Vertebrate Ecophysiology

An Introduction to its Principles and Applications

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Contents

1

Homeostasis: a fundamental organising paradigm in ecophysiology

The concept of 'homoiostasis' is now a central one in many sciences and its widespread use and utility attests to the genius of the American physiologist Walter Cannon, to whom we owe the original insight. Cannon coined the term in 1929 and defined homeostasis as '. . . the coordinated physiological processes which maintain most of the steady states in the organism' (Cannon, 1929). He then went on to employ it with great success in his later books and publications (see Cannon, 1939) and the concept is now a central one in biology as well as in other fields such as engineering, economics and information technology. The idea of a process of self-regulation is based, however, on the earlier studies and speculations of the great French physiologist Claude Bernard, who first suggested that animals regulate and hold constant an internal state or *milieu intérieur* that is quite different from that of the environment around them. As he states in his famous textbook of 'lessons' published in Paris in 1878:

> I believe that I am the first to have proposed this idea that animals in reality possess two environments: an external environment in which the animal is situated and an internal environment in which are found the tissue elements[1] (Bernard, 1878).

The more recent concept of an idea, or theory, functioning as a paradigm comes from the work of the American philosopher Thomas Kuhn, who coined this term to describe the way in which whole scientific communities suddenly change the way in which they interpret and describe phenomena. In studying the ways in which the ideas of the obscure sixteenth century astronomer

[1] My translation.

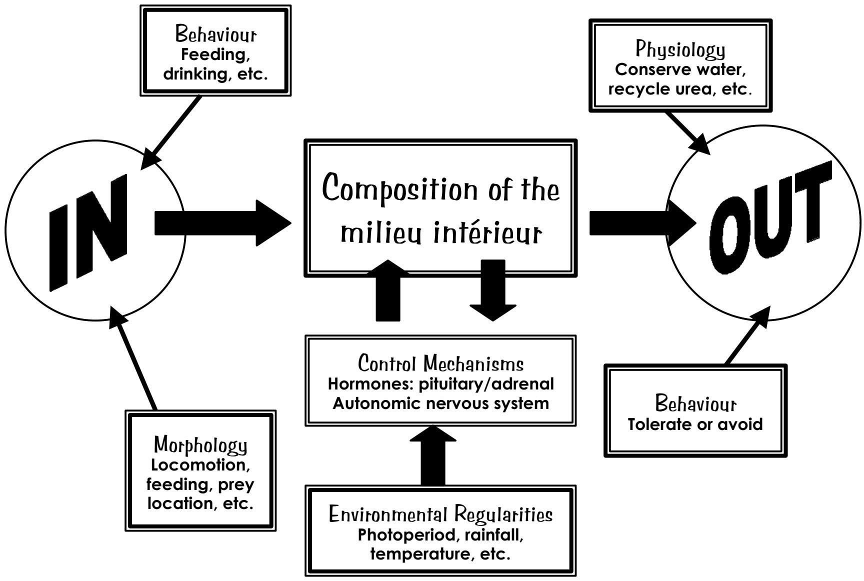

Figure 1.1. Schema illustrating the essential components of the process of homeostasis in a living system and the means by which the *milieu intérieur* is regulated.

Nicolas Copernicus revolutionised our understanding of the universe, and the Earth's position in relation to the sun (Kuhn, 1976). Kuhn developed his general theory of 'scientific revolutions' and coined the term 'paradigm' to describe '. . . a coherent, universally-recognised scientific explanation, or theory, of a hitherto unresolved set of data' (Kuhn, 1962). He describes the process by which scientists are quite content to accept, sometimes for long periods of time, explanations that are often contradicted by published data, and then, quite suddenly, they are supplanted by a new explanation or set of explanations. A good example of such a scientific revolution in recent times is the acceptance of Alfred Wegener's once heretical ideas on drifting continents (Wegener, 1966) and the central rôle now played by the concept of plate tectonics in geology.

