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How Self-Organisation Can Guide Evolution

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Abstract

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How Self-Organisation Can Guide Evolution

by Jonathan P. Glancy

Self-organisation and natural selection are fundamental in shaping the natural world. Substantial progress in understanding how these two forces interact as biological systems evolve has been made through the study of abstract models, for example by evolving boolean networks on computers. Further progress may be made by identifying a model system in which the interaