Effect of load on preferred speed and cost of transport

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Wickler, S. J., D. F. Hoyt, E. A. Cogger, and K. M. Hall. Effect of load on preferred speed and cost of transport. J Appl Physiol 90: 1548–1551, 2001.—Horses have a tendency to utilize a relatively narrow set of speeds near the middle of a much broader range they are capable of within a particular gait, i.e., a preferred speed. Possible explanations for this behavior include minimizing musculoskeletal stresses and maximizing metabolic economy. If metabolic economy (cost of transport, CT) and preferred speeds are linked, then shifts in CT should produce shifts in preferred speed. To test this hypothesis, preferred speed was measured in trotting horses (n = 7) unloaded on the level and loaded with 19% of their body weight on the level. The preferred speed on the level was 3.33 ± 0.09 (SE) m/s, and this decreased to 3.13 ± 0.11 m/s when loaded. In both conditions (no load and load), the rate of O2 consumption (n = 3) was a curvilinear function of speed that produced a minimum CT (i.e., speed at which trotting is most economical). When unloaded, the speed at which CT was minimum was very near the preferred speed. With a load, CT decreased and the minimum was also near the preferred speed of horses while carrying a load.

PREFERRED SPEED IS THE TENDENCY of animals to utilize a restricted range of speeds near the middle of a much broader range they are capable of using within a particular gait. Pennycuick (12), measuring locomotion in large ungulates, indicated that they tended to use a restricted range of speeds during their migrations. This concept of preferred speed was empirically demonstrated in one pony by Hoyt and Taylor (9). They measured the preferred speed at the walk, trot, and canter and found that it occurred at the speed where the metabolic cost to move a given distance, i.e., the cost of transport (CT), was a minimum. In a two-species comparison (white rats and kangaroo rats), Perry et al. (13) demonstrated that, despite difference in body mass and gait, musculoskeletal stresses were nearly identical at their preferred speed. Other aspects of vertebrate locomotion have been studied that might have been expected to provide an explanation of preferred speed, such as internal power (5), external power (7), and the connection between mechanics and energetics (11). One of the most promising has been the description of the mechanics of bouncing gaits (1, 3), which predicts changes in response to load carrying (6). However, none of these important studies provide a mechanistic explanation of why animals prefer to use particular speeds.

If metabolic economy (CT) and preferred speeds are linked, then shifts in CT should produce changes in the preferred speed. To test this, preferred speed and CT were measured in horses on the level and while carrying a load. Loading increases metabolic rate (15) and musculoskeletal stresses in ponies (4) and, therefore we hypothesized, should reduce preferred speed.

MATERIALS AND METHODS

Preferred speed. The methods and procedures were approved by the institutional Animal Care and Use Committee. Seven Arabian horses (4 mares and 3 geldings, age 7–15 yr) were trained to walk and trot, in response to a voice command, along a 50-m fence line on compacted soil. Horses were warmed up 15 min before data collection.

The weight saddle was made of a light-weight wooden-framed saddle, modified to hold bags of lead shot. Saddle and lead had a total mass of 85 kg (19% of body mass). The distribution of weight approximated the normal distribution of weight (60% on forelegs) as verified by alternately weighing the horses with only the forelegs or hindlegs on the scale. The horses had an average mass of 466 ± (SE) 20 kg.

O2 consumption. O2 consumption (Vo2) was measured at trotting speeds (2.25–4.5 m/s) using an open-flow system on a high-speed equine treadmill (Sato I, Equine Dynamics, Kansas City, MO). Animals were conditioned to wear a loose-fitting facemask connected to a 23-cm-diameter hose. Air was drawn past the mask at ~6,000–9,000 l/min with a centrifugal fan. A sample for O2 analysis (Ametek S3A/II O2 analyzer, Pittsburgh, PA) was taken downstream of the flowmeter, and CO2 and water were removed before analysis (Ascarite, Thomas Scientific, Swedesboro, NJ, and Drierite, Hammond Drierite, Xenia, OH, respectively). This sample