Homeostasis is certainly one of the most durable of these paradigms and, as yet, shows no signs of being supplanted. It helps to focus on the myriad dynamic processes that occur within a living organism, and the plethora of interactions that occur constantly with the surrounding environment, and place them in a meaningful context. This is best illustrated diagrammatically, and Figure 1.1 attempts to portray the processes that are involved in the homeostatic maintenance of a constant internal state in a vertebrate animal. The constancy of the *milieu intérieur* is maintained through the interplay of fluxes, both in and out of the body, of essential elements and molecules, such as water, oxygen, carbon dioxide, sodium, glucose, nitrogen, etc. Both behavioural and physiological processes in turn influence these. Animals need to seek their food, and morphological adaptations and behaviours that control food acquisition have a major impact on influxes of water and essential nutrients. The extent to which these resources are ultimately made available to the body, however, depends on many physiological factors, such as the rate of passage of the food through the gut, the efficiency of digestive enzymes, and the efficacy of absorptive processes in the small intestine.

Effluxes, or outfluxes, of temperature, water, CO_2, and molecules such as urea, sodium and potassium are again influenced by both behavioural and physiological processes. Behavioural changes can markedly influence rates of heat gain and loss in animals, especially ectotherms such as reptiles that use the sun to maintain their body temperature constant when active during the day (see Bradshaw, 1986). Physiological processes are also very much involved in regulating heat loss from the body of animals such as mammals, where heat flow from the interior to the exterior of the body is modulated by varying blood flow through the dermis and hence modifying its conductance. Although many lower vertebrates lose much of their body water via evaporation from the skin, birds and mammals are able to produce a hyperosmotic urine that is more concentrated than their body fluids, and the kidneys are thus the major site of water conservation in these animals. The development of impressive concentrating mechanisms with large medullae in the kidneys of desert rodents (see Figure 1.2) has long been interpreted as an adaptation for the conservation of water but, as we shall see in Chapter 6, ecophysiological studies of the animals in their own environment suggest that they are never short of water and this interpretation may be too simplistic.

The composition of the internal environment or *milieu intérieur* is also monitored and regulated constantly by elements of the autonomic nervous system and by hormones, especially those elaborated by the pituitary and adrenal glands. The pituitary gland produces a large number of protein and peptide hormones whose secretion is controlled in turn by 'releasing factors' secreted in the hypothalamus of the brain and transported by a discrete portal blood system to the pituitary. These releasing factors, which are peptide hormones themselves, activate gene expression in the special cells of the anterior pituitary (adenohypophysis), each of which is dedicated to the secretion of a separate hormone (some examples are the two gonadotrophins that stimulate the gonads to secrete sex hormones, follicle stimulating hormone (FSH)

