/*h* (lateral extension of midleg/height of centre of mass, actual value=1.4). Points above the critical lines indicate loss of equilibrium for a given *l*/*h* ratio.

Data for speed and curvature are given for *Cataglyphis bombycina* in Fig. 2. In this species, transverse accelerations of $6.2\,\mathrm{m\,s^{-2}}$ are attained; the l/h ratio was found to be 1.4. Plotting curvature against speed shows that, during curve-walking, the mechanical limitations imposed by body morphology are reached: in a few cases, critical values of v_{max} for a given curvature are attained (Fig. 2). In most cases, however, the speed–curvature relationship follows submaximal l/h lines.

Discussion

Morphological constraints and stability

In general, at moderate speed the walking trajectory of ants is characterized by stride lengths well below the maximum span between legs. At high speed, however, this figure is exceeded and there are gaps between succeeding tripods, indicating a temporary loss of static equilibrium and even some aerial phases. Comparable behaviour has been reported for other fast-running animals. Loss of ground contact is well known in insects (*Periplaneta americana*: Full and Tu, 1991), in crabs (*Ocypode quadrata*: Blickhan and Full, 1987) and in vertebrates (Heglund *et al.* 1974). The results presented here suggest that it is a common feature of ant locomotion.

Cataglyphis bombycina has been reported to exhibit a quadrupedal (diagonal) gait at top speed, indicating that the forelegs lose ground contact and that static equilibrium is lost. The same behaviour has been described in *Periplaneta americana* (Full and Tu, 1991). Both findings suggest that the forelegs play a minor role in generating forward thrust. Direct force measurements in *Carausius morosus* (Cruse, 1976), *Acheta domestica* (Harris and Ghirardella, 1980) and *Periplaneta americana* (Full *et al.* 1991) demonstrate that the forelegs act as supports to maintain equilibrium, whereas the rear legs exert substantial amounts of propulsive force.

It has been shown that the position of the centre of mass relative to the supporting legs is crucial for stability during curve-walking. Ants never seem to risk being tilted over by centrifugal force. Maximum speed is lowered as curvature increases (Fig. 2), yielding transverse accelerations well below their critical limits. However, workers of *C. bombycina* occasionally reach the limit of stability (Fig. 2). Turning at high angular velocity in this species may be interpreted as an adaptive strategy and will be discussed below.

Comparative aspects of ant locomotion

To compare the locomotion of ants with that of larger animals, stride length and speed were scaled to dynamically similar conditions, yielding dimensionless numbers $\hat{s}$ and $\hat{v}$. Compared with ants, the crab *Ocypode quadrata* (Blickhan and Full, 1987) exhibits higher values of $\hat{s}$, and estimates made for cockroaches (Delcomyn, 1971; Full and Tu, 1990, 1991) suggest that $\hat{s}$ is even larger. However, mean values of $\hat{s}$ and $\hat{v}$ for ants and vertebrates lie in the same area of the graph, i.e. these animals seem to walk in a dynamically similar way. This observation gives rise to some tentative conclusions. In walking vertebrates (Heglund *et al.* 1982), an important percentage of the potential energy of the centre of mass is converted to kinetic energy by the inverted pendulum

mechanism. Energy transfer is less pronounced in crabs (Blickhan and Full, 1987) and is virtually absent in fast-running cockroaches (Full and Tu, 1990, 1991). While the range of $\hat{v}$ is similar in the taxa represented in Fig. 1, the values of $\hat{s}$ are diverse. If we assume a relationship between a pendulum-like gait and $\hat{s}$, it may be inferred that, with respect to efficient energy transfer, ants behave more like vertebrates than like crabs or cockroaches.

The log–linear regression equations relating stride length to speed in ants yielded a mean exponent of 0.44, ranging from 0.26 to 0.60 (Table 3). Comparable values have been found in Carabidae (Evans, 1977; exponent 0.27), *Periplaneta americana* (Delcomyn, 1971; exponent 0.24) and in vertebrates (Alexander, 1977; exponent 0.60). The exponent may be interpreted as the relative contribution of lengthening stride and increasing stride frequency to increases in walking speed. In ants, the exponent is comparatively high. Thus, the contribution of stride length plays a major role in ants and vertebrates, whereas in Carabidae as well as in *Periplaneta americana*, frequency modulation appears to be more important. Compared with Carabidae, *Periplaneta americana* (Delcomyn, 1971; Full and Tu, 1991) and *Carausius morosus* (Jander, 1985), ants appear to be relatively long-legged insects; the ranges of leg movements relative to the body are considerable and show substantial overlap between adjacent legs. Furthermore, stride length is relatively large compared with body size. By 'trotting' from one tripod to the next, stride length can be extended beyond the limits imposed by the maximum spans between the legs.

The $\log s = a + b \log v$ relationship allows me to draw some general conclusions on scaling and species-specificity of worker ant locomotion. The intraspecific effects of body size on the s/v relationship are restricted to variations in the proportionality factor a, which scales in a geometric manner to the height of the centre of mass above ground and, likewise, to leg length in each species (Fig. 1A). Marked between-species differences were found in the strategies used to attain a given speed by a specific combination of stride length and frequency. These differences are expressed by the exponent b. Evidence for similar scale effects was found in Carabidae (Evans, 1977). The above findings, together with the data presented in Table 3, indicate that species-specific traits of locomotion may be characterized and related to environmental constraints.

All measurements of the four *Cataglyphis* species were at one temperature (30 °C). Thus, the results of the locomotor analyses of these species are directly comparable. The most striking results were found in *C. bombycina* and *C. fortis*. In these ants, mean speed is comparatively high (1 m s^{-1} in field observations; Wehner, 1983) as a result of their high stride frequency and their long legs. Compared with these species, *C. bicolor* and *C. albicans* run with a significantly lower mean stride frequency but with a similar relative mean stride length. The four *Cataglyphis* species mentioned here are desert inhabitants, mainly feeding on arthropods that succumb to heat stress (Wehner, 1983, 1987). The sublethal conditions outside the nest force these ants to minimize their foraging time. Thus, selection favouring high-speed locomotion may have led to a variety of adaptations, such as long legs, 'trotting', a high stride frequency and, in the case of *C. bombycina*, quadrupedal locomotion. The high rotation velocities reported in the latter species (Wehner, 1987) are most often observed in escape behaviour: when threatened,

the animal starts to run in erratic trajectories, evading potential predators (R. Wehner, personal communication). There is further selective pressure favouring long legs in these species. The temperature gradient a few millimetres above the desert ground is very steep. Thus, each millimetre that the body of the ant is raised above the ground helps to lower heat stress (Wehner, 1987).

The locomotory behaviour of the *Formica*, *Lasius* and *Myrmica* species was measured at 22 °C. As mean speed in ants exhibits a strong Q_{10} and little is known about the optimal temperature for each species, these factors potentially confound interspecific comparisons. However, the myrmicine species *M. ruginodis* does not exhibit any specific locomotory trait that would allow the separation of Formicinae from Myrmicinae with respect to walking behaviour.

The females and males of *L. niger* have been shown to differ from workers in most aspects of their locomotory behaviour. Although workers can be regarded as highly specialized wingless runners, in females and males, as a result of their ability to fly, terrestrial locomotion appears to be of minor importance. The legs of the males are probably more important in copulation than in locomotion, while in females burrowing may be more important than covering long distances on the ground.

The above arguments demonstrate that the comparative analysis of walking behaviour helps to establish group-specific features of locomotion that can be related to morphological and ecological constraints.

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