

## BIOPHYSICS

## Leg force interference in polypedal locomotion

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The examination of gaits and gait changes has been the focus of movement physiology and legged robot engineering since the first emergence of the fields. While most examinations have focused on bipedal and quadrupedal designs, many robotic implementations rely on the higher static stability of three or more pairs of legs. Thus far, however, the effect of number of pairs of legs on locomotion dynamics has not been examined. Accordingly, the present approach aims to extend available theory to polypedal designs and examines how the number of active walking legs affects body dynamics when combined with changing duty factors and phase relations. The model shows that ground force interference of higher numbers of active pairs of walking legs can prevent effective use of bouncing gaits, such as trot, and their associated advantages, such as energy efficiency, because significantly higher degrees of leg synchronization are required. It also shows that small changes in the leg coordination pattern have a much higher impact on the center-of-mass dynamics in locomotor systems with many legs than in those with fewer legs. In this way, the model reveals coordinative constraints for specific gaits facilitating the assessment of animal locomotion and economization of robotic locomotion.

## INTRODUCTION

Usually, intermediate and fast-legged locomotion in terrestrial arthropods, such as insects and arachnids, is considered as closely connected to the synchronous activity of diagonally adjacent legs, for instance, tripodal sets of legs in insects (1, 2). By contrast, recent research revealed deviating symmetrical (3) leg coordination patterns in a couple of fast-running species such as cockroaches, mites, and spiders (4–6). Given appropriate leg properties, alternating sets of legs facilitate the employment of spring-mass dynamics well known from running bipeds and trotting terrestrial vertebrates (7, 8). Locomotor apparatuses with legs acting similarly to mechanical springs that support the body during stance are found to be energy-efficient structures, which provide high degrees of dynamic stability (5, 7, 9).

Locomotor apparatuses rely on the mechanical and physiological properties of their components, that is, the legs that constitute it. In arthropods moving straight ahead on level substrate, frontal leg pairs only decelerate, and rear legs only accelerate (10, 11). Accordingly, most arthropod legs experience either flexion or extension during a contact phase, which effectively prevents energy storage and recovery within the legs. With sprawled legs, the only structures that can store elastic energy are the hips if they were first deflected in a dorsal direction and flexed ventrally in the later stance phase (12). This implies that only vertical forces and movement energy can be recovered, and vertical amplitudes of the center of mass (COM) directly affect the capacity of elastic energy storage. The propensity to only recover vertical energy is less significant in fast-moving vertebrates with their flexible spines and erect legs. In vertebrates, all legs can contribute to deceleration and acceleration (7, 13). Each leg can store movement energy in the initial stance phase and recycle it in the later stance phase, while energy storage and recovery involve both vertical and fore-aft directions. Accordingly, the vertical amplitude of the COM is not necessarily equivalent to the length changes of the legs and the amount of temporarily stored elastic energy in vertebrates (13), although the stiffness per leg appears to be similar among a wide range of species and body plans (7).

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However, with increasing running speed and declining contact durations, spring-mass dynamics require increasing vertical amplitudes of the COM (14, 15), which might be hampered by the typically sprawled legs and the low COM positions in arthropods. If required vertical oscillations cannot be maintained due to limitations of the material properties of the load-bearing skeletal components (16), the specific design or position of the legs (5), or limitations of the muscular system (17), the elastic capabilities of tendons and other compliant structures can no longer be appropriately exploited.

If legs are considered as damped mechanical oscillators (12, 18), the ratio of potentially recovered and dissipated energy, that is, the damping ratio, gains importance. While oscillation energy grows with the second power of the oscillation amplitude, energy dissipation relies on viscoelastic processes and increases with the second power of speed. The mean vertical speed of the COM in spring-mass systems during stance depends on the amplitude and the available time frame, that is, the contact period. Since contact periods decrease hyperbolically with running speed (4, 6, 19), the vertical speed of the COM increases exponentially even if amplitudes would remain constant. The dissipated energy grows with the second power of this speed, such that the slope of the dissipated energy becomes much steeper than that of the potentially recovered oscillation energy (fig. S1). Consequently, with increasing running speed and depending on the damping ratio, the locomotor system may transform from an underdamped to an overdamped oscillator, which would eventually prevent energy-efficient oscillations. Small animals, such as insects, are particularly prone to high damping ratios (20, 21). Accordingly, gait changes are to be expected if the animals pass through significant ranges of contact durations and running speeds, even though arthropods and most other animals maintain high running speeds only for short periods of time (22).

