

What explains the trot–gallop transition in small mammals?

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Summary

The transition from trot to gallop in quadruped mammals has been widely hypothesized to be a strategy to minimize the energetic costs of running. This view, however, has been challenged by some experimental evidence suggesting instead that this transition might be triggered by mechanical cues, and would occur when musculoskeletal stresses reach a certain critical value. All previous experiments to test those hypotheses have used relatively large species and their results, therefore, may not be applicable to small mammals. In this study we evaluated the effect of carrying loads on the locomotor energetics and gait transitions of the rodent *Octodon degus* running on a treadmill. Metabolic rate and cost of transport increased about 30% with a 20% increment in body mass. This increment was higher than expectations

based on other mammals, where energy consumption increases in proportion to the added mass, but similar to the response of humans to loads. No abrupt change of energy consumption between gaits was observed and therefore no evidence was found to support the energetic hypothesis. The trot–gallop transition speed did not vary when subjects were experimentally loaded, suggesting that the forces applied to the musculoskeletal system do not trigger gait transition.

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Introduction

Most quadrupedal mammals use one of three main types of gaits during locomotion (walk, trot and gallop) and switch from one to another as speed varies. Investigations have sought to explain the underlying mechanisms that dictate when an organism changes gait (Farley and Taylor, 1991; Vilensky et al., 1991; Hreljac, 1993; Minetti et al., 1994; Diedrich and Warren, Jr, 1995; Kram et al., 1997). Early studies proposed that gait transition served to reduce the energetic costs of locomotion (Hoyt and Taylor, 1981; Taylor, 1985; Alexander, 1989). This hypothesis was supported by two observations. First, animals tend to use only a narrow range of speeds within a particular gait (Pennycuick, 1975; Hoyt and Taylor, 1981; Perry et al., 1988; Kenagy and Hoyt, 1989). For horses, these preferred speeds have been shown to minimize metabolic energy costs within a gait (Hoyt and Taylor, 1981), suggesting that energetic economy might be an important determinant of terrestrial locomotion. Second, in humans and horses, each gait displays a particular relationship between metabolic energy expenditure and speed. These metabolic curves intersect in such a way that it is energetically less expensive to switch to

another gait at speeds beyond the intersection point than to maintain the same gait (Margaria et al., 1963; Hoyt and Taylor, 1981). The speed at which the energy cost curves intersect has been referred to as the ‘energetically optimal transition speed’ (EOTS) (Hreljac, 1993). However, the experimental support for this ‘energetic hypothesis’ is contradictory: some studies have shown that the walk–run transition in humans and the trot–gallop transition (TGT) in horses occurs at the EOTS (Mercier et al., 1994; Diedrich and Warren, Jr, 1995; Wickler et al., 2003), but others have shown, for the same species, that gait transitions occurred at significantly lower speeds (Farley and Taylor, 1991; Hreljac, 1993; Minetti et al., 1994).

A second hypothesis to explain gait transitions proposes that animals switch gait as a mechanism to reduce the forces applied to the musculoskeletal system (Biewener and Taylor, 1986; Farley and Taylor, 1991). *In vivo* measurements of peak principal strains showed that peak limb bone strains in horses and goats increased linearly with speed within each gait, but decreased significantly at the transition of trot to gallop (Rubin and Lanyon, 1982; Biewener and Taylor, 1986). Despite the differences in body size and absolute speed between those

species, maximum peak bone strains were similar at the TGT, suggesting that this transition might be determined by a critical value of peak limb bone stress (Rubin and Lanyon, 1982; Biewener et al., 1983; Biewener and Taylor, 1986). To test this hypothesis, Farley and Taylor (Farley and Taylor, 1991) added weights to horses, thereby increasing the forces on the limbs for any given velocity. They found that when loaded, horses transitioned to galloping at significantly lower speeds than when unloaded, but maintained similar peak musculoskeletal forces at the TGT. This suggested that the TGT is triggered mechanically when musculoskeletal forces reach a critical level (Farley and Taylor, 1991). Support for a mechanical cue for gait transitions, however, remains tenuous. It was recently shown that the TGT in horses running uphill occurs at lower speeds than in horses running on level (Wickler et al., 2003). Given that uphill running should not increase the total forces applied to the limbs (e.g. Roberts et al., 1997), these authors suggested that their results contradict the idea of a mechanical trigger for the TGT. However, Wickler et al. did not directly measure the forces applied to the limb bones (Wickler et al., 2003), and although average forces for all limbs may not be elevated on an incline, it seems reasonable that there may be a shift in weight distribution, with more weight on the hind limbs when ascending.

