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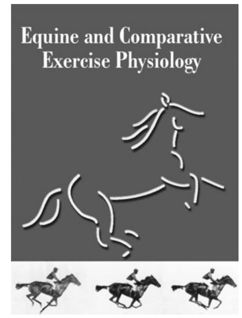

Effects of endurance training on VO_{2max} and submaximal blood lactate concentrations of untrained sled dogs

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Abstract

Five previously untrained yearling sled dogs were evaluated for endurance training-induced changes in maximum oxygen consumption (VO_{2max}) and submaximal blood lactate concentrations. Following 3 weeks of light training followed by 4 weeks of moderate training, VO_{2max} increased by 10%, from 180.2 ± 9.9 to 198.7 ± 19.2 ml kg min^{-1} ($P = 0.046$). Light training was not associated with any increase in VO_{2max}. Blood lactate concentrations at the same absolute intensity decreased by 215%, from 9.2 ± 4.7 to 4.3 ± 2.4 mmol l^{-1} ($P = 0.022$). Speeds associated with oxygen consumptions of 70% VO_{2max} increased by 12%, from 4.8 ± 0.4 to 5.4 ± 0.5 m s^{-1} ($P = 0.008$) and speeds associated with VO_{2max} increased by 21%, from 6.7 ± 0.3 to 8.2 ± 0.7 m s^{-1} ($P = 0.012$).

Keywords: exercise; sled dogs; oxygen consumption

Introduction

Sled dogs, or Alaskan huskies, are elite endurance athletes, as evidenced by their ability to maintain high speeds (>25 km h^{-1}) for long distances[52]. Their most famed athletic feat is competing in the Iditarod Trail Sled Dog Race, an 1100 mile (1770 km) race that involves travel from Anchorage to Nome, Alaska every March. The race crosses varied terrain, ranging from a 5000-foot (1524 m) mountain pass to windy coastal plains. Due to their unique ability to perform in extreme environments, sled dogs have recently become subjects of field research for comparative exercise physiologists. Unfortunately, little research has been done in the laboratory to establish baseline cardiovascular fitness parameters or to evaluate how these parameters respond to training. Reynolds *et al.* reported that 12 weeks of endurance training did not result in a significant change in VO_{2max}[42]. However, the method by which VO_{2max} was measured was not described. Additionally, their dogs had been previously trained and their level of residual fitness was unknown at the beginning of the study.

There are currently no known objective parameters that can be used to predict performance in endurance dog racing. Constable *et al.* examined cardiac variables, conformation and athletic ranking of dogs that finished the Iditarod and those that did not[4]. Only athletic ranking by the musher differed significantly between finishers and non-finishers. Establishing non-invasive methods to predict performance may assist in selective breeding programmes and team member selection. VO_{2max} has long been a major indicator of endurance performance capability in humans[9]. Among human athletes with similar VO_{2max} values, it has been demonstrated that differences in endurance capacities at submaximal exercise intensities are correlated with blood lactate concentration and muscle capillary density[6].

Therefore, the objectives of this study were to develop a method to measure oxygen consumption (VO_2) in exercising sled dogs, to measure VO_{2max}, to determine blood lactate concentrations at submaximal exercise intensities and to assess responses of these parameters to periods of light and moderate submaximal training.

Material and methods

Prior to all testing, this study was approved by the Institutional Animal Care and Use Committee at Washington State University.

Development of techniques – mask and airflow

An open-circuit flow through a system of the type developed for exercising horses was adapted for use with running dogs[2]. A face mask was developed that allowed for panting while still providing a complete collection of expired gases. A biased airflow rate was identified that allowed for the measurement of VO_2 without compromising on gas exchange. Previous studies in horses have indicated that the biased flow rate must exceed the peak inspiratory flow that can be generated by the subject[1].

A healthy, proven sled dog (female, aged 10) was used to develop the system. After undergoing treadmill acclimation, this dog completed three incremental exercise tests in harness to fatigue, while wearing a mask that housed a Fleisch #2 pneumotachometer (Gould Systems, Cleveland, OH). Maximal inspiratory and expiratory flows ($13.4\,l\,s^{-1}$) did not change during the three separate runs. To ensure that this flow rate was adequate in the untrained yearling sled dogs, three of them completed an incremental exercise protocol with biased flow rates ranging from 13 to $27\,l\,s^{-1}$. Resistance was similar with all flow rates.