Mathematical models are widely used for the computation and analysis of legged locomotion in men, birds, and to some extent, even for quadrupedal and hexapedal animals and robotic implementations. However, reduced analytic and numerical model concepts struggle with temporally overlapping activities of more than two legs or synchronized sets of legs [for example, (23)]. In polypedal organisms with temporally shifted activities and varying degrees of overlap between

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successive stride phases, these simple spring-mass models are not applicable. Kinematic models, in turn, are well suited for the description of the temporal activities of the single legs within locomotor apparatuses with arbitrary numbers of legs [for example, (2, 3)]. However, these model approaches largely disregard locomotion dynamics and ground reaction forces exerted by the legs. Therefore, they do not give any insight into the consequences of the legs' activities on movement dynamics or whether requirements for certain COM dynamics can be fulfilled by an animal.

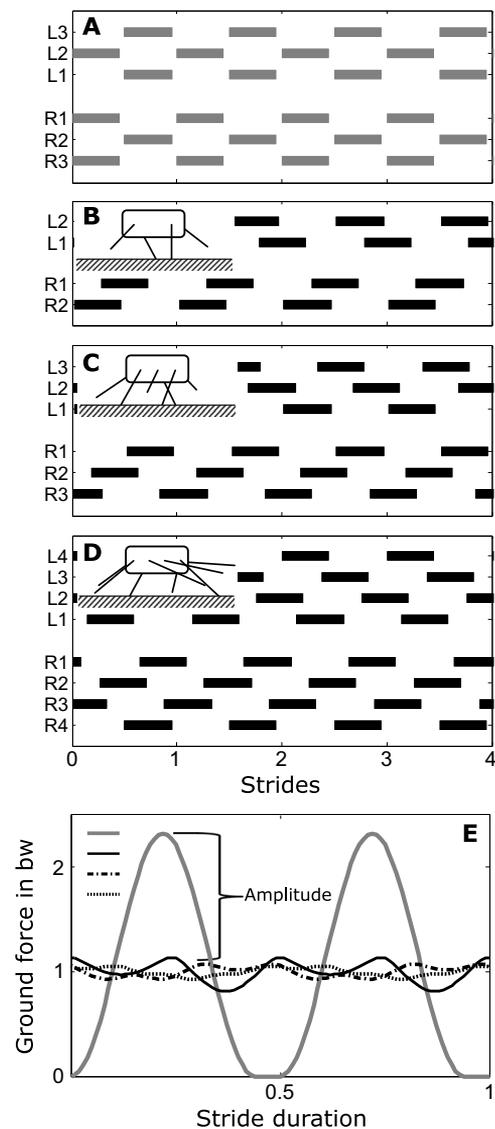
Therefore, the present study aims to combine the best of both worlds by introducing typical single leg ground forces to a kinematic model approach. Major outcomes of spring-mass dynamics are as follows: similar, approximately symmetrical vertical ground reaction forces of all walking legs and summed-up vertical forces that oscillate about body weight (bw) (7, 24). Ground reaction forces induce changes in the momentum and kinetic energy of the animal's body. Accordingly, oscillation amplitudes of an animal's body are determined by those of overall ground reaction forces (11, 25). In particular, the vertical ground force and oscillation amplitudes of the COM are crucial for the efficacy of elastic structures in the walking legs with regard to the storage and recovery of movement energy (12, 26).

The essential parameters in kinematic descriptions of gaits are the duty factor, that is, stance period divided by stride period, and the phase shifts between ipsilateral adjacent legs  $\theta$  (3). In many species, the speed dependency of the duty factor is highly nonlinear (4, 6, 8), whereas phase relations seem to be adjusted both continuously and in discrete steps, depending on the particular biomechanical constraints (3, 27, 28). Both measures directly affect the maximum total forces exerted by the legs and the resulting COM dynamics.

The present approach provides insight into the effects of changing leg numbers, duty factors, and  $\theta$  on the fluctuation amplitudes and frequencies of the total vertical ground reaction forces. It shows that maximum force amplitudes decline more quickly with increasing deviation from alternating leg coordination as the number of walking legs increases. Duty factors, in turn, markedly affect the absolute force amplitudes but have no effect on the relative decline over the phase range. Phase shifts between adjacent ipsilateral walking legs deviating significantly from 0.5 (alternation) or 1 (concurrency) increase the minimum number of legs in contact with the ground, which presumably leads to increased proprioception and controllability of the locomotion.

