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Aestivation and time dilation in anurans

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ABSTRACT: Aestivating frogs are able to withstand long periods of immobilisation whilst appearing to maintain their muscle mass and contractile performance. The functional capacity of critical muscles is also not compromised upon emergence from aestivation. Years of starvation and immobilisation endured by aestivating anurans has no deleterious effect on their muscles, bones, water content, or stomach and liver integrity, which suggests there is some sort of time dilation at work in aestivating frogs that makes months or years inside their aestivation cocoon pass as days or weeks would when active normally.

KEYWORDS: Aestivation, time dilation, anurans.

INTRODUCTION

Aestivation is a state of aerobic torpor, which is believed to be a survival strategy for animals living in arid conditions. It is typically associated with a lack of food availability and frequently associated with high environmental temperatures (Pinder et al., 1992; Abe, 1995; Land and Bernier, 1995). Animals that aestivate normally do so for 9–10 months of the year, but there are numerous examples of continuous aestivation lasting two or more years. Aestivating animals are triggered to emerge from their underground burrows by the first torrential rains of summer, at which time they “break their dormancy” or “end their aestivation.”

Aestivating animals enter dormancy to avoid adverse environmental conditions (Guppy et al. 1994). In doing so, they are exposed to a number of physiological challenges, including fasting for months or years, exposure to extreme temperatures, hypoxia and prolonged immobilisation (Guppy and Withers 1999).

Some of these challenges are countered by the characteristic habit of dormant animals to depress their metabolic activity (Storey and Storey 1990). Reduced respiration rates minimise the impact of hypoxia and a decreased rate of ATP turnover lowers the energy demand; thereby prolonging fuel reserves (Guppy et al. 1994).

Several of the frog species that aestivate produce cocoons made from multiple layers of shed epidermis alternated with glandular secretions (Loveridge and Withers, 1981; Pinder et al., 1992). During aestivation, burrowing frogs undergo fasting (Cramp et al. 2009) and are immobilised by the cast-like cocoons (Seymour 1973a; Withers 1993, 1995). Aestivating amphibians dramatically slow down their breathing, heart rate, and metabolic processes, such as digestion.

DISCUSSION

The Green-striped burrowing frog, Cyclorana alboguttata, routinely aestivates as part of a physiological strategy to avoid desiccation in semi-arid environments. During aestivation, the hind limbs are immobilised in a cocoon for months at a time and the frogs experience starvation.

EFFECT OF STARVATION DURING AESTIVATION ON MUSCLE PROTEIN LEVELS

The loss of body protein affects the function of important organs, eventually resulting in death. Starvation in mammals typically leads to a breakdown of muscle protein, however, the Sartorius protein concentration in frogs has been found to be unchanged during aestivation. The protein content in the cruralis increased significantly after prolonged aestivation and remained unchanged in other muscles (Mantle et al. 2010). Furthermore, the protein content of the adductor magnus muscle of the burrowing frog, Neobatrachus centralis, is maintained during aestivation (Fuery et al. 1998).

EFFECT OF STARVATION DURING AESTIVATION ON HYDRATION

Starvation in mammals typically results in dehydration. In aestivating frogs, however, the water content of the Sartorius muscle is significantly above control levels after prolonged aestivation (Mantle et al. 2009). In other muscles, the water content level tends to rise, but less than in the Sartorius. The water content of muscles is conserved throughout aestivation (Withers 1998a), and the water content of most muscles (excluding in the Sartorius, where it increases) has been found to remain stable (Donohoe and Boutilier 1998).

EFFECT OF IMMOBILISATION DURING AESTIVATION ON MUSCLE INTEGRITY

Periods of inactivity due to disuse typically leads to degenerative changes culminating in the atrophy of muscle fibres. Muscle growth depends on the dynamic balance between synthetic and degradative processes (Schimke, 1975). Hudson & Franklin (2002a), however, found no reduction in muscle size, isometric force production or locomotive performance in Cyclorana alboguttata after three months of inactivity associated with aestivation.

This can be contrasted with the significant muscle disuse atrophy (characterised by a reduction in muscle fibre diameter and concomitant loss of performance) typically found in mammals that have had limbs artificially restrained or immobilised with casts or splints (Booth, 1982).

Studies have shown that aestivating frogs are able to withstand long periods of immobilisation during aestivation whilst maintaining whole muscle mass and contractile performance. The functional capacity of critical muscles is not compromised when they emerge from aestivation. (Mantle et al. 2010).