Whether the same determinants apply to small running mammals is not known. There is little information about gait transitions in species other than humans and horses. The objective of this study is to evaluate the effect of experimental manipulations of body mass on the TGT and the energetics of locomotion of a small south American mammal, the degu *Octodon degus* (Rodentia, Caviomorpha). If the switch from trot to gallop in degus is triggered to reduce locomotory costs, the TGT should occur at the EOTS, even if body mass is experimentally altered. On the other hand, if the TGT is a mechanism to reduce peak musculoskeletal stresses, the speed at which the transition occurs should decrease in animals with increased body mass.

Materials and methods

Animals and experimental treatments

Eleven adult male degus *Octodon degus* Molina were captured in sites surrounding Santiago, Chile, and were transported to the laboratory where they were kept individually in plastic cages (30×30×15 cm) with rabbit food pellets, and water *ad libitum*. Initial body mass was 180.5±6.4 g (mean ± s.e.m.; Table 1). Subjects were trained to run on a treadmill enclosed in a Plexiglas metabolic chamber (46×22×17 cm), following the design of Hoyt and Kenagy (Hoyt and Kenagy, 1988). All animals experienced three treatments: (1) 'control', no body mass modification; (2) 'overfed', ~20% increase in body mass *via* overfeeding; and (3) 'injected', ~20% increase in body mass through intraperitoneal injection of 0.9% saline solution (Jones, 1986). No rodents seemed to be affected by the injection. In a previous experiment, the same injection treatment applied

Table 1. *Body mass of experimental animals for each body mass treatment*

| Individual | Body mass (g) | | |
|------------|---------------|-----------|-----------|
| | Control | Injected | Overfed |
| 1 | 140.9±0.8 | 170.1±0.7 | 167.1±0.9 |
| 2 | 181.5±0.8 | 218.4±0.6 | 214.4±1.0 |
| 3 | 152.3±1.0 | 183.0±0.7 | 186.4±1.1 |
| 4 | 169.5±0.7 | 203.5±0.7 | 207.3±1.6 |
| 5 | 209.3±1.2 | 250.5±0.5 | 254.6±1.5 |
| 6 | 197.1±1.4 | 237.1±0.6 | 238.5±1.4 |
| 7 | 201.0±1.1 | 239.3±0.8 | 244.1±1.8 |
| 8 | 190.4±0.8 | 229.5±0.6 | 230.4±1.7 |
| 9 | 178.6±0.9 | 214.6±0.7 | 217.4±1.5 |
| 10 | 168.8±1.1 | 201.9±0.9 | 200.8±1.5 |
| 11 | 196.3±1.0 | 236.6±0.7 | 238.4±1.8 |

Body mass data are expressed as means ± s.e.m.

Individuals in bold (1–6) were used for the respirometry experiments.

to degus did not modify their resting metabolic rate, suggesting that the procedure does not produce excessive levels of stress (R.A.V., unpublished results). Body mass remained constant for about 3–4 h after the injection and animals returned to their original body mass within 24 h. The order and sequence of treatments for each individual were randomly assigned. The overfed condition was achieved by providing food *ad libitum*. Animals reached the desired body mass in about 2–3 weeks. Because of the random assignment of treatments, some animals were first overfed, then had their body mass reduced to their original state. This weight-loss protocol consisted of limiting the daily food available to 80% of the amount necessary to maintain constant body mass. Body mass was measured daily to ensure continuous and gradual weight loss. Subjects achieved their original body mass in about 4–6 weeks. Because the increase in body mass produced by overfeeding the animals might be a result of increments of metabolically active tissue (i.e. muscle and organs), inactive tissue (body fat), or a combination of both, body fat content was measured in three control and three overfed individuals. The subjects were killed and the whole body (excepting the head) was homogenized and subjected to a Soxhlet extraction procedure, which entails the removal of lipids using an ether-based solvent (Van Soest, 1982). A sample was taken, dried at 100°C and weighed with an analytical balance (±0.001 g). Lipid content was removed using a petroleum ether solution and the dry mass was measured again. The difference corresponded to the fat content of the sample. Fat content is reported as the percentage of body mass and metabolically active body mass is calculated as body mass×(1–% body fat). The fat content of control individuals was 20.86±3.97% (N=3) and 30.82±1.24% (N=3) for overfed individuals. All procedures were reviewed and approved by the Ethics Committee of the Faculty of Sciences, Universidad de Chile.