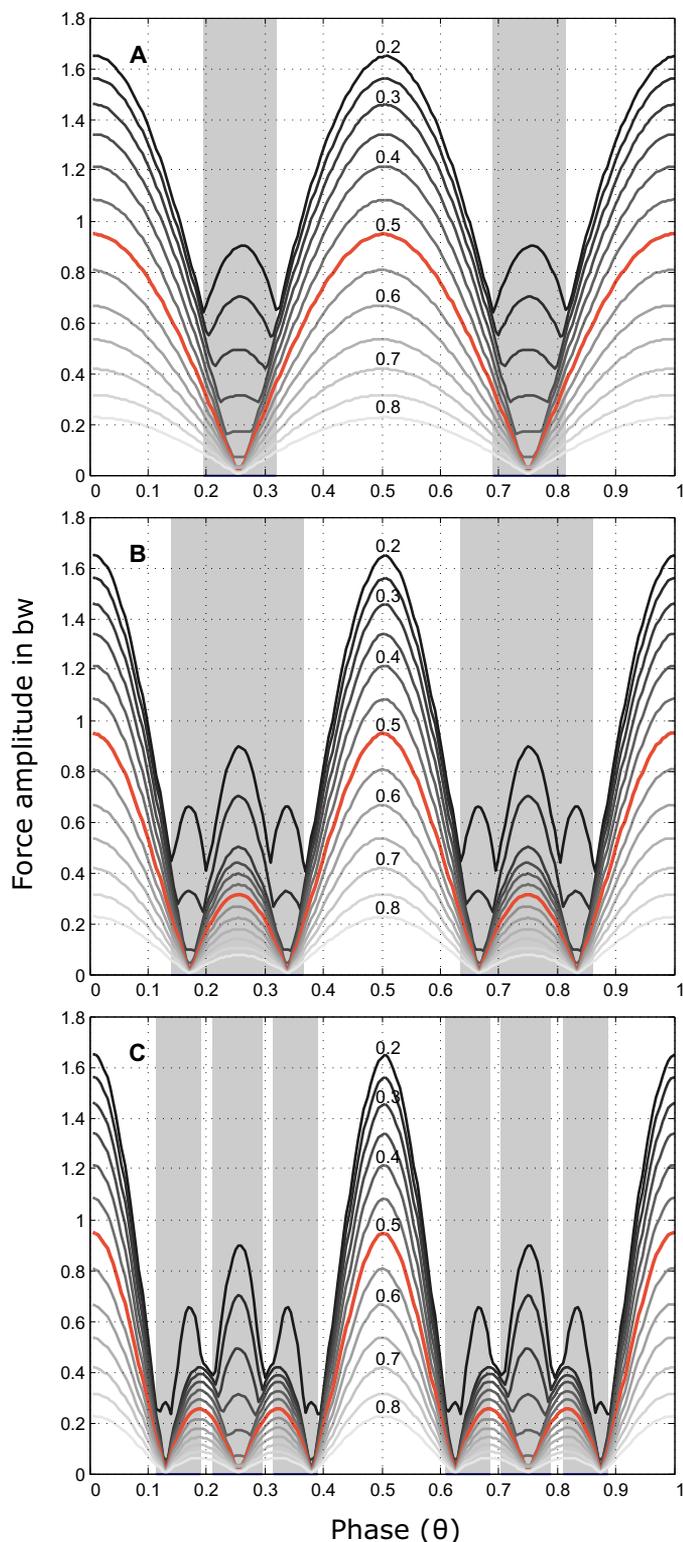
## RESULTS

Depending on the number of legs involved in the generation of ground reaction forces, even relatively small changes in  $\theta$  may result in significant alteration of the vertical force amplitudes (compare Fig. 1 for examples). However, the absolute changes are small if duty factors are high, and become substantial if duty factors are lower than about 0.7 (Fig. 2). Independent from the number of legs, maximum amplitudes of vertical forces are about 1 bw with duty factors of 0.5. Since the vertical momentum generated by the walking legs has to compensate for body weight over a stride, peak-to-peak values (that is, the difference between the lowest and highest force values) are twice as high (Fig. 1E). Maximum force amplitudes are 1.65 bw with duty factors of 0.2 and decrease almost linearly with increasing duty factors (Fig. 2). At a duty factor of 0.8, maximum force amplitudes are 0.23 bw, which is only about one-seventh of the former value.

