CAMBRIDGE

Cambridge University Press
978-0-521-81797-4 - Vertebrate Ecophysiology: An Introduction to its Principles and Applications
Don Bradshaw
Excerpt
More information

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.

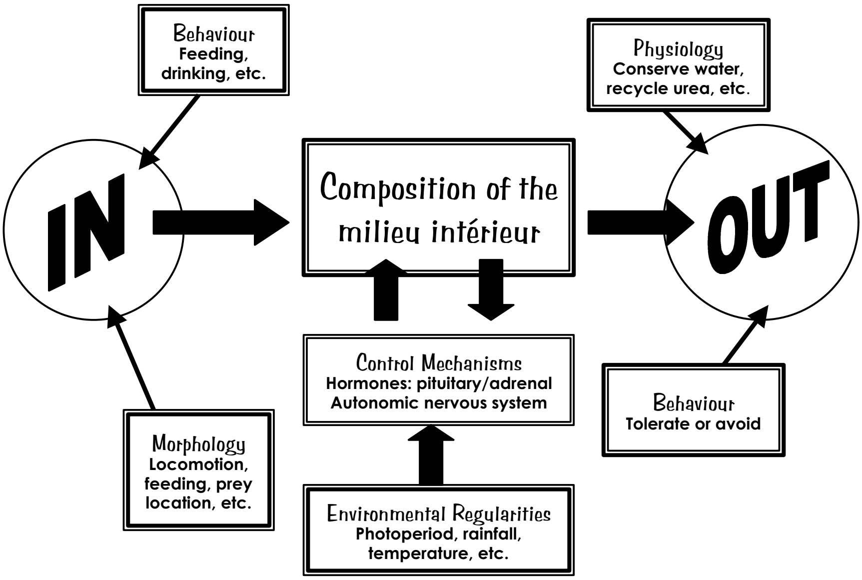

Figure 1.1. Schema illustrating the essential components of the process of homeostasis in a living system and the means by which the *milieu intérieur* is regulated.

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)

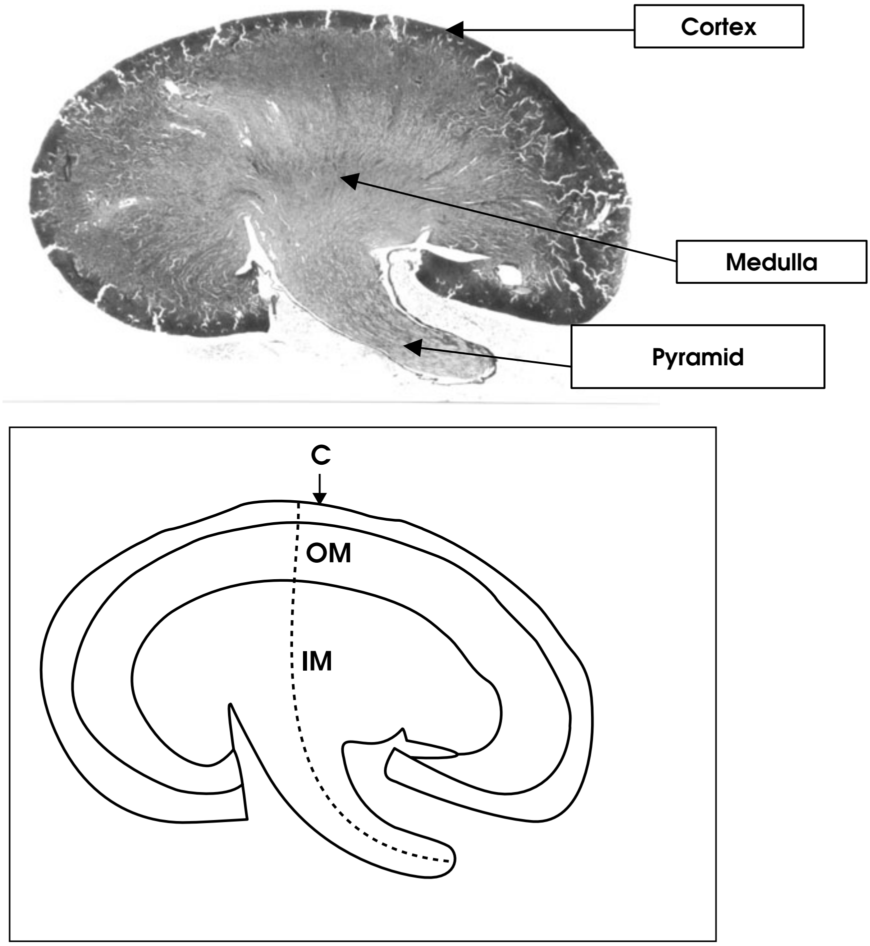

Figure 1.2. Mid-sagittal longitudinal section of left kidney of the Lakeland Downs short-tailed mouse (*Leggadina lakedownensis*) from Thevenard Island, Western Australia, showing zones of cortex (C), outer medulla (OM) and inner medulla (IM) identified by staining. Scale: 1 cm = 1 mm. (Photo courtesy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

and luteinising hormone (LH); thyroid-stimulating hormone (TSH), which stimulates the thyroid gland to secrete the hormones thyroxine and tri-iodothyronine; 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.