Stride frequency and trot–gallop transition determination

After several weeks of training, stride frequency was measured in 11 individuals while they ran at a constant speed. Stride frequency was determined by timing a videotaped interval (Canon A1 digital camera, 30 frames s^{-1} , shutter speed of 1/500 s, with a time code registration). Because the recording rate of the camera was not high enough to reliably estimate an instantaneous step frequency, an average value was calculated by dividing the number of stride cycles (at least 12) by time. Assuming the worst-case scenario, measurement error for both foot touch down and take off will be 2/30 s (two frames error). Thus, for a rodent running at 6 strides s^{-1} , a sequence of 12 strides (2 s approximately) will give an error of 3–4% for the estimation of stride frequency. For each gait, a least-square linear regression model was fitted to stride frequency *versus* running speed of each individual, and the intersection between the regression lines for trotting and galloping was used as the TGT speed (Heglund and Taylor, 1988).

Running energetics

During running, metabolic rate (running \dot{V}_{O_2}) was measured concurrently with video recording using an open-flow respirometry system (Sable Systems, Nevada, USA) at ambient temperature (19–21°C). Not all individuals run long enough at a particular speed to give reliable respirometry measurements and only six animals were used to estimate running energetics. All subjects were acclimated to the stopped treadmill for about 20 min; after their metabolic rate had stabilized, the belt was brought to the desired speed. Instantaneous metabolic rate (Bartholomew et al., 1981) was recorded for at least 2 min while dried air was drawn at a rate of 4012 ml min^{-1} . Before and after entering the chamber, air was passed through carbon dioxide (Baralyme[®]=Ba(OH)₂) and water (Drierite[®]=CaSO₄) absorbent granules. Oxygen consumption was monitored by a Datacan V-PC program every 0.5 s with an applied electrochemistry oxygen analyzer (model S-3A/I; Ametek, Pittsburgh, Pennsylvania, USA). The metabolic rate (\dot{V}_{O_2} , in ml $O_2 g^{-1} h^{-1}$) was calculated by equation 4a of Withers (Withers, 1977) using the metabolically active body mass and correcting gases by STP. The net cost of transport (COT; in ml $O_2 g^{-1} km^{-1}$) was obtained by dividing the metabolic rate by the running speed. Only trials in which degus ran steadily at a fixed position on the treadmill were included for further analysis.

Results*Trot–gallop transition speed*

Subjects ran on the treadmill using speeds between 0.6 and 1.4 $m s^{-1}$. A positive linear relationship was found between stride frequency and treadmill speed, but the slope decreased significantly when subjects switched from trotting to galloping (see Fig. S1 in supplementary material). The range of slopes was 5.2–7.3 and 0.5 to 2.8 strides m^{-1} in trotting and galloping subjects, respectively. The trot–gallop transition speed was $1.05 \pm 0.02 m s^{-1}$ (mean \pm s.e.m.) in control degus, while for

injected and overfed subjects the transition occurred at 1.04 ± 0.02 and $1.04 \pm 0.02 m s^{-1}$, respectively. No difference was found in the TGT between treatments (repeated measures ANOVA, $F=1.40$, d.f.=2,20, $P>0.1$). The observed speeds for the control group were slightly higher ($t=2.28$, d.f.=10, $P<0.05$) than the allometric prediction of $1.01 m s^{-1}$ for the TGT for a 180 g mammal (Heglund et al., 1974).