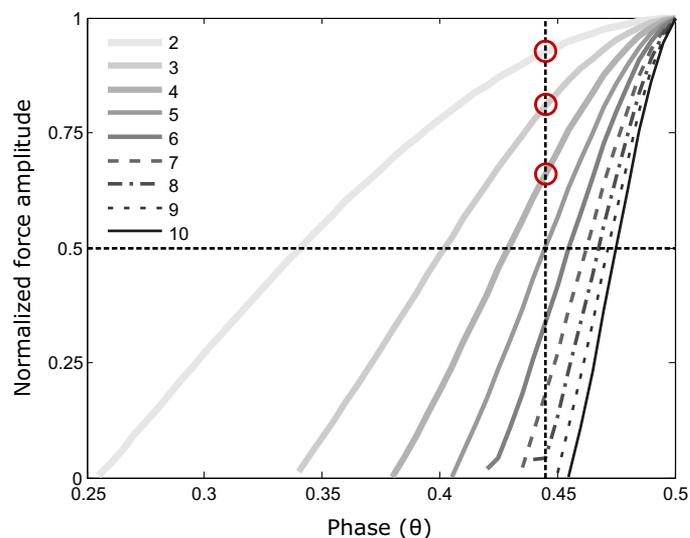


**Fig. 1. Gait patterns of four-, six-, and eight-legged locomotor systems (A to D) and corresponding overall ground forces over a stride (E) for single leg duty factors of 0.45 (that is, contact duration < swing duration).** Bars represent contact phases; left (L) and right (R) legs are counted fore to aft. (A) Gait pattern of a trotting hexapod; ipsilateral phases are 0.5. (B to D) Ipsilateral phase shifts (0.26, 0.34, and 0.38) and corresponding gait patterns produce minimal vertical force amplitudes for given numbers of legs (four, six, and eight). These gait patterns correspond to the overall vertical ground forces shown in (E). The gray solid line refers to (A), the black solid line refers to (B), the dash-dotted line refers to (C), and the dotted line refers to (D).

In locomotor apparatuses with three pairs of legs, vertical ground forces maintain only half of their maximum amplitude if  $\theta$  is 0.4 (Fig. 3). The phase shift at which amplitude values are halved is independent of the duty factor but changes with the number of legs and adopts a saturation curve (Fig. 4). Thus, the halving phase shift is 0.427 in locomotor apparatuses with four pairs of legs and 0.443 in those with five pairs of legs. In locomotor systems with higher leg numbers, values progressively converge to 0.5. However, with only two pairs of active walking legs, the critical phase shift is 0.34, representing the



**Fig. 2. Dependency of total vertical leg force amplitudes on the phase shift of ipsilateral adjacent legs and duty factor for locomotor apparatuses with two to four leg pairs.** (A) Two pairs of walking legs: Duty factors range from 0.2 (dark gray) to 0.8 (light gray) with the duty factor of 0.5 highlighted in red. With low duty factors and intermediate phase shifts, the peak frequency of the force oscillations deviates from two times the stride frequency; these intervals are shaded in gray. (B) Three pairs of legs. (C) Four pairs of legs.

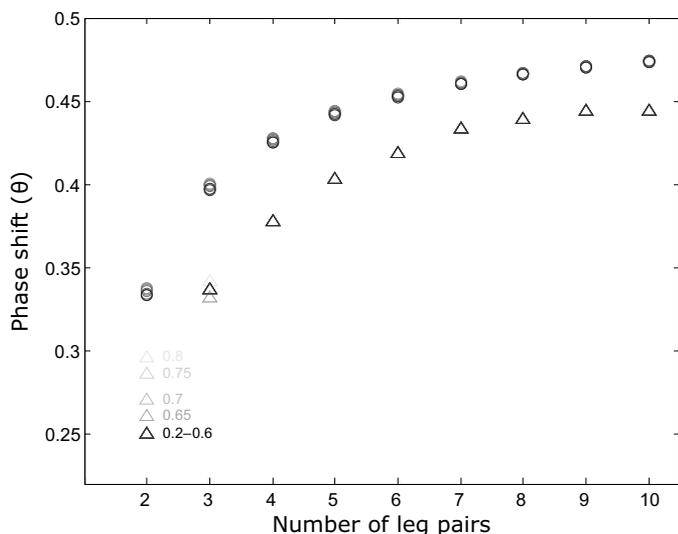


**Fig. 3. Specific amplitudes of the overall vertical ground reaction forces for locomotor apparatuses with 2 to 10 pairs of legs (see legend).** Data are shown for a duty factor of 0.5 in the phase range from the amplitude minimum closest to alternating leg coordination to the amplitude maximum at alternating sets of legs (compare Fig. 2). The slope of the amplitudes increases significantly with an increasing number of leg pairs. The trajectories' points of intersection with the horizontal dashed line indicate those  $\theta$  at which only one-half of the maximum force amplitude is retained (see Fig. 4). The vertical dashed line represents a deviation of 0.06 from the strictly alternating gait pattern as found in fast-running desert ants (see main text for further explanations). The red circles indicate the force amplitude values for locomotor systems with two, three, and four pairs of legs at such a deviation from strict alternation.

highest difference from the alternating case. The force amplitude minima show a similar behavior to the half peak values with respect to  $\theta$  (Fig. 4). In locomotor apparatuses with three pairs of legs, minimum force amplitudes occur at  $\theta = 0.34$ ; with four pairs of legs, it is 0.38; and with five pairs of legs, it is 0.4. With higher leg numbers, minimum force amplitudes occur at even larger phase shifts, that is, smaller deviations from  $\theta = 0.5$ . Locomotor apparatuses with only two pairs of legs experience relatively high force amplitudes in the phase range from 0.2 to 0.3 if duty factors are low (Figs. 2 and 4); therefore, the position of the force amplitude minimum changes with the duty factor. The values are as high as 0.32 with a duty factor of 0.3 and decrease toward 0.25 at higher duty factors.