Cambridge University Press
978-0-521-81797-4 - Vertebrate Ecophysiology: An Introduction to its Principles and Applications
Don Bradshaw
Excerpt
More information

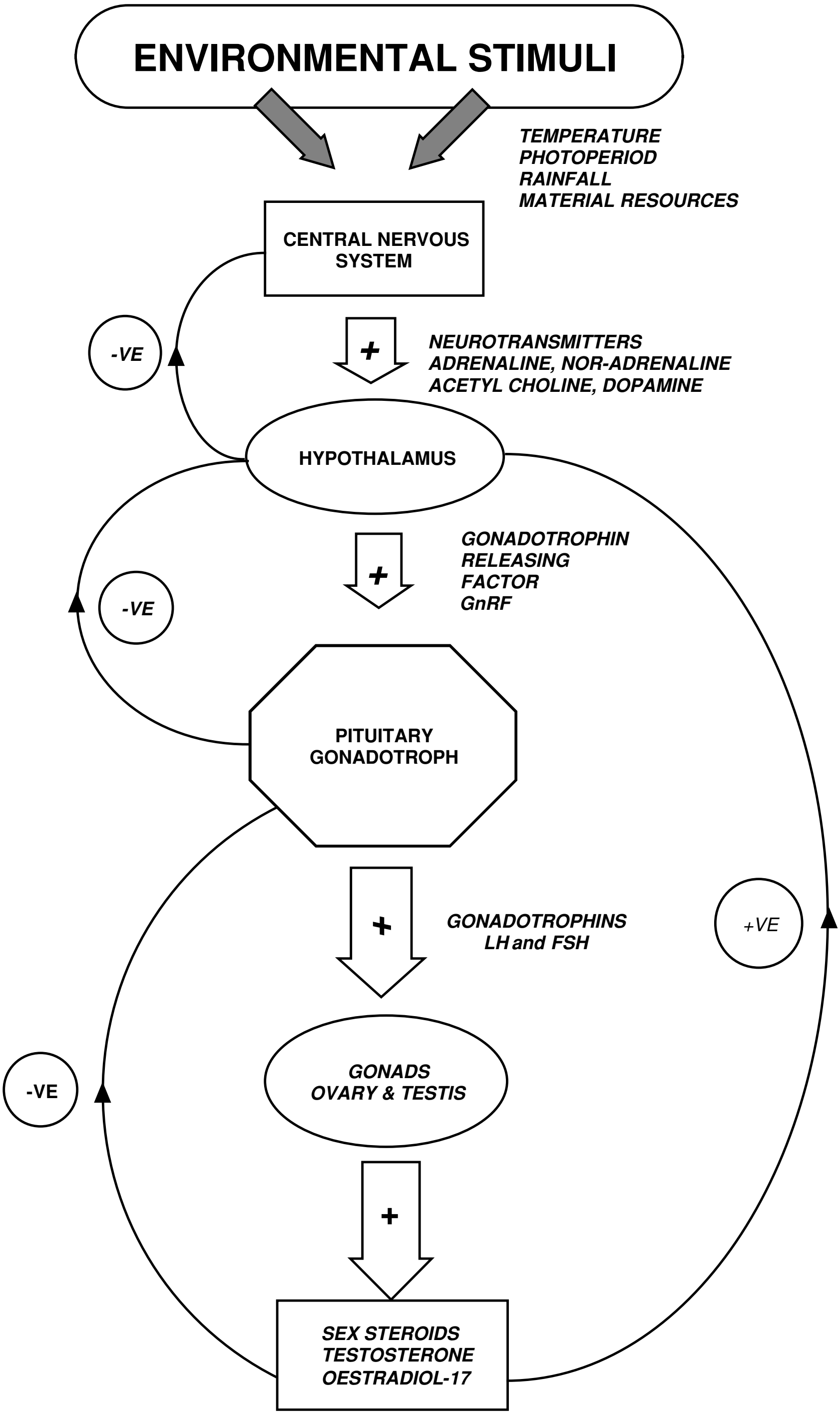

Figure 1.3. Schema illustrating the hierarchical nature of the hormonal control systems regulating the secretion of steroid hormones by the vertebrate gonads.

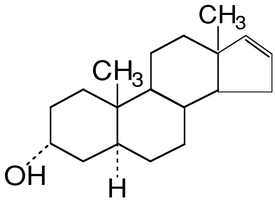

Figure 1.4. Structure of the steroid molecule, androstenol (5α-androst-16-en-3α-ol).

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).

2

Stress: the concept and the reality

We talk very glibly these days of stress, especially the 'stress of modern-day living', and in the scientific literature one often finds mention of things such as 'temperature stress', 'water stress' and 'the stress of reproduction'. It has proven extraordinarily difficult, however, to agree on a common definition of the term, let alone develop methods for measuring the incidence and intensity of stress in animals.

