

THE JOURNAL OF EXPERIMENTAL BIOLOGY

VOLUME 160

OCTOBER 1991

# The comparative physiology of exercise



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The Journal of  
Experimental  
Biology

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A pair of desert iguanas (*Dipsosaurus dorsalis*): 60 g lizards resident in the low deserts of the southwestern United States and northern Mexico. These and other iguanid lizards have been used to study reptilian skeletal muscle and cardiovascular function during and after exercise. Photographed by Todd T. Gleeson.

Published and Printed by The Company of Biologists Limited,  
Department of Zoology, University of Cambridge,  
Downing Street, Cambridge CB2 3EJ

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**This Publication  
is available in Microform**

**University Microfilms International**

300 North Zeeb Road, Dept P R , Ann Arbor, MI. 48106

## ACKNOWLEDGEMENTS

The meeting on which the contributions to this volume are based was organized jointly with the Respiration Group of The Society for Experimental Biology. We are grateful to the Society for their financial contribution and to Margaret Clements, who made everything run smoothly.

We are indebted to Cambridge University Press, Macmillan Magazines Ltd, Oxford University Press and The University of Chicago Press for granting permission to reproduce text illustrations.

# THE JOURNAL OF EXPERIMENTAL BIOLOGY

## The comparative physiology of exercise

Exercise lies at the heart of the struggle for existence. The exercise abilities of animals are constantly being refined by the relentless process of natural selection. An increased production of muscular power and its efficient translation into locomotory activity can allow more effective movement, extend foraging ranges and may lead to the development of migration. The salmon ascending the cataract, the lizard pursuing its mate and the falcon stooping on its prey are all descendants of generation upon generation of individuals that successfully performed these activities in the past. This volume reviews the energetic requirements of locomotion throughout the animal kingdom and investigates the wide range of adaptations required to support increasing levels of exercise, from the molecular level to the whole organism, from invertebrates to birds. It provides both general principles and specific information in a form that is accessible to student and researcher alike.

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## PREFACE

This volume was prepared from invited papers presented at the annual meeting of the Society for Experimental Biology held at the University of Birmingham, UK, in April 1991. This session, organised by the Respiration Group of the Society, was first proposed in 1989. The then editor of the *Journal of Experimental Biology*, John Treherne, suggested that it would also form an ideal basis for the Journal's annual review meeting, as the subject area covered many of the interests represented by the Journal. John died before arrangements for the meeting could be started, but his successor as editor, Charlie Ellington, decided to carry on (and participate) with number thirteen in a series that was very much the result of John's enthusiasm and drive. Previous review meetings had been held as small workshops, but collaboration with the Society enabled the presented papers to be opened up to a wider audience. However, in the evenings, the fifteen participants, drawn from around the world, were able to withdraw and discuss their mutual interests in the exciting and technically challenging field of animal exercise.



## INTRODUCTION

Exercise plays a pervasive role in the lives of all animals. The animal that is faster or has the greater stamina will succeed in the hunt, and either feast or flee. The increased production of muscular power, and its efficient translation into locomotory activity, allows new avenues of movement, an extended foraging range and the capability of migration.

The capacity of an animal for exertion has been shown to be both highly variable within a population and to be heritable, thus providing a basis for natural selection (Bennet). However, increases in strength and in stamina are essentially two separate paths to improved performance, with strength (and therefore maximum speed) being determined by the maximum power output of the muscles. The peak forces generated by the muscle are inherently limited by the basic structure of the contractile mechanism, but the maximum power levels are determined in addition by the velocity of contraction. Muscle fibres are optimized for operation under the specific conditions of locomotion required of them (Johnston), but the duration of this type of activity is strictly limited by the finite level of the substrates used to fuel the contractions and by the deleterious accumulation of metabolites (Wood, Gleeson).

The continuous production of power requires aerobic metabolism, and the higher the oxygen consumption, the greater is the sustained power output. However, improving oxygen uptake, transport and delivery to the active muscles requires significant developments in the respiratory and cardiovascular systems (O'Dor and Webber; Butler). The function of these systems must be finely controlled so as to match the supply of oxygen and substrates to the demands of the active muscles (Turner). The structure and function of transport and storage mechanisms at the capillary, cellular and biochemical level must also be able to sustain the resulting increased flux of substrates and metabolites (Hoppeler and Billeter). The maintenance of an optimum internal environment is obviously essential for the most efficient operation of these mechanisms. Homeostatic functions, already stressed by exercise itself, can be compromised by external environmental conditions (Randall and Brauner) and thus lead to a reduction in oxygen transport. Exercise also induces changes in muscle and plasma amino acid concentrations, with the state of training determining the magnitude of any change (Henriksson). Training also produces a shift in protein turnover from a balance between synthesis and catabolism towards a predominance of synthesis. Muscle hypertrophy and/or changes in its phenotypic properties will occur, depending upon the type of exercise (Goldspink).

Locomotion is the driving force for the development of adaptations that allow the production of high levels of muscular power. However, the absolute power levels required for locomotion vary markedly, depending not only on animal size (Heusner) but also on the mode of transport. Flight demands the highest power

but, because of the high velocities achieved, allows a low cost of transport (Ellington, Butler). Terrestrial locomotion is more expensive, but many mechanisms have evolved to improve the efficiency of this mode of transport (Alexander), including skeletal improvements, energy storage techniques and respiratory/locomotory coupling (Baudinette).

Exercise is arguably the most important factor in driving evolution. Its ramifications are around us. The fish that swim, the birds of the air, ourselves, are all here because of the need to succeed and survive.

A. J. Woakes

May 1991