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was obtained such that changes in pressure in the upstream air sample would not impact pressure at the analyzer. Flow rate was monitored using a 15.2-cm orifice plate (model 304SS, Meriam Instruments, Cleveland, OH) and differential pressure transducer (model 2110 Smart Pressure Gauge, Meriam Instruments). Flow rates were calibrated at the speed at which each VO$_2$ measurement and dividing it by the speed at which Eq. 4b

was calculated using Eq. 4b of Withers (18), and all gases were corrected to STP. All metabolic rates presented are mass specific. Analog data from the O$_2$ analyzer, flowmeter, and tread speed were recorded simultaneously using a commercial data acquisition program (Datacan, Sable Systems, Las Vegas, NV) and a computer. The coefficient of variation for VO$_2$ of one animal at the same speed was ~3%. Horses were conditioned to the collection system for ≥2 mo before collection of data for analysis.

For VO$_2$ measurements, horses were warmed up on the treadmill for 15 min at the walk and trot, run at their first experimental speed for 15 min, walked for 3 min, and then trotted at another speed for 15 min. The speeds chosen for this study were near the preferred speeds (3.2–3.5 m/s), at a low trotting speed near the walk-trot transition speed (2.25 m/s), and at a high trotting speed near the trot-gallop transition speed (4.5 m/s). Only two speeds were used on any one sampling day to eliminate fatigue as a confounding variable, and the speeds were varied randomly. Heart rates were measured to assess fatigue and recovery from exercise. VO$_2$ was calculated from the lowest consecutive 2-min average obtained during the 15-min bout. CT was calculated by taking each VO$_2$ measurement and dividing it by the speed at which it was determined. Metabolic measurements were limited to three horses because of soundness and behavioral considerations that occurred after the collection of preferred speed data. However, preferred speed data were collected on the three remaining horses, interspersed with metabolism measurements. Twenty metabolism measurements were made for each horse for each condition (unloaded and loaded).

**Statistical analysis.** Preferred speed data for each individual horse were analyzed using t-tests. A paired t-test was used to compare preferred speed of all seven horses. Comparisons of VO$_2$ and condition (unloaded control and loaded) were made using analysis of covariance with speed as the covariate. If $P < 0.05$, then means were subject to a protected least significant difference post hoc test. To determine whether the relationships between VO$_2$ and speed and CT and speed were linear or curvilinear, a stepwise regression was used. Stepwise regressions with speed and the square of speed as independent variables were performed with a probability to enter set at 0.05, while the probability to remove was set at 0.10. Values are means ± SE.

**RESULTS**

**Preferred speed, unloaded and loaded.** On the treadmill, horses trotted between ~2.25 and 4.5 m/s (the range over which metabolism was measured on horses trotting). When given the behavioral opportunity to choose trotting speeds, the horses utilized a much narrower range of speeds (Table 1). The means for the individual horses on the level ranged from 3.0 to 3.7 m/s. Addition of a load (19% body wt) significantly decreased preferred speed from 3.33 ± 0.09 m/s on the level to 3.13 ± 0.11 m/s.

**VO$_2$ on the level and speed.** A simple linear regression of VO$_2$ vs. speed for each of the three horses was significant, but a stepwise regression, using the square of speed as a variable, indicated that the nonlinear dimension described the data significantly better. When the data for the three horses were combined, VO$_2$ (ml·g$^{-1}$·h$^{-1}$) vs. speed (m/s) was also described better by a second-order polynomial ($P < 0.0001$ for the regression, with $P$ for the speed term = 0.173 and $P$ for the speed$^2$ term = 0.0005). The equation for the metabolism vs. speed relationship was as follows: VO$_2$ = 1.02 – (0.161 × speed) + (0.089 × speed$^2$) ($r$ = 0.97; Fig. 1).

