

Effects of Nutritional State on Physiological Responses and Heat Production During Exercise of the Animal – a Review

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ABSTRACT : This review was conducted to analyse the effect of nutrition on physiological responses; heat production of domestic animal during exercise. Overall, it can be concluded that the major factors likely to affect heat production in domestic animals during exercise (including work load) are body weight, speed, the gradients attempted, feed intake, ambient conditions (including temperature and solar radiation) and altitude.

On nutrition-exercise interactions, for example, it has been concluded that animals on better quality diets produce more heat than those on poorer quality ones, and that glucose as well as acetate are metabolized as energy sources during both rest and exercise.

(Key Words: Nutrition, Exercise, Domestic Animal, Heat Production, Physiology)

THE EFFECTS OF NUTRITIONAL STATE ON PHYSIOLOGICAL RESPONSES DURING EXERCISE

Many researches have been done on nutrition-exercise interactions, and as a general rule it has been concluded that animals on better quality diets produce more heat than those on poorer quality ones, and that glucose as well as acetate are metabolized as energy sources during both rest and exercise. Confirmation of this is provided, for example, by Jarrett et al. (1976), who reported that the utilization of glucose was greatly increased by exercise: during work glucose supplied about 27% of the energy for respiration in an exercising limb whereas acetate supplied only about 2%. In complete contrast, little utilization of glucose in the resting limb was recorded although acetate oxidation accounted for about 20% of the oxygen uptake. Concurrently, Judson et al. (1976) reported that the total entry rate of blood glucose at rest was 0.44 ± 0.03 mmol/min, while during exercise it was 0.84 ± 0.004 mmol/min.

At different physiological level, further information was found in the work of Clark and Quin (1947), who reported that when sheep were exposed to environmental temperatures of 9-23°C in the field, thin sheep on a poor diet (600 g/d grass hay) showed a suppressed panting reflex (20-40 vs 90-150/minute) and an excessive rise in RT (37.2-39.3°C vs 38.3-39.5°C) in comparison to those on a better diet (350 g/d maize and 790 g/d lucerne hay).

Moreover, the ability to control RT returned when body condition improved. This result was supported by Robinson and Lee (1947), who noted that a high-plane diet fed to ewes induced very highly significant increases in RT and RR in both hot-wet and hot-dry atmospheres when compared to a low-plane diet. Subsequently, an experiment using 3 different levels of diet ("low", 300-400 g/d; "medium", 500-850 g/d; and "high", 800-1,400 g/d) for Merino and Corriedale ewes (Riek et al., 1950) revealed that these sheep were generally relatively tolerant of hot conditions; the exceptions were the high-plane Corriedales, which had to be removed before the completion of seven hours of exposure to 40°C and 40 mmHg. water vapour pressure, with a RT over 41.7°C. Subsequently, in cattle Purwanto et al. (1993) reported that both RR and RT at a high level of TDN intake (72.5 g/kg^{0.75} day) were the same as at a medium level (80% of the high level), but both those values were higher ($p < 0.05$) than at a low level (60% of the high level). At all levels of TDN intake, the mean of standing HP (heat production) was higher ($p < 0.05$) than the resting (lying) HP. The differences between standing and lying HP at low, medium and high feeding levels were 4.4, 4.7 and 5.4 kJ/kg^{0.75} h, respectively; values which represent only 7% of total HP. In sheep, Graham et al. (1959) found that low (600 g/d), medium (1,200 g/d) and high (1,800 g/d) levels of feeding in sheep produced heat at rates of 0.23, 0.35 and 0.42 KJ/h, respectively when environmental temperature varied from 24 to 40°C. Also in sheep, Clapperton (1964a) reported that the mean apparent

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digestibilities (%) of dietary constituents (at a submaintenance feeding level) by the Cheviot and Scottish Blackface breeds, when at rest or walking on a treadmill at 2.9 km/h on a gradient of 17° for 260 minutes, were showed in table 1.