Specifically, at low duty factors and intermediate ipsilateral phases, harmonics may occur that result in oscillation frequencies of the vertical forces adopting multiples of two times the stride frequency (that is, the value to be expected for alternating leg coordination and required for appropriate loading of elastic structures in the leg). In locomotor apparatuses with two pairs of legs, phases with oscillation frequencies higher than two range between 0.2 and 0.32; in locomotor apparatuses with three pairs of legs, they range between 0.14 and 0.36 and between 0.12 and 0.39 in those with four pairs of legs (Fig. 2).

Ipsilateral phase shifts significantly deviating from 0.5 result in an increase of the minimum number of legs in contact with the ground. Sufficiently high deviations can even prevent phases without any legs on the ground, although single leg duty factors are then significantly lower than 0.5 (Fig. 5).



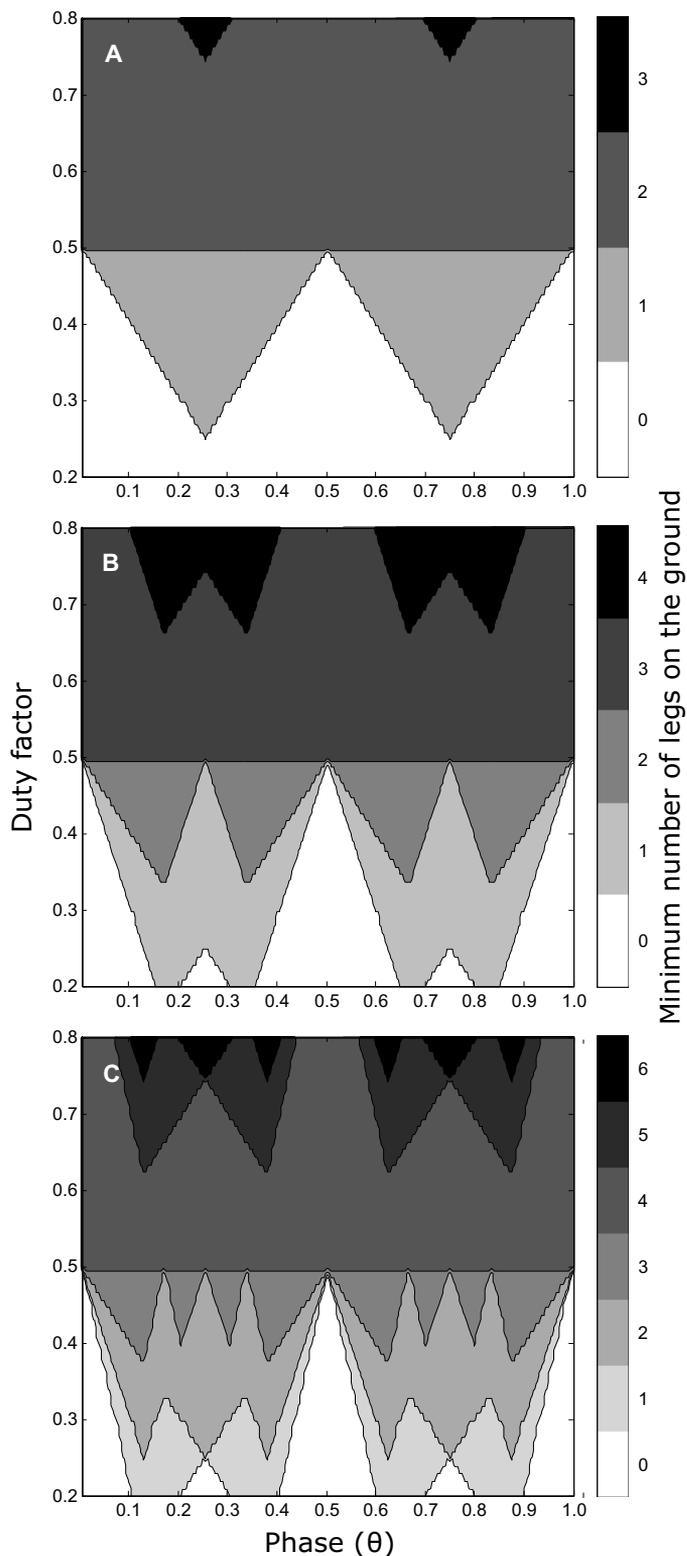
**Fig. 4. Position of the first amplitude minimum (triangles) and half peak values (circles) with respect to  $\theta$  for locomotor apparatuses with 2 to 10 pairs of walking legs.** Particularly for low leg numbers, the position of the force amplitude minimum decreases with increasing duty factors (decreasing brightness; compare Fig. 2A and labeling at the first column of triangles), while duty factors have virtually no impact on the phase shift at which force amplitudes are halved (see also Fig. 2).