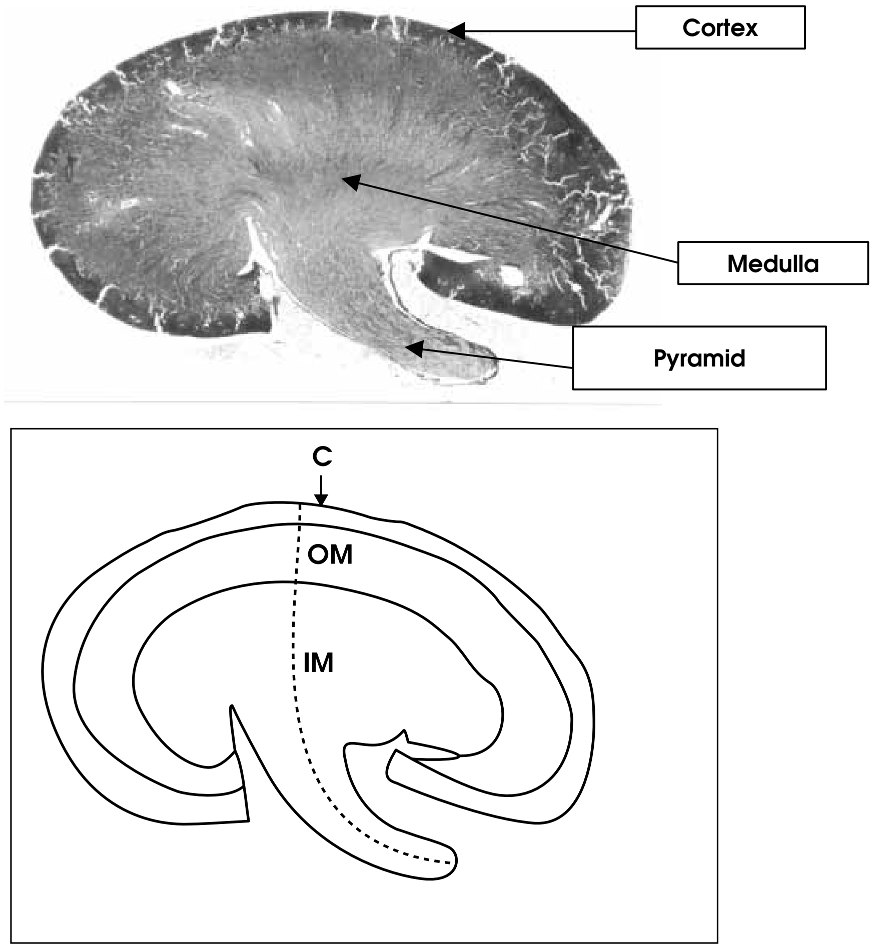

Figure 1.2. Mid-sagittal longitudinal section of left kidney of the Lakeland Downs short-tailed mouse (*Leggadina lakedownensis*) from Thevenard Island, Western Australia, showing zones of cortex (C), outer medulla (OM) and inner medulla (IM) identified by staining. Scale: 1 cm = 1 mm. (Photo courtesy of Dr Dorian Moro.)

and luteinising hormone (LH); thyroid-stimulating hormone (TSH), which stimulates the thyroid gland to secrete the hormones thyroxine and triiodothyronine; adrenocorticotrophic hormone (ACTH), which controls both the size and the secretory activity of the adrenal glands; growth hormone (GH); and prolactin). The hierarchical arrangement of brain, pituitary and effector endocrine glands is shown diagrammatically in Figure 1.3 for the main hormones regulating reproduction.