Prolonged immobilisation of mammalian limbs can result in muscle atrophy. However, aestivating anurans do not exhibit skeletal muscle atrophy or decreased functional performance even after long periods of inactivity (Hudson and Franklin 2002a, 2002b, 2003, Hudson et al. 2004, Symonds et al. 2007). The frog, Cyclorana, can withstand long periods of immobilisation whilst maintaining overall muscle mass and contractile performance (Hudson and Franklin 2002a; Hudson et al. 2006; Symonds et al. 2007). The structural characteristics of some muscles, however, such as the cross-sectional area of whole muscle and individual fibres, change significantly during nine months of aestivation. These changes appear to correlate with muscle function (Mantle et al. 2009).

EFFECT OF IMMOBILISATION DURING AESTIVATION ON THE 3D STRUCTURE OF CAPILLARIES

In mammals, prolonged immobilization of the limbs can result in a loss of capillary tortuosity; in turn resulting haemorrhaging of the skeletal muscles if rapid remobilization is permitted. By comparing the scanning electron micrographs from control (active) and aestivating (for four months) C. alboguttata, no differences in the three-dimensional structure of capillaries was detected. Quantification of the tortuosity of the capillaries in the semimembranosus muscle of controls and aestivating C. alboguttata revealed no significant difference. There was also no significant difference in the diameter of the capillaries in the semimembranosus muscles of control and aestivating frogs. The preservation of capillary structure in the hind limb muscles of C. alboguttata in part accounts for their remarkable ability to emerge with a fully competent locomotive system after prolonged immobilisation (Hudson & Franklin, 2003).

EFFECT OF IMMOBILISATION ON BONE DURING AESTIVATION

Extended periods of immobilisation in mammals typically results in bones being remodelled and a decrease in bone strength. Frogs that aestivated in soil for three and nine months and were compared with control animals that remained active, were fed, and had a continuous supply of water. In comparison to the controls, the long bone size, anatomy and bending strength of the aestivating frogs' bones remained unchanged, indicating an absence of osteoporosis due to disuse

(Hudson and Franklin 2004). The effect of aestivation and, hence, prolonged immobilisation, does not appear to have a deleterious effect on the cross-sectional area, histology, or bending strength of the femur and tibiofibular of C. alboguttata.

EFFECT OF STARVATION DURING AESTIVATION ON STOMACH INTEGRITY

Starvation in mammals typically results in atrophy (wasting away) of the stomach, however, the nutrient assimilation following prolonged food deprivation during aestivation can be enhanced (Cramp and Franklin 2003). The last meal before aestivation might be properly processed even if the overall metabolic activity is being reduced.

THE EFFECT OF DECREASED METABOLIC RATES DURING AESTIVATION ON LIVER FUNCTION

The metabolic capacity of the liver has been shown to be maintained during aestivation in some frog species (Berner et al. 2009), even though the in vitro metabolic rate of the liver is reduced significantly during amphibian aestivation (Fuery et al. 1998).

Berner et al. (2009) found that the liver enzyme activity in C. alboguttata remained stable throughout aestivation. Aestivation decreases the hepatic contribution to metabolic requirements, even though the mass-specific enzyme activities remain constant. In vitro liver metabolism may be depressed by up to 55 percent in an aestivating amphibian (Fuery et al. 1998).

Similarly, the accumulation of urea in the plasma of aestivating anurans could be toxic at high levels because of the alteration of protein function. Urea causes a general and consistent inhibitory effect on enzyme activity in rats and in non-aestivating anurans, however, the enzymes in the muscle tissue of speedfoot toads were found to be almost unaffected, or even activated by urea (Cowan and Storey 2002).

THEORY

The extraordinary findings listed above for aestivating frogs suggest that there is some sort of time dilation at work, which makes their months or years inside a cocoon pass as days or weeks would when normally active. Everything is slowed down for the frogs in the time dilation, for example, the basal heart rate is decreased by 60 percent and the metabolic rate by up to 80 percent during aestivation. No deleterious effects from the extended periods of immobilisation or starvation occur. We suggest that frogs can utilise this time dilation via heat isolation and that the duration they can sustain it depends on the surface area of the frog.

More research is needed to calculate the time spent inside and outside the cocoon and the corresponding functional age of the frog before and after the aestivation period.

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