**DISCUSSION**

**General considerations on leg (de-)synchronization**

The efficiency of bouncing gaits, such as running, trotting, or the alternating tripodal gait of insects and harvestmen, largely depends on elastic structures in the walking legs. Since stress-strain dependencies of tendons and equivalent structures are mostly nonlinear and characterized by significant hysteresis (12, 29), these springs have to undergo sufficient strain to be useful as energy storage, which requires sufficient load during the legs' stance phase (30). In steady locomotion, the vertical force components dominate leg loading [for example, (31, 32)]. The changes of these forces result in length changes of elastic structures within the legs and can therefore be used for cyclic energy storage and recovery. However, just as temporally largely overlapping ground contacts—reflected by high duty factors—decrease force amplitudes and may prevent sufficient loading of elastic structures, the use of spring-mass dynamics may also be hampered if loading forces exceed the physical abilities of the legs' musculoskeletal structure (16, 33). Accordingly, in horses, the change from fast trot to slow gallop minimizes the peak values of total vertical forces (34), and single leg forces drop slightly (35). In many species, the change from trot to gallop seems to coincide also with an optimization of metabolic costs (36). In sideways running ghost crabs, however, such an energy optimization could not be validated (22), and the strain in the exoskeleton of their legs even increases at the gait transition (37). This might relate to a lack of elastic energy recovery in these animals' gallop.

In bouncing gaits, increasing running speeds result in increasing relative swing phase durations and decreasing duty factors. The synchronized leg activity leads to phases without any contact with the ground if duty factors fall below 0.5. Metachronal coordination of ipsilateral legs enables increasing relative swing phase durations without ballistic phases (6). Accordingly, in both cases, muscle activity during



**Fig. 5. Minimum number of legs on the ground as function of duty factor and phase shift of ipsilateral adjacent legs. (A) Two pairs of legs. (B) Three pairs of legs. (C) Four pairs of legs.** With sets of legs close to alternating activity and duty factors below 0.5, the minimum number of legs on the ground is always 0, while phase shifts deviating from alternation (0.5) and synchrony (0 and 1) result in increased minimum numbers of legs in contact with the ground.

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swing can be slower and more energy-efficient (38, 39), which may trigger reduced metabolic costs as found in fast-moving desert beetles (40).

### Disturbances

In gaits with strictly alternating leg coordination, maximum vertical ground forces and duty factors depend on each other. While duty factors and contact duration decline with increasing running speed, peak forces increase to keep the momentum constant (14). If leg synchronization declines, running speed can be increased, and the duty factors can decline without significant increases in total vertical peak forces (Fig. 1). With declining duty factors, and a relative increase of coordination errors as found in fast-running desert ants (41) or on rough terrain (42), with alternating leg coordination and high vertical amplitudes of the COM, the animals are at risk of touching down initially only with one leg. When duty factors are low, resulting high single leg forces might exceed the physical properties of the leg adjusted to shared force application as typical for straight, level locomotion. Overload, in turn, can cause a failure of the locomotor apparatus. Metachronal leg coordination—that is, coordination patterns with ipsilateral phase shifts significantly deviating from those found in bouncing gaits—results in minimized total force maxima (Fig. 2). Consequently, desynchronization of the sets of legs also minimizes the maximum feasible load on a single leg and thereby may help to avoid such collapses. Accordingly, blaberid cockroaches change from an alternating tripod leg coordination scheme at intermediate running speeds to metachronal leg coordination at maximum speeds (6), preventing large vertical amplitudes of the COM and vertical force peaks. Nevertheless, some arthropod species specialized for high-speed escape runs are able to move even bipedally using specifically adjusted legs when extremely high speeds are required (43, 44).

Even in specialist polypodal high-speed runners, the maintenance of synchronicity among the legs of the alternating sets seems to be challenged at high running speeds. Although contact duration typically decreases exponentially with speed [for example, (4, 19)], the tripod synchrony factor, that is, the normalized fraction of contact phase overlap between legs in the same set of legs (45), does not exceed 0.8 in fast-running desert ants of the species *Cataglyphis fortis* (41). Accordingly, with increasing running speeds, the impact of internal and external disturbances seems to increase as well. Decreased synchronization, however, results in reduced amplitudes of total vertical forces, lower vertical amplitudes of the COM, and a lower capacity for elastic energy storage in the legs. It seems likely that variable and disturbed gait patterns as found on slippery or rugged substrates yield similar effects.