Dogs

Five harness-broken but otherwise untrained sled dogs completed the study (three males, two females; all being the progeny of a 2004 Iditarod champion sire). Each was 17 months old at the start of the study. They began the trial weighing 21.9 ± 2.8 kg (mean ± standard deviation) and ended it weighing 22.2 ± 2.9 kg.

Nine weeks prior to the start of the study, the dogs were moved into kennels (10 feet × 10 feet), started on a diet composed of 27% protein and 44% fat on an energy basis, and began acclimating to exercise on a treadmill. The dogs were run in harness, with the harness attached to the back of the treadmill to simulate pulling. The acclimation runs were limited to <2 min at an average speed of *c.* $4.2\,m\,s^{-1}$ (range, $2.7–6.0\,m\,s^{-1}$). The dogs were generally exercised on the treadmill twice a week.

Experimental protocol – VO_{2max}

Peak oxygen consumption was measured prior to the start of the training regimen (week 0), after 3 weeks of light training (week 4) and following another 4 weeks of moderate training (week 9).

Dogs completed an incremental exercise test in which speed was increased by $0.5\,m\,s^{-1}$ increments at 1-min intervals until there was no increase in VO_2 despite an increase in speed. Starting speeds varied between dogs. At rest and during the last 15 s at each speed, mixed expired O_2 was measured using an oxygen analyser (Ametek S-3A, Pittsburg, PA). VO_2 was corrected to standard temperature, standard pressure and dryness (STPD).

Ambient temperature varied from 16 to 27°C. Each dog was weighed prior to each exercise trial. The dogs were shaved and sprayed with water to assist in cooling during the exercise trial.

Air flow rates through the mask were set at *c.* $16\,l\,s^{-1}$, which was *c.* 20% higher than the maximum inspiratory flow ($13.4\,l\,s^{-1}$) of the adult sled dog measured previously. Flow rates were verified indirectly by integrating signals generated using 1–7 l volumes from a 14 l syringe with laser-designated 1 l increments (Hans Rudolph, Kansas City, KS).

Experimental protocol – submaximal exercise tests

Two days after each VO_{2max} protocol, a 20 g catheter was placed in the cephalic vein and each dog completed a submaximal run at a speed calculated to be 70% of pre-training (week 0) VO_{2max} (i.e. at the same absolute speed) for 5 min. During each of these protocols, blood was drawn at rest and following 5 min of exercise. During the week 4 and week 9 submaximal trials, a strain gauge (MLP-50, Transducer Techniques, Temecula, CA) was attached between the harness and the treadmill. Tension readings were taken every 20 s. The tension readings over the 5-min period were averaged. This was integrated into the formula: work = tension × speed, in order to determine the work performed by each dog during the run[49].

Whole blood (250 μl) was deproteinized with 500 μl of cold perchloric acid (7% solution). The samples were centrifuged for 10 min at 4000 rpm; the supernatant was decanted and stored at −80°C until analysis. The supernatant was analysed spectrophotometrically for lactate based on the appearance of NADH when lactate was converted to pyruvate (Milton Roy Spectronic 401, Rochester, NY).

Training protocol

The dogs completed a 9-week training programme during the autumn. The dogs were run 3 days per week in teams of two. Due to temperature constraints (the room in which the treadmill was housed was not air-conditioned), the dogs underwent light submaximal training for the first 3 weeks (*c.* 3 days week^{-1}, average distance 1.7 ± 0.1 km; average speed 4.7 m s^{-1}, range 4.0–6.2 m s^{-1}). Following assessment of VO_{2max} and lactate responses to standardized exercise as described above, the dogs subsequently underwent a 4-week training programme of moderate intensity. Speed, distance and frequency were gradually increased until the dogs were running up to 34 km divided over 4 days, 9 weeks after beginning the entire study (*c.* 4 days week^{-1}, average distance 5.6 ± 0.4 km, average speed 4.9 m s^{-1}, range 3.6–5.7 m s^{-1}). Mean total distance run by each dog over the 9 weeks was 161 ± 9.1 km at *c.* 4.9 m s^{-1}.

During the moderate training, the dogs' training bouts were split between controlled treadmill training as described above and exercise, consisting of pulling a person on a bicycle. Distances and average speeds of exercise training undertaken outside were monitored by a global positioning system (eTrex Vista, Garmin International, Inc., Olathe, KS). The bicycle training was undertaken in order to accomplish longer training runs.