There is general agreement among biologists that 'stress' is an important ecological factor, often contributing to the extinction of rare and endangered species (Bradshaw, 1996, 1999). There are thus a number of important questions that need to be addressed concerning stress, including:

What is stress?
How do we define it and measure its effects?
How does one measure its incidence and severity?
What effects does stress have on an animal's ability to maintain homeostasis?
Does prolonged stress reduce fitness?
Are threatened and endangered species more susceptible to the effects of stress than are other species?
Can we use instances of stress physiology to gauge the level of susceptibility of animal species to environmental change and their likelihood of extinction?

Definitions

It was Walter Cannon again who, as early as 1914, first developed the idea that organisms react to unfavourable situations in terms of highly integrated metabolic activities. Cannon's concept of stress was derived by simple analogy from Newtonian physics where an imposed force (stress) produces a deformation (strain) in an object, with the strain being proportional to the stress. He further developed this mechanistic analogy by introducing the concept of a 'critical stress level' in biological systems, producing a 'breaking strain' in the appropriate homeostatic mechanism, which then failed to counter the stress (Cannon, 1929).

By far the greatest contribution to the study of stress, however, was made by Hans Selye who, in his monumental paper, defined stress as 'a state of non-specific tension in living organisms', thereby engendering the current problem of how best to identify its presence and also measure its intensity (Selye, 1946). Selye (1936) clearly identified what he termed the 'stress triad' of adrenocortical enlargement, atrophy of the thymus and lymphoid tissues, and ulceration of the digestive tract, which may be observed in experimental animals subjected to a wide variety of nociceptive (i.e. harmful) agents of high biological intensity. He then formulated his famous 'General Adaptation Syndrome', comprising three stages:

(i) a stage of '*alarm*',
(ii) a stage of '*adaptation*' and
(iii) a stage of '*exhaustion*' (Selye, 1946).

Unfortunately, Selye came to regard the 'stress triad' as an extreme manifestation of a normal non-specific 'stress response' necessary for the maintenance of the specific homeostatic states identified by Cannon. He later described this non-specific response as a 'state of stress', as exemplified in his definition above, and believed that a minimal level of stress was essential for normal existence ('eustress') and distinguished this from potentially harmful levels of stress ('distress') leading to pathological states (Selye, 1976).

Selye's approach to the concept of stress has not escaped criticism, because of its inherent vagueness and imprecision, and the essence of such criticism is that the term 'stress' should rather be applied instead to the environmental factors that elicit homeostatic adjustments as defined by Cannon (Mason, 1975; Levitt, 1980; Hoffman *et al.*, 1993).

Stress is thus defined by Brett (1958) and Koehn and Bayne (1989) as:

> any factor that inhibits the growth and reproduction of individuals in a population

and by Sibley and Calow (1989) as:

> . . . an environmental condition that, when first applied, impairs Darwinian fitness.

Stress and stressors

I personally think that Selye's approach is the better and that those environmental factors inducing stress in organisms should be called *'stressors'* and that the term 'stress' should be restricted to the effect, rather than the cause. I would thus not consider abnormally high temperatures, or a severe shortage of water, as a stress, but as a stressor with the potential to induce stress in an animal. Whether it does so or does not, however, depends on how effective the animal's homeostatic mechanisms are in combating and controlling the impact of the stressor. We thus need to know more about the animal's defences against environmental perturbations; in the face of a given stressor, it should be possible to determine whether stress is engendered or not by what happens to the animal's *milieu intérieur*.

A stressor that leads to a change in the animal's internal state, from whatever might be considered to be optimal, is one that we can say has produced a stress state in the animal. Take the case of a mammal that is short of water. The normal reaction would be for the animal to experience thirst and search for water to drink. If this is not available then there would be a slight elevation of the osmotic pressure of the blood that would lead to the secretion of increased amounts of antidiuretic hormone (ADH) from the pituitary gland. This, in turn, would increase the rate of water reabsorption in the collecting ducts of the renal medulla and, thus, increase the concentration of the urine being produced and decrease its volume. In this way the animal protects its body water and avoids the potentially deleterious effects of dehydration by conserving water that would otherwise be lost via the kidneys.

There is no way that one would interpret this as an animal experiencing stress. It is exposed to a stressor (the shortage of water) to which it is responding adequately by the use of its normal homeostatic mechanisms. If, however, the animal starts to experience dehydration, despite secreting maximal amounts of ADH in the blood, and its kidney producing urine of the maximum concentration possible for that species, we can consider that it is experiencing stress. Dehydration is simply loss of body water and it leads to an increase in the osmotic pressure of the remaining body fluids, which may be easily measured with an osmometer.

Our definition of stress thus encompasses two aspects: a maximal stimulation of regulatory mechanisms (in this case ADH from the pituitary) opposing the stressor, which are none the less inadequate to prevent a significant change in state of the *milieu intérieur*. By using this approach it should be possible to identify the existence of stressful states in biological organisms through their reaction to specific stressors, and also measure the intensity of the stress induced by the extent of the subsequent physiological reaction. This