Table 1. Mean digestibilities (%) and heat production (%) of Cheviot and Scottish Blackface breeds

Breed	Dry matter digestibility (%)		Heat production (%)	
	rest	walk	rest	walk
	Cheviot	65.9±1.5	66.7±1.3	64.4±1.6
S. Blackface	64.6±0.8	65.1±1.3	64.0±1.8	64.1±2.2

From a combination of the above results it can be seen that different breeds of sheep have different capabilities to digest feedstuffs, and that in general sheep digest more efficiently as well as produce more heat, when walking than when resting.

In working animals, Bakrie et al. (1989a) reported that buffalo had a significantly higher RT during work when given a roughage diet than when fed a concentrate diet. In addition, while the RT of buffalo on the concentrate diet remained lower at all times during work, RR followed the opposite trend and remained higher on this diet compared to the roughage diet. This differential responses in RT and RR is not unexpected, since increased evaporative cooling from a high RR would automatically reduce RT. Nevertheless, the use of diets of lower heat increment seems to reduce the heat load in working animals, particularly buffalo. Moreover, Bird et al. (1981) reported that treadmill exercise at 2.5 km/h on a 10 degree slope for 60 min in sheep caused a six- to seven-fold increase

in hind-limb oxygen uptake (364 vs 2,360 $\mu\text{mol}/\text{min}$), due mainly to an increase in blood flow, assisted by an increase in the oxygen-carrying capacity of arterial blood. Subsequently, at rest, the oxygen uptake was 355 and 373 $\mu\text{mol}/\text{min}$ when feed was given at maintenance (5.8 MJ/day) and 1.5 times maintenance (8.6 MJ/day), respectively. Meanwhile, during exercise the corresponding oxygen uptake values were 2,114 and 2,606 $\mu\text{mol}/\text{min}$ ($p < 0.05$). Subsequently, Richter et al. (1992) reported that in the human leg the oxygen uptakes at rest and during 30 minutes exercise were 89 and 4,192 $\mu\text{mol}/\text{min}$ respectively.

Experiments on exercise in steers fed low and high plane diets (Murray et al., 1981) revealed that the RT response to exercise was greater in the high than in the low plane group. For example, after 2 h of exercise the high plane group showed increases in mean RT of 2.1 to 2.2°C compared with values of 1.7 to 1.8°C for the low plane group ($p < 0.05$). Compared with high plane animals, low plane animals also had lower RR before and after 2 h of exercise, although mean values were not significantly different (125 ± 17 vs. 161 ± 4 and 202 ± 6 vs. $219 \pm 11/\text{minute}$, respectively). In addition, high plane animals had significantly greater ($p < 0.05$) sweating rates than low plane animals (474-615 vs. 267-332 $\text{g}/\text{m}^2/\text{h}$, respectively). The same patterns were reported by Slee et al. (1988) in sheep; after 1 h of heat exposure, sheep on unrestricted feeding had slightly higher RT (40.0 ± 0.0 vs. $39.6 \pm 0.2^\circ\text{C}$; $p < 0.05$) and much higher RR (138.7 ± 58.4 vs $32.0 \pm 20.0/\text{min}$; $p < 0.05$) than those on restricted feeding.

The values for the energy cost of walking and working in various draught animal species are illustrated by the following (after Lawrence and Stibbards, 1990).

Table 2. Mean energy expenditure in various draught animal species

	Average value	Species	Source	Comments
Energy cost of walking (J/m/kg live weight)	1.9	Cattle (<i>Bos taurus</i>)	Brody (1945)	Weights 383 to 430 kg; speeds 1.8 to 3.2 km/h
	2.0	Cattle (<i>Bos taurus</i>)	Ribiero et al. (1977)	Speeds 2.5 to 5.0 km/h
	0.5 to 2.8	Cattle (<i>Bos taurus</i>)	King (1981)	200 kg animals fed at maintenance; speeds 1.4 to 5.8 km/h
	2.1	Brahman cattle/buffaloes	Lawrence and Stibbards (1990)	Speeds 1.4 to 5.8 km/h