Rate of oxygen consumption and net cost of transport

The rate of oxygen consumption increased with treadmill speed in all subjects and the percentage of increase in \dot{V}_{O_2} in loaded animals compared to controls was similar across the range of speeds (see Fig. S2 in supplementary material). Metabolic rate of injected and overfed individuals increased by 34 ± 5 (mean \pm s.e.m. for all speeds) and $27 \pm 4\%$, respectively, above the control rate. Average metabolic rate of overfed animals was not significantly different from that of injected subjects ($t=1.712$, d.f.=100, $P>0.05$). The COT kept a rather constant value or did not show a clear pattern as a function of speed (Fig. 1). The coefficient of variation of COT was between 2 and 9% for all subjects. As the COT just before and after the trot–gallop transition speed did not differ within each treatment (control: $T^+=15$, $P=0.345$; injected: $T^+=17$, $P=0.173$; overfed: $T^+=11$, $P=0.917$; Fig. 1), the COT for trotting and galloping for each treatment were pooled to estimate the COT at the transition speed. The COT estimated for the gait transition differed between treatments (repeated-measures ANOVA, $F=29.22$, d.f.=2,10, $P<0.001$), being lower in control individuals ($3.44 \pm 0.13 ml O_2 g^{-1} km^{-1}$) than in injected and overfed animals (4.42 ± 0.25 and $4.35 \pm 0.24 ml O_2 g^{-1} km^{-1}$, respectively; Holm–Sidak test, for control *versus* injected: $t=6.86$, $P<0.0001$; for control *vs* overfed: $t=6.35$, $P<0.0001$).

Discussion

The experimental manipulation of the subjects' body mass by 20% produced a significant effect on the energy expenditure for locomotion. In general, adding mass to an animal increases the force that must be generated by muscles (Farley and Taylor, 1991) and has been shown to increase the metabolic rate proportionately in several mammal species (Taylor et al., 1980). When normalized by total mass (i.e. body mass + load), the addition of 20% weight produced an increment of about 30% in metabolic rate in our rodents. This increment is higher than that predicted by Taylor et al. (Taylor et al., 1980), but their proportionality is not universally observed. Some studies have not detected any increase in metabolic rate when carrying loads of 5–10% of body mass (Cooke et al., 1991), whereas others have shown increments in metabolic rate higher and lower than those predicted by Taylor et al.'s proportionality (e.g. Griffin et al., 2003; Marsh et al., 2006). In our experiments, total metabolic rate (measured as ml $O_2 min^{-1}$) increased 38% with a 20% increment in body mass. This 17% deviation from proportionality is close to the 18% deviation observed in humans carrying loads of 30% their body mass (Griffin et al., 2003). The increment in metabolic rate during

loaded locomotion was similar regardless of the overweight treatment used. Only one individual (individual 2) showed a higher metabolic rate when injected than when overfed. This suggests that artificial loading and increment in adipose tissue have the same effect on the energetic of locomotion, as has been suggested for humans (Browning et al., 2006).

The energetic hypothesis predicts that the TGT should occur at speeds that minimize the energetic cost. For degus, no association was found between gait switching and energetic economy. Unlike the concave energy expenditure curve with a clear energetic minimum observed in studies of humans

(Saibene and Minetti, 2003) and horses (Hoyt and Taylor, 1981), degus showed a linear relationship between rate of oxygen consumption and running speed for a given gait, as noted in previous studies (Taylor et al., 1982; Hoyt and Kenagy, 1988). The COT remained relatively constant with running speed. Similarly, a study of locomotion energetics in *Spermophilus saturatus*, a degu-sized squirrel, found that COT decreased exponentially with running speed, reaching a constant value at high speeds instead of the U-shaped curve (Hoyt and Kenagy, 1988). Degus may not show an energetic minimum because they could not be trained to run beyond their normal range of speeds within each gait. It is possible that there is an EOTS for degus but that it could not be detected by this study. Even so, it seems unlikely that animals are able to sense their metabolic rate and/or COT to trigger a change of gait. A more likely scenario would be a proprioceptive signal that could be correlated to locomotion energetics. Some indirect evidence, however, suggests that this might not be the case; Vásquez et al. (Vásquez et al., 2002) found that natural travel speeds of degus depend on travel distance and habitat structure, showing that factors other than energetic economy influence locomotor behaviour.