**VO$_2$ and load.** When the horses were loaded, metabolism was increased an average of 17.6% for all speeds ($P < 0.0001$ for all comparisons, e.g., from 1.53 ± 0.02 to 1.80 ± 0.03 ml O$_2$·g$^{-1}$·h$^{-1}$ at the intermediate trotting speeds). As with unloaded horses, the relationship between metabolism and speed was better described as a curvilinear function ($P < 0.0001$ for the regression, with $P$ for the speed term = 0.729 and $P$ for the speed$^2$ term = 0.0064). The equation for the metabolism vs. speed relationship was as follows: VO$_2$ =

![Fig. 1. Curvilinear relationship between metabolism and speed in horses trotting (n = 3) without a load (unloaded) and loaded with 19% of the body mass (n = 3). VO$_2$, O$_2$ consumption.](http://jap.physiology.org/)

Table 1. Preferred speeds at the trot in loaded and unloaded conditions

<table>
<thead>
<tr>
<th>Horse</th>
<th>Weight, kg</th>
<th>Unloaded</th>
<th>Loaded</th>
<th>$P$</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>405</td>
<td>3.66 ± 0.08</td>
<td>3.57 ± 0.05</td>
<td>0.03</td>
<td>129</td>
</tr>
<tr>
<td>B</td>
<td>423</td>
<td>3.24 ± 0.02</td>
<td>3.08 ± 0.08</td>
<td>&lt;0.001</td>
<td>154</td>
</tr>
<tr>
<td>C</td>
<td>458</td>
<td>3.01 ± 0.02</td>
<td>2.83 ± 0.02</td>
<td>&lt;0.001</td>
<td>153</td>
</tr>
<tr>
<td>D</td>
<td>487</td>
<td>3.46 ± 0.04</td>
<td>2.96 ± 0.03</td>
<td>&lt;0.001</td>
<td>100</td>
</tr>
<tr>
<td>E</td>
<td>484</td>
<td>3.49 ± 0.02</td>
<td>3.46 ± 0.03</td>
<td>0.19</td>
<td>180</td>
</tr>
<tr>
<td>F</td>
<td>432</td>
<td>3.44 ± 0.07</td>
<td>3.06 ± 0.08</td>
<td>0.008</td>
<td>45</td>
</tr>
<tr>
<td>G</td>
<td>380</td>
<td>3.03 ± 0.02</td>
<td>2.90 ± 0.02</td>
<td>&lt;0.001</td>
<td>125</td>
</tr>
<tr>
<td>Avg</td>
<td>446</td>
<td>3.33 ± 0.09</td>
<td>3.13 ± 0.11</td>
<td>0.016</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SE. Preferred speeds (PS) at the trot are significantly decreased when the animal is loaded with a weight saddle approximating 19% of body weight. df, Degrees of freedom (total number of replicates for each animal for both conditions).
1.09 - (0.144 \times \text{speed}) + (0.105 \times \text{speed}^2) (r = 0.98; Fig. 1).

$C_T$ on the level, unloaded. When $C_T$ (in ml O$_2$·kg$^{-1}$·m$^{-1}$) was plotted against speed for each individual horse (Fig. 2), the relationship was better described by a second-order polynomial. The equation relating $C_T$ to speed was as follows: $C_T = 0.230 - (0.0599 \times \text{speed}) + (0.0084 \times \text{speed}^2) (r = 0.58)$. The minimum $C_T$, calculated from the derivative of the equation for $C_T$ vs. speed, occurred at 3.55 m/s, and the minimum average preferred speed of these same three horses was 3.53 m/s.

$C_T$ and load. Loading increased the $C_T$ in all three animals ($P < 0.0001$ for all comparisons) an average of 18% at all speeds (from 0.123 ± 0.002 to 0.146 ± 0.002 ml O$_2$·kg$^{-1}$·m$^{-1}$ at the intermediate speeds). The relationship between $C_T$ and speed was better described by a polynomial for all three horses, and when combined, the $C_T$ was also better described as a curvilinear polynomial [$C_T = 0.254 - (0.0631 \times \text{speed}) + (0.0091 \times \text{speed}^2)$, $r = 0.58$]. The minimum $C_T$ occurred at 3.46 m/s, and the average preferred speed of these three horses carrying a load was 3.37 m/s.