Statistical analysis

Results were expressed as the mean ± standard deviation and analysed using a one-way ANOVA for repeated measures. When the *F* statistic was significant, individual means were compared using a *post hoc t*-test, with *P*-values adjusted using a Bonferroni correction. Since it was not possible to control for the harness tension and, therefore, the work that was done, a subsequent analysis of covariance was conducted with calculated workload as the covariate.

Results

Results are summarized in Table 1. VO_{2max} increased significantly in response to moderate-intensity training but did not increase significantly in response to light training. Speeds at which VO_{2max} also increased significantly with moderate training but not light training.

During the submaximal runs at the same absolute speed, there was a significant and substantial decrease in blood lactate concentrations post-exercise. Harness tensions at the same absolute speed in weeks 4 and 9 did not differ significantly, resulting in similar workload. When expressed relative to week 9 VO_{2max}, the absolute speeds were equivalent to 63.9 ± 2.3% VO_{2max}. The speed associated with an exercise intensity of 70% of VO_{2max} increased significantly from week 0 to week 9.

Discussion

Since aerobic metabolism depends on body size, allometric scaling has been developed to determine the relative aerobic capacity of various species[48]. Several notable exceptions to the allometric curve exist. For example, the smallest mammal, the Etruscan shrew, exhibits a VO_2 of 1000 ml kg min^{-1} during submaximal exercise[53]. Pronghorn antelopes, known for their endurance abilities on the plains, have a VO_{2max} of 300 ml kg min^{-1} [30]. Wild canids, including the coyote (179 ml kg min^{-1})[54], wolf (157 ml kg min^{-1})[54] and Arctic blue fox (217 ml kg min^{-1})[31], all demonstrate high aerobic capacity for body size.

VO_{2max} has long been accepted as a primary indicator of cardiovascular and endurance capacity in humans[9]. Elite human athletes show VO_{2max} values of 65–85 ml kg min^{-1} [5,12,45].

Unfortunately, there are limited data available on athletic trained quadrupeds. Arabian horses are regarded as the premier endurance horse breed but have not been evaluated in controlled environments to the same extent as Thoroughbreds and Standardbreds. A VO_{2max} of *c.* 130 ml kg min^{-1} has been reported in one study involving lightly exercised Arabians[37]. In contrast, trained Thoroughbreds and Standardbreds exhibit maximal oxygen consumption values of *c.* 150 ml kg min^{-1} [11,15,18,28,29,37,38,44], although these have not been elite competitors. Mongrel dogs, by comparison, have VO_{2max} values ranging from 30.3 to 170 ml kg min^{-1} [32,33,34,39,46,47,54]. Our five yearling sled dogs demonstrated a mean trained VO_{2max} value of 198 ml kg min^{-1}, which, in comparative terms, reinforces the impression that they are elite endurance athletes.

Table 1 Submaximal lactate concentrations at the same absolute workload (mmol l^{-1}), harness tensions (kg), work (J), speed (m s^{-1}) and maximal oxygen consumption (ml O_2 kg^{-1} min^{-1}) in response to light- and moderate-intensity training

Parameter	Week 0	Week 4 (light training)	Week 9 (moderate training)	*P*-value
Blood lactate (5 min) (A)	9.2 ± 4.7	8.0 ± 2.9	4.3 ± 2.4	*P* = 0.047
Tension (A)	NA	6.0 ± 1.1	5.9 ± 0.7	
Work (A)	NA	1741 ± 242	1721 ± 97	
VO_{2max}	180.2 ± 9.9	186.0 ± 17.0	198.7 ± 19.2	*P* = 0.046
70% of VO_{2max} speed	4.8 ± 0.4	4.8 ± 0.4	5.4 ± 0.5	*P* = 0.008
100% of VO_{2max} speed	6.7 ± 0.3	7.5 ± 0.8	8.2 ± 0.7	*P* = 0.012

Many species demonstrate a significant increase in VO_{2max} with training. In an 8-week training protocol, previously untrained humans demonstrated a 9% increase in VO_{2max}[8], while longer training protocols frequently result in an even greater increase in VO_{2max} of 13–26%[10,13,19,26]. Foxhounds had a 28% increase (114–146 ml kg min^{-1}) in calculated VO_{2max} with an 8- to 12-week endurance training programme[34]. Adult Thoroughbreds that had been previously trained and then detrained demonstrated a 17% increase in VO_{2max} with another 12 weeks of exercise training on a treadmill[14].