THE EFFECTS OF EXERCISE ON HEAT PRODUCTION

Generally, animals need energy for the maintenance of body functions and activities, particularly when they are walking or exercising (Taylor et al., 1974; Borut et al., 1979; and Lawrence and Stibbards, 1990) and this is considered as heat production. The energy is mainly derived from carbohydrate oxidation via pathways described by the general formula $C_6H_{12}O_6 + O_2 \rightarrow CO_2 + H_2O + \text{energy}$. Harman and Pethick (1994) reported that the contribution of glucose to whole body CO_2 production in sheep was low at rest, with values in close agreement with previous works (Wilson et al., 1983, Oddy et al., 1985). However, during exercise oxidation increased dramatically, with the absolute rate of glucose oxidation increasing by about 5- and 9-folds when walking below and above the anaerobic threshold, respectively. This work confirms that glucose is an important aerobic energy source during physical work. In addition, heavier animals have been shown to use more energy for walking than lighter ones (King, 1981) and there is a general tendency for energy utilization to increase with increases in walking speed (Lawrence and Stibbards, 1990) according to the general equation for all animals:

$$E_w = 0.974V + 1.199 \quad (E_w = \text{Joules above standing/m/} \\ \text{kg live weight; } V = \text{speed m/s}).$$

In running gazelle, Taylor et al. (1974) described heat balance as: heat production = heat storage \pm total evaporative heat loss \pm non evaporative heat loss, and noted that heat production increased linearly with increasing running speed. For example, at a speed of 3 km/h, heat production was 1.8 times the observed resting levels, and this increased to 8.4 times at 21 km/h (14.9 times predicted standard metabolic rate). Heat storage increased by 32, 74 and 77% as treadmill speed increased to 9.6, 15.8 and 20.2 km/h, respectively. While evaporative heat loss increased over 6-fold as running speed increased from 0 to 9.6 km/h, nonevaporative losses declined as treadmill speed increased to 3 and 9.6 km/h (by 50 and 24%, respectively). Therefore, most heat loss was through evaporation, particularly by panting rather than sweating since the latter did not increase significantly and remained at approximately 30 g/m²/h. Taylor et al. concluded that exercise would not have a major effect on the water balance of gazelles due to the fact that they normally either move slowly when they graze or sprint for only short periods to avoid predators.

In comparing different species, Taylor and Rowntree

(1973) reported that goats appear to be intermediate between the "regulator" and "heat storer" classes of animal, in that they store about 35% of heat production; compared to the cheetah and rhea in which 65 and 20%, respectively of heat production were stored during 15-30 min on a treadmill at 9 km/h and 22°C. In addition, there were two important differences in the heat balance between cheetahs and goats that were running. Firstly, heat storage was much more important in cheetahs than in goats. Secondly, neither evaporative nor nonevaporative heat loss of the cheetah increased with increasing heat production, whereas both increased in the goat. For example, as the cheetah increased speed from 2 to 11 km/h, heat storage increased from 5.0 to 31.4 KJ/kg/h, and about 70% of the heat produced while running at 11 km/h was stored. In contrast, total evaporation increased only from 6.2 to 10.5 KJ/kg/h, and only 24% of the heat produced at 11 km/h was lost by evaporation. Nonevaporative heat loss from the cheetah actually decreased (from 5.9 to 2.8 KJ/kg/h) and accounted for only 6% of the heat produced at 11 km/h. A quite different heat balance occurred in goats. As speed increased from 1 to 9 km/h, heat storage increased from 2.0 to 12.6 KJ/kg/h, but accounted for only 34% of the heat produced at 9 km/h. Evaporation from goats increased nearly 10-fold (from 1.8 to 17.0 KJ/kg/h) and 43% of the heat produced at 9 km/h was lost by evaporation, while nonevaporative heat loss also increased (from 6.8 to 10.3 KJ/kg/h) and accounted for about 26% of heat produced at the same speed. In conclusion, it can be said that the cheetah has not developed evaporative cooling mechanisms for maintaining a constant body temperature during running and instead stores heat, while goats have developed the opposite strategy.