DISCUSSION

With the exception of Shetland ponies (9) and horses (17), the study of preferred speeds has not been approached systematically. Preferred speeds have been reported for ponies (9), squirrels galloping in the wild (10), and kangaroo rats hopping and rats galloping over a force plate (13).

The study on rodents (13) demonstrated that the preferred speed, which is lower than the maximal speed for that gait, resulted in peak muscle stresses that were only one-third of maximum isometric stresses achievable by the muscles. This reduction in stress would permit more repetitions (longer endurance) with less potential for injury. Although this rationale can explain why preferred speed might be lower than the maximal speed at a gait, it does not suggest why preferred speed falls at an intermediate speed. Heglund and Taylor (8) provided an allometric equation for preferred speeds based on the assumption (not actually measured) that it falls in the middle of the range of speeds for that gait. Indeed, the average preferred speed of our horses was 3.33 m/s, a speed intermediate between the maximal and minimal speeds for these same horses trotting on the treadmill. The analysis of Heglund and Taylor predicts that preferred trotting speed increases with body size, and this would seem to be necessary given the allometry of the trot-gallop and walk-trot transition speeds. However, the preferred speed of the 140-kg pony of Hoyt and Taylor (9), 3.25 m/s, was virtually identical to that of our 450-kg horses (3.33 ± 0.09 m/s). The allometric equation of Heglund and Taylor predicts a difference in preferred trotting speed of 0.9 m/s between ponies and horses with these body masses (3.3 vs. 4.2 m/s).

Another explanation of the preferred speed was offered by Hoyt and Taylor (9). In their ponies, the relationships between $V_{O_2}$ and speed are described as curvilinear. The relevance of linear vs. curvilinear relationships between metabolism and speed is important when an animal’s $C_T$ or the mass-specific cost of moving a unit distance is calculated. If $V_{O_2}$ increases linearly with speed, then the slope of this relationship (which equals $C_T$) is constant and independent of speed. In a curvilinear relationship, there is a speed where $C_T$ reaches a minimum value. In the present study, the speed of minimum $C_T$, i.e., highest metabolic economy, coincided with the animal’s preferred speed.

In the present study, we found that the relationships between the metabolic rate and speed (Fig. 1) were better fit by a curvilinear equation resulting in a speed where $C_T$ was minimum (Fig. 2). This speed where movement was most economical was virtually identical to the preferred speed of the horses analyzed.

What happens when the horse carries an additional mass? Adding mass to an animal increases the force that must be generated by muscles (4) and increases metabolic rate proportionately in a number of animals (15), including the horse (16). In our study, addition of a 45-kg weight saddle, equal to an average of 19% of the animals’ body masses, increased the metabolic rate an average of 17.6%, close to the predictions by Taylor et al. (15). However, this increase in metabolism with additional mass is not universally observed. Some studies on humans fail to detect an increase in metabolic rate with vertical loading with weights from 5 to 10% of body mass (2).

The increase in mass increases $C_T$ uniformly if $C_T$ is expressed per kilogram of body mass. If $C_T$ is calculated using the mass of the horse plus the mass of the weight saddle, $C_T$ per kilogram is not different. Again, the speed that produced a minimum $C_T$ for the horses with a load occurred at a speed that correlated well with their measured preferred speed while they carried that additional mass.

Although the above results are an appealing argument for metabolic economy setting preferred speeds, it is still correlative. It seems unlikely that a horse can directly sense its $C_T$ and use this as a reason for selecting a particular speed. It seems more likely that
a proprioceptive input is what the animal senses and that the source of this input correlates with metabolic rate. The muscles are the most likely candidate for this source, because they are the transducers that convert metabolic energy to mechanical power. Little is known about how muscle function changes with speed, but it seems possible that there might be regular changes that the animal could sense in the force or velocity required to trot at different speeds.

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REFERENCES