When trained at a relative intensity equivalent to 40 or 80% of their VO_{2max} speeds, Thoroughbreds demonstrated a 10% increase in VO_{2max} after only 2 weeks[29]. In contrast, our dogs did not demonstrate a significant increase in VO_{2max} following 3 weeks of light training. During this time, our dogs were only trained *c.* 3 days week^{-1} for *c.* 1.7 km at an intensity equivalent to *c.* 70% VO_{2max} speed, whereas the horses used by Knight *et al.* were trained 6 days per week for 1.5 km[29]. However, our sled dogs did demonstrate a 10% increase in VO_{2max} when trained at moderate intensity for 5 weeks from week 4 to week 9 (an average of 5.62 km at *c.* 4.9 m s^{-1}, 4 days week^{-1}). Despite the increased workload during the last 6 weeks, our dogs were still probably undertrained in comparison with normal racing sled dogs. Dogs under training for the Iditarod are typically running >90 km week^{-1} by the end of week 9 of their training; our peak weekly training distance never exceeded 34 km.

There was no untrained control group in this study due to the lack of suitable subjects. Therefore, the possibility that the increase in VO_{2max} was associated with normal growth and development cannot be completely ruled out. However, we think it is highly unlikely that the detected increase in VO_{2max} was due to anything but training. Had this been the case, it would have been reasonable also to observe changes while the dogs were being lightly trained. This did not happen. Although the VO_{2max} of Thoroughbreds continues to increase in untrained yearlings as they grow[35], these animals are still not fully grown 2 years after being born[21], whereas dogs enter oestrus at *c.* 6 months of age and reach 99% of adult weight by 1 year of age[23]. Our dogs completed the current study when they were between 17 and 20 months of age.

It has been previously reported that VO_{2max} values of sled dogs did not change significantly following a 12-week endurance training programme[42]. However, the dogs in that study were older dogs that had been previously trained. They were given no systematic training for the 3 months prior to the onset of the study. However, during this time, they were kept restrained on chains, which allowed for unmonitored exercise. Therefore, it is unclear as to how much endurance capacity they retained in the detraining period. In trained humans[7] and Thoroughbreds[51], VO_{2max} has been shown to decrease significantly with detraining, even though values had remained above those measured prior to training in the Thoroughbreds. In order to prevent residual effects of previous training or any undocumented conditioning, our dogs had never previously been trained and were kept in 10′ × 10′ kennels for the 9 weeks preceding the study.

A previous study comparing dog breeds found that highly conditioned Labrador Retrievers fed a high-fat (60% on an energy basis) diet had a VO_{2max} (167 ml kg min^{-1}) that was indistinguishable from that of trained sled dogs (179 ml kg min^{-1}) on the same diet[40]. Due to these findings, Reynolds *et al.* postulated that diet, rather than breeding, was responsible for the endurance capacity of sled dogs[41]. In light of our recent findings, it appears that although diet might play a role in aerobic capacity, the effects of selective breeding and physical training cannot be disregarded.

Previous research has demonstrated that there is a high correlation between blood lactate concentrations during submaximal exercise and endurance performance[16,22]. In humans[43] and horses[50], it is well established that blood lactate concentrations at the same absolute speed are lower following training. It has also been demonstrated that blood lactate concentrations at the same relative intensities are lower in trained than untrained individuals at work loads ranging from 30 to 75% VO_{2max}[3,27], and a significantly lower blood lactate concentration was elicited at the same relative exercise intensity following training in humans[10,26] and in Standardbred horses[36]. These findings are similar to those found in this study. When exercising at the same absolute exercise intensity, blood lactate concentrations in our sled dogs following 5 min of exercise decreased as fitness increased. This most likely reflects a training-related improvement in metabolic control and a change in the pattern of substrate utilization in the progressively better-conditioned dog[20,25]. The lactate concentrations before and after the light training programme were higher than expected. These dogs were experiencing their first form of any type of controlled or sustained exercise and it may be that the unexpectedly high lactate concentrations reflected a lack of metabolic control in these athletically naïve subjects. Similar findings have been reported in members of other species in association with their first exposure to training[13,17,24,50].

In conclusion, it appears that sled dogs have comparatively high VO_{2max} and that 4 weeks of moderate training resulted in a significant increase in VO_{2max}

and a significant decrease in submaximal blood lactate accumulation at the same absolute workload. An easier or lighter training programme has no effect on VO_{2max}. In future studies, it would be informative to measure tension more frequently during runs in order to better quantify both absolute and relative submaximal workloads. It would also be relevant to expose the dogs to a training protocol that better emulates training conditions of elite racing sled dogs in order to help better understand the full extent of these athletes' aerobic capacities and their abilities as elite endurance competitors.

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