Subsequently, in goats, Borut et al. (1979) reported that while under mild conditions, in the morning at 26°C, evaporation accounted for up to 50% of the heat produced, at 40°C in a climatic chamber it equaled heat production, and at 12:00 h in the desert it had increased to about 150% of heat production. The goats in the climatic chamber relied mainly on panting to dissipate heat. In the desert, however, the amount of heat dissipated by sweating was twice as great as that lost through the respiratory system. These high rates of sweating (up to 143 g/m²/h) were attributed to increases in ST consequent on the absorption of solar radiation, which does not exist in the laboratory but is very prominent in the desert environment. Borut et al. however, did not compare the different sexes, which only used the female animal. In a separate experiment comparing buffalo and cattle (Zebu and Hereford), Taylor et al. (1970) reported that

cutaneous water losses from buffalo, Zebu and Hereford animals corresponded to 4.1, 4.3 and 4.7% of their body weight or 58, 69 and 61% of total water losses, when water was given by free access at 22-40°C environmental temperature in the African desert. The remaining water was lost in the faeces and urine. When water intake was restricted, evaporation was reduced by an amount equal to or greater than the combined reduction of faeces and urine in cattle (300%), but less in buffalo (60%). Thus evaporation was clearly the major avenue of water loss from bovids under desert conditions, and the fact that the buffalo had the lowest water loss could be due to it being a non sweating animal.

Similar patterns were found by Taylor and Lyman (1972) in two different types of gazelle: the Thomson gazelle stored large amounts of heat during running which led to an increase in RT as much as 4.6°C, but their corresponding increase in sweating was relatively low (56 vs 78 g/m²/h before and after running, respectively). Under the same conditions, Eland increased RT only slightly (less than 1°C), but experienced an increase in sweating of from 96 to 266 g/m²/h.

Overall, it can be concluded that animals of different breeds and species have different ways to maintain heat balance, and that these vary to a considerable degree with body size, environmental conditions and sweat gland output.

In general, a ruminant needs energy for any of the purposes of maintenance, pregnancy, growth, fattening, lactation and work and these are known as net energy requirements, because an animal has to expend energy on the nutrients it absorbs in order to use them for any such processes (Lawrence and Stibbards, 1990). While, the ARC (1980) stated the standard energy requirement for horizontal locomotion to be 1.2 MJ/km for a 600 kg cow, the corresponding figure according to Taylor et al. (1989) is 1.0 MJ/km and Taylor et al. (1970) concluded that the energy cost of running is related to body weight. Subsequently, Taylor (1974) reported that a 400-kg ox, walking at a speed of 2 km/h could be expected to expend an amount of energy 11% higher than its resting metabolic rate. Moreover, experiments on the heat production of calves of different body weights kept out-of-doors (Holmes et al., 1976) suggested that heat production increased (6.2 vs 6.5 kJ/kg/h) with increasing body weight (94 vs 122 kg respectively). Ribeiro et al. (1977) reported that the rates of heat production of cattle walking on a treadmill on the level and at a gradient of 6° were 2 and 26 J/kg/m, respectively. Values (J/kg/m) for other species during horizontal locomotion are: man 2.3 (Hall and Brody, 1934); dog, 2.5 (Lusk, 1931); horse, 1.6

(Hall and Brody, 1934); sheep, 2.3 (Clapperton, 1964b) and red deer 2.6 (Brockway et al., 1965) and it appears that between these species the energy cost of moving 1 kg of body horizontally is fairly constant.

Leng (1985) concluded that the total daily heat production of a tethered animal is 1.5 times higher than its basal metabolism; in an animal walking with a companion when ploughing the increase is to 2.0 times its basal metabolism whereas an animal actually ploughing increases its daily heat production by 3.8 times its basal metabolic rate. Other factors such as temperature levels are also known to affect dairy heifers (Purwanto et al., 1994); heat production at 20°C was almost the same as at 10°C, but that at 30°C was 11% higher than at 10°C; such an increase could partly be associated with the high energy cost of standing (Clapperton, 1964b), since animals at 30°C stood for 104 min/d longer than those at 10°C. Pirwanto et al. (1994) estimated the energy cost of this additional standing to be 9.2 kJ/kg^{0.75}d, as compared to about 64.8 kJ/kg^{0.75}d as a result of increased metabolic and thermoregulatory activities associated with the concurrent 1.3°C rise in RT. With regards different altitudes, Hays et al. (1978) pointed out that exercise effects in oxen were greater at 3,500 m than at 400 m (in heart rate, RR, Hb, blood pH, blood lactate and blood pyruvate by 26, 11, 4, 0.3, 39 and 56%, respectively) and suggested that energy expenditure was greater at high than low altitude.