### Impact of the number of walking legs

The number of active pairs of legs significantly affects the requirements for coordination accuracy. While in locomotor systems with three pairs of legs a phase deviation of 0.1 from the alternating pattern results in halving of the total vertical peak forces, this occurs at deviations of only 0.07 in systems with four pairs of legs and at even smaller deviations in locomotor systems with more pairs of legs (Fig. 4). Assuming a duty factor of 0.3, a tripod synchrony factor of 0.8—as found in fast-running *C. fortis* (41)—already leads to phase shifts of approximately  $0.3 - (0.3 \times 0.8) = 0.06$  away from the strict alternating pattern. Such a shift reduces the ants' vertical force amplitudes by 19% (Fig. 3). In locomotor systems with four pairs of legs, however, the same shift would result in a reduction by a third. Quadrupeds, in turn, can cope with higher phase variations since phase deviations of 0.06

reduce peak forces by only 7%. Accordingly, in animals with fewer legs, ipsilateral phase shifts can be relatively large without causing significant reductions in total vertical peak forces, vertical amplitudes of the COM, and the capacity for elastic energy storage. Animals with more than about five pairs of active legs, even fast species frequently using low duty factors such as centipedes (46), are practically incapable of using spring-mass dynamics in the sagittal plane. In such species, the tiny inaccuracies induced by internal and external perturbations prevent sufficient synchronization of the putative sets of diagonally adjacent legs.

Ipsilateral phase shifts that differ significantly from 0.5 result in an increased minimum number of legs on the ground (Fig. 5). Sufficiently high deviations from  $\theta = 0.5$  completely prevent airborne intervals, even though duty factors are considerably lower than 0.5. Consequently, such gaits facilitate permanent proprioceptive feedback and may increase controllability and stability of the locomotion (47, 48).

### Comparative considerations

Many advantages of spring-mass dynamics as found in running and trotting gaits, such as energy efficiency and running stability (49), are fully effective only on relatively firm and smooth substrates and require specialized locomotor apparatuses enabling transient elastic energy storage. For many species that lack these specific adaptations, such as spiders (4, 5), many bugs, beetles (50), amphibians (51), or tortoises (52), disadvantages of bouncing COM trajectories may prevail. Increased peak forces due to constructive interference of single leg ground forces may then rather be a perturbation of movement stability and vision (53), which are avoided by high duty factors and intermediate  $\theta$ .

Close to and between the positions of the force amplitude minima (that is, between 0.14 and 0.36 in hexapedal locomotor systems), the peak frequency of the force oscillations differs significantly from two times the stride frequency, specifically at low duty factors (Fig. 2 and fig. S2). Harmonics occurring in this range lead to multiples of the value expected for spring-mass dynamics. Accordingly, within this range, COM oscillations cannot be effectively used for the initiation and maintenance of symmetrical bouncing gaits. In horses, typical gaits using ipsilateral phase shifts in the range of minimum vertical COM amplitudes and high oscillation frequencies are ambling gaits such as tölt, single-foot, and rack (3, 27). The equivalent in hexapedes is the high-speed metachronal gait as found in cockroaches and mites (5, 6).

Since contralateral phase shifts are not considered, the present model is not suitable for examination of asymmetric gaits such as gallop (3). For gait patterns as found in mammals galloping at high speeds (54) in addition to ipsilateral phase shifts of about 0.3, contralateral phase shifts lower than 0.3 are required. These leg coordination patterns, however, would reestablish bouncing dynamics of the COM at which the sequenced and overlapping ground contacts of the four legs substitute a single leg ground contact of the traditional spring-mass model (54). The prime example for galloping arthropods are semiterrestrial, sideways moving ghost crabs that reach impressive speeds in their typical flat sand habitats in the intertidal zone (22). However, among fully terrestrial fast-moving arthropods, so far, no such contralateral phase adaptations have been found except for a brief notice referring to the peculiar high-speed jumping gait of the jumping bristletail *Petrobius* (55).

### Further effects of leg (de-)synchronization

High total vertical ground reaction forces as typically resulting from synchronized leg coordination patterns are also transferred onto the

substrate, which may transmit the elicited vibrations to potential predators or prey organisms (56). The temporally distributed force application of gait patterns with intermediate  $\theta$  may camouflage the signals and prevent the assessment of the producer's location, speed, and size. Granular and other flowable substrates can, in turn, dissipate significant proportions of movement energy, particularly if peak forces are high, largely preventing energy recovery (57). This external energy dissipation also makes lower speeds with resulting high duty factors and intermediate  $\theta$  preferable [compare (47)].