Unlike metabolic rate, the TGT speed was not affected when degus' body mass was increased. Hence, we found no evidence indicating that the gait transition in degus is triggered by mechanical signals from the musculoskeletal system. Considering that two different procedures (i.e. saline injection and overfeeding) produced similar results, it seems unlikely that the lack of effect of loads on locomotion is a product of a particular methodology. It is possible that the estimated speed for the TGT depends on how the determination of transition speed was made. Estimates derived from extrapolation of stride frequency curves, as in our experiment, might be slightly different than more direct estimates from experiments where treadmill speed is gradually modified until the gait change is apparent (e.g. Kram et al., 1997; Wickler et al., 2003). Unfortunately, direct estimation of gait transitions was impractical to adopt in these experiments because of the high stride frequencies of the rodents and some technical limitations of the experimental setup. Differences between methodologies might make it difficult to compare TGT speeds from this work with speeds recorded in other studies where a more direct determination of gait transition has been made. This study, however, focuses on the individual responses to different treatments and thus any significant difference observed is likely to be the effect of the increased body weight treatment rather than a methodological artefact.

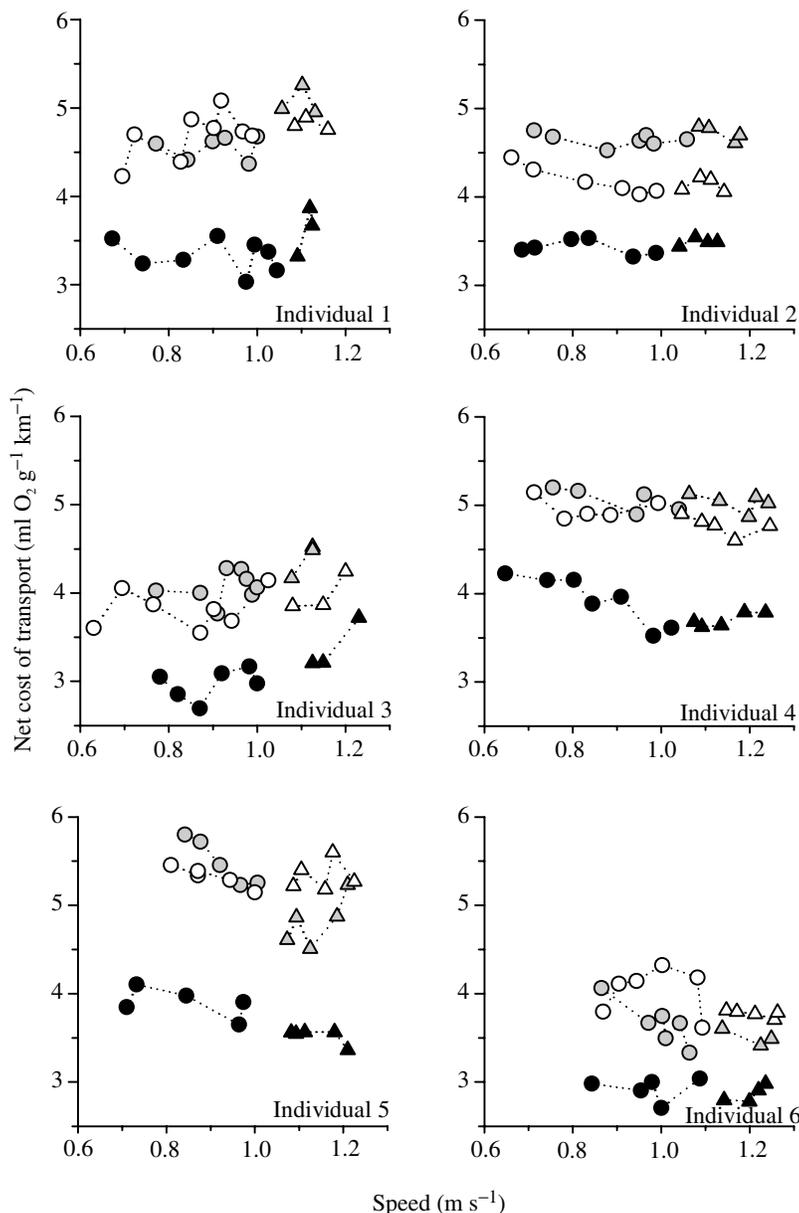


Fig. 1. Net cost of transport (COT) as a function of treadmill speed for measured individuals. Circles, values obtained during trotting; triangles, values obtained during galloping; black, grey and open symbols, control, injected and overfed treatments, respectively.