Yamamoto (1989a, 1989b) observed that in cattle the levels and daily fluctuations in heat production were closely related to feed intake and feeding time. For example, heat production decreased gradually by 40, 39, 35 and 28 kJ/kg^{0.75}h, when level of TDN intake declined from 15.5 to 14.2, 11.0 and 8.8 kg/day, respectively. Such a finding was supported by Matsumoto et al. (1990), who reported that calves at 100 kg body weight with feeding levels of 100, 85, 70 and 55% TDN produced heat at rates of about 40, 33, 30 and 27 kJ/kg^{0.75}h, respectively. Additionally, it was found that heat production declined with increasing body weight. For example, cows weighing 330 kg and fed similar TDN levels produced heat at rates of 33, 32, 29 and 26 kJ/kg^{0.75}h, respectively.

In working buffalo and cattle (3.6 km/h treadmill speed, 13-20°C environmental temperature and 47% relative humidity) Pearson and Smith (1994) reported that heat production was 0.1 and 0.2 kJ/kg^{0.75}h when dry matter intakes were 2.6 and 3.2 g/kgM^{0.75}h, respectively and feeding time was restricted (food troughs were removed at 08:30 h and replaced at 15:30 h). However, daily exercise (0.5-3 km/day) did not significantly affect voluntary dry matter intake and heat production in dairy

cows (Gustafson et al., 1993). It is assumed that different levels of heat production are closely associated with different levels of oxygen consumption during exercise. For example, in exercising goats, Fukura et al. (1986) observed an increase in oxygen consumption from 0.71/kg^{0.75}/h when resting to 1.1 and 1.41/kg^{0.75}/h when walking at 1.5 or 3.7 km/h. In exercising sheep, (2.6 km/h) Bell et al. (1983) suggested that oxygen consumption increased by 4.5-fold in the thermoneutral zone (14-17°C), a response that was slightly higher than at 23 to 40°C (4.3-fold). The sheep at 40°C relied particularly on panting (RR increased from 84 to 134/min) as the major avenue of heat loss, a condition supported by the finding that blood flows to the nasal mucosa and turbinates of the upper respiratory tract increased about 12- and 30-fold, respectively. Subsequently, Pethick et al. (1991) observed increases in the oxygen consumption of both the gut and liver of sheep as treadmill speed and inclination were increased.

The heat production of cattle and buffalo during walking, carrying and pulling increased from 2.1 to 4.2 KJ/kg live weight as speed increased from 1.4 to 5.8 km/h; and the animals became visibly uncomfortable (Lawrence and Stibbards, 1990). Those results were in general agreement with Hales and Findlay (1968), who concluded that the oxygen consumption of cattle increased during exposure to severe heat.

CONCLUSIONS

Overall, it can be concluded that animals on better quality diets produce more heat than those on poorer quality ones, and that glucose as well as acetate are metabolized as energy sources during both rest and exercise. For example, during work glucose supplied about 27% of the energy for respiration in an exercising limb whereas acetate supplied only about 2%. During exercise oxidation increased dramatically, with the absolute rate of glucose oxidation increasing by about 5 to 9-folds. Additionally, sheep on a poor diet showed a suppressed panting (20-40 vs 90-150/minute) and an excessive rise in RT (37.2-39.3°C vs 38.3-39.5°C) in comparison to those on a better diet. Compared with high plane animals, low plane animals also had lower RR before and after of exercise. In addition, high plane animals had significantly greater ($p < 0.05$) sweating rates than low plane animals.

At different levels of TDN intake, the mean of standing HP (heat production) was higher ($p < 0.05$) than the resting (lying) HP. It can also be concluded that different breeds of sheep have different capabilities to

digest feedstuffs, and sheep digest more efficiently as well as produce more heat, when walking than when resting.

Within different species, they were concluded that goats appear to be intermediate between the "regulator" and "heat storer" classes of animal, they store about 35% of heat production compared to the cheetah and rhea of 65 and 20%, respectively.

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