Apparently, locomotor systems of bipeds with only one pair of walking legs and those of multilegged animals employing bipedal gaits such as American cockroaches (44) and a range of lizard species (58, 59) largely avoid force interference problems, particularly at high running speeds and duty factors below 0.5 (25). Consequently, also perturbations caused by interfering leg forces may not occur, and the stability of the COM dynamics and the coordination patterns should be higher. In this regard, the control effort (60) is expected to be much lower than in polypedal locomotion, which probably outweighs reduced static stability and may represent a major advantage at high running speeds [compare also (59)].

## MATERIALS AND METHODS

Changes of ipsilateral phase shifts and changed duty factors were examined with regard to total vertical forces for locomotor systems with 2 to 10 pairs of walking legs. All analyses were performed using MATLAB scripts (MATLAB 7.10.0; MathWorks). Since the study is focused on the general understanding of polypedal locomotion, specific anatomies of walking legs have not been taken into regard.

Phase relations between the legs were defined with regard to stride durations that were set to 1; time was given in multiples of this stride duration. The phase shift  $\theta$  was determined by the occurrence of one leg's touchdown within the stride period of another leg; it was always between 0 and 1. Thus, the phase shift was 0.2 if the touchdown of the second leg occurred after 20% of the stride period of the first one. Since phase relations follow a circular distribution, phase shifts of 0 and 1 were equivalent (4). The analyses went through all  $\theta$  from 0 to 1; duty factors from 0.2 to 0.8 were examined, that is, the study focused on physiologically relevant values (4, 6, 41, 58).

In previous studies, it has been shown that the contralateral phase relation between the rear legs of cockroaches and mites is 0.5, irrespective of running speed (5, 6). Accordingly, and to reduce the number of variables, contralateral phase relations between the rear legs were set to 0.5, that is, rear legs alternated strictly. Setting contralateral phases of the rear legs to 0.5 restricted the approach to symmetrical gait patterns (3). During straight, level, terrestrial locomotion of animals with segmented walking legs, such as many vertebrates and arthropods, the vertical ground force component is always the largest, irrespective of the number of legs used or which class of animals is taken into account [for example, (31, 32)]. Moreover, vertical force components are most decisive and characteristic for the COM dynamics of certain gaits, although lateral forces can reach significant values in animals with sprawled legs (7, 10, 11). Accordingly, the present study is focused on vertical forces. As a first approximation, the force applied during the stance phase of a leg has been modeled as  $\frac{1}{2}(1 - \cos(2\pi t))$  for the time interval  $t$  from 0 to 1, that is, the start and the end of the stance phase (compare Fig. 1). However, in a preliminary study on locomotion in mites, half-sine-shaped force profiles did not significantly alter the calculations of total forces and

their amplitudes (5). Each stride comprised an initial stance and a subsequent swing phase where no forces were applied onto the ground. The quotient of contact duration and stride duration defined the duty factor of a leg. Stride duration, duty factors, and ground forces were modeled as equal for all legs. To generate different gait patterns, ipsilateral leg activities were shifted against each other according to prescribed  $\theta$  from 0 to 1. Ipsilateral phase, duty factor, and leg number were the only changed parameters; oscillations of total vertical forces then emerged from the interplay of these kinematic measures and the stereotyped single leg ground forces.

With strictly alternating sets of legs, overall ground forces over a stride had two maxima, which were caused by the consecutive activity of the sets of legs (Fig. 1E). All forces were summed up and divided by the mean value resulting in normalization onto body weight. Spectral analyses of the resulting force oscillations were accomplished by using the fast Fourier transformation algorithm implemented in MATLAB. To this end, the time series was expanded to 10 strides, and the mean force value was subtracted. Resulting amplitudes corresponded to one-half of the peak-to-peak values of the respective ground forces, that is, the difference between the absolute maximum and minimum values of summed-up overall ground forces. Amplitude values change symmetrical about the alternating pattern ( $\theta = 0.5$ ). Accordingly, amplitude values for  $\theta = 0.4$  and  $\theta = 0.6$  were equivalent. In Results, therefore, values for local minima, half peak values, etc. were provided only for the phase range between 0 and 0.5.

The minimum number of legs in contact with the ground can serve as proxy for the requirement of dynamic stabilization of a gait (5). The number of legs on the ground was determined equivalent to the ground forces by summing up the legs in contact with the ground for each instant of time; minimum values were determined for the increments of  $\theta$  and duty factor subsequently.

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/9/eaat3721/DC1>

Fig. S1. Speed-dependent transformation of a locomotor system from an underdamped to an overdamped vertical oscillator.

Fig. S2. Example force spectrums for locomotor apparatuses with three pairs of walking legs at a duty factor of 0.3.

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