But why did body mass increments not modify TGT as observed in horses? One possible answer comes from the diverse mechanisms that mammals adopt to cope with bone stresses as body mass increases. Given that mammal long bones tend to scale nearly isometrically, large species are expected to experience higher stresses on their limb bones than small species, and therefore to put bones under mechanical loads that are closer to their mechanical limit (Biewener, 1983; Biewener, 1990). Mammals, however, use several mechanisms to keep peak bone stresses within safe functional limits. In small to medium-sized species (i.e. less than 100 kg), peak bone stresses are kept relatively constant by changes in limb posture from very crouched in small species to more upright in larger ones (Biewener, 1983; Biewener, 1989). Adopting a more erect posture reduces not only the bending moment on the bones but also the moments around the joints, reducing the muscular forces needed to support the animal's weight (Biewener, 1989). In species larger than 100 kg, however, postural changes become insufficient to maintain low peak bone stresses and additional mechanisms are implemented. These include more robust limb bones due to negative allometry of bone length (McMahon, 1975; Prothero and Sereno, 1982; Bertram and Biewener, 1990; Christiansen, 1999) and strong reduction of locomotor performance as size increases (Garland, Jr, 1983; Iriarte-Díaz, 2002). Thus, small-sized mammals seem to be less constrained than large species in compensating for changes in body mass. A rodent, for example, might acquire a more upright posture than usual to decrease the stresses induced by additional weight, whereas in large-sized species this mechanism is not longer available.

Dynamic similarity is a particularly interesting concept that has been applied to the study of animal locomotion (Alexander, 2005; Vaughan and O'Malley, 2005). If gravitational force is important, two moving objects, despite differences in speed and size, would move with the same dynamics only if the ratio between inertial and gravitational forces for the two objects is the same at corresponding stages of their motions. This ratio is known as the Froude number (Fr) and is represented by the equation v^2/gL , where v is velocity, g is gravitational acceleration and L is the limb length. Alexander and Jayes (Alexander and Jayes, 1983) showed that mammals of different sizes, running with equal Fr , tend to move in a dynamically similar way, using equivalent limb kinematics and exerting similar patterns of forces on the ground. In this scenario, the change from one gait to another is expected to happen at equal Fr and, accordingly, several quadrupedal mammals, ranging from small mice to rhinoceros, transition from trot to gallop at Fr between 2 and 3 (Alexander and Jayes, 1983). Furthermore, since the Fr is mass independent, experimental alterations of body mass are expected to produce no change on the Fr of the TGT. We made a rough estimation of Fr at the TGT for our degus from a calibrated lateral camera view using an average hip height obtained from two individuals during midstance while running on the treadmill. Degus switched from trot to gallop at Fr of 2.8 ± 0.1 , 2.7 ± 0.1 and 2.8 ± 0.1 for control,

injected and overfed individuals, respectively. These values fall into the normal range of Fr observed in mammals for the TGT.

The applicability of Fr and dynamic similarity models in animal locomotion has been further tested experimentally in humans using reduced gravity conditions. These models have been unable to predict the kinetics and kinematics of human walking and running but have successfully predicted gait transitions (Donelan and Kram, 1997; Donelan and Kram, 2000). Humans, independent of the amount of gravity, switch from walking to running at different absolute speeds but at the same Fr of approximately 0.5 (Kram et al., 1997). It has been argued that Fr might not be adequate to describe the mechanics of running gaits and that additional dimensionless numbers should be considered to capture the contribution of elastic elements to locomotion (Alexander, 1989). However, the fact that several mammal species, regardless of their size, switch between running gaits at the same Fr suggests that its use may be justified to study the TGT, at least as an initial heuristic approach. As in the energetic case, it is unclear how Fr could be sensed to trigger a change of gait. And the fact that several mammals of diverse body size switch gaits at similar Fr could be the coincidental result of additional correlated factors. Thus, studies analyzing the influence of different forces, including gravitational forces, could provide some insights about gait transitions in small mammals. For example, a recent study by Gallardo-Santis et al. (Gallardo-Santis et al., 2005) found that spontaneous running speed on vertical surfaces (tree climbing in several species of small mammals) does not differ from horizontal speed, suggesting that gravitational forces do not affect speed/body size relations in small mammals.

List of abbreviations

| | |
|-----------------|--|
| COT | net mass-specific cost of transport |
| EOTS | energetically optimal transition speed |
| Fr | Froude number |
| STP | standard temperature and pressure |
| TGT | trot-gallop transition |
| \dot{V}_{O_2} | oxygen consumption rate |

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