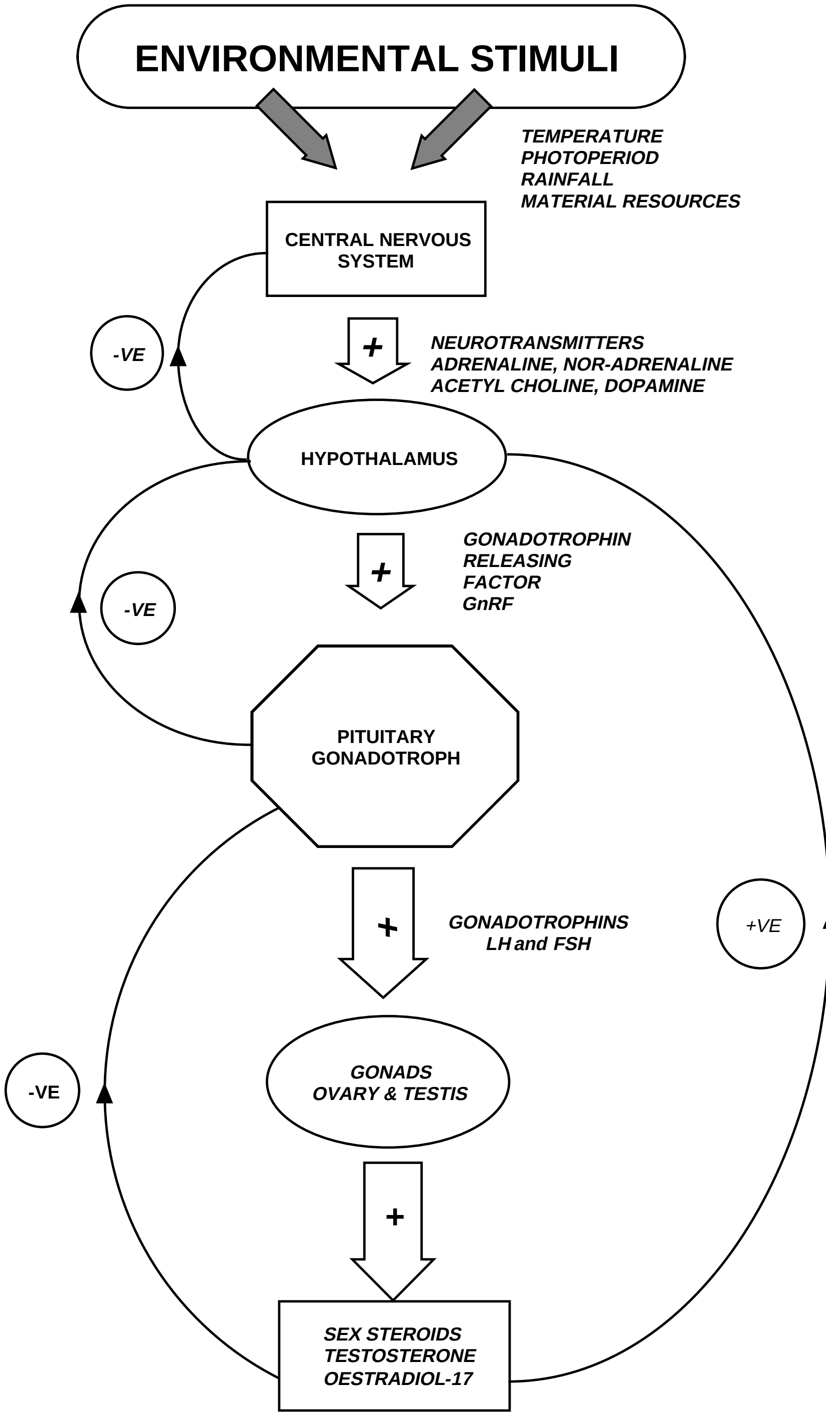

Figure 1.3. Schema illustrating the hierarchical nature of the hormonal control systems regulating the secretion of steroid hormones by the vertebrate gonads.

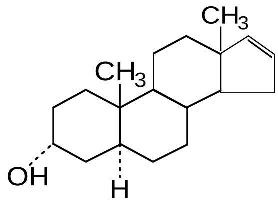

Figure 1.4. Structure of the steroid molecule, androstenol (5α-androst-16-en-3α-ol).

The rates of secretion of these hormones into the blood are in turn influenced markedly by changes in the external environment, and it is the hypothalamus of the brain, with its many specialised neurosecretory neurones, that is most involved in transducing environmental cues such as temperature and photoperiod into hormonal cues which help maintain homeostasis. The pineal gland in the centre of the brain in mammals also produces the hormone melatonin, which is secreted with a marked diurnal–nocturnal rhythm, and has a strong influence on reproductive processes in many mammals (Reiter, 1978; Reiter and Follett, 1980; Tang *et al.*, 1996).

Pheromones are also chemicals produced by animals that are released into the surrounding air and water and communicate information between different individuals in a population, particularly in relation to sexual and social status. These are often steroid molecules and a fascinating example of how plants and animals may co-evolve interlocking strategies is provided by the steroid molecule androstenol (5α-androst-16en-3α-ol) shown in Figure 1.4. Truffles are fungi that have long been known for their aromatic properties and these are prized in cooking, especially in France and Italy. The subterranean truffles were traditionally located with the aid of a sow or 'truie' as seen in Figure 1.5. Nowadays dogs (and even portable gas chromatographs) are used to locate the valuable truffles, but the mystery of why female pigs were particularly susceptible to the smell of the truffles became apparent when the identity of the mating pheromone of the boar was discovered by Claus *et al.* (1981). This is also androstenol and the male secretes it in foam around the mouth when trying to mate. The sow, on smelling it, adopts the lordosis posture and allows the male to mount her. One can only surmise that the sow in the forest assumes that a handsome boar is buried for some reason underground and, on unearthing the truffle, shows her disgust by trampling on the truffle and thus releasing its spores into the atmosphere. In this way, the truffle is using a mammal and its reproductive signalling system to complete its own amazing reproductive cycle. Nor does the story end here. Gower and Ruparelia (1993) have recently carried out tests that suggest that the musky-smelling androstenol functions as a mild aphrodisiac in humans.

Figure 1.5. Searching for truffles in France, using the ancient method with 'la truie', or a sow.

There are periods of an animal's life, however, when the internal state is not maintained constant but varies systematically. The most important of these is during the period of growth from the juvenile to the adult state, but there are also other periods – such as during the process of reproduction – where there may be important changes in the *milieu intérieur*, especially that of the female, engendered by the presence of an embryo in viviparous vertebrates (see Hytten, 1976). Pathological states are often associated with dramatic changes of the *milieu intérieur* and, in some of these, a new homeostatic régime is established by an apparent 'resetting' of the upper and lower set-points. Fever is a good example of this: the body temperature is maintained homeostatically, but at a higher set-point than normal, owing to changes in the ionic composition and osmolality of the cerebrospinal fluid (CSF) (Myers *et al.*, 1971; Turlejska and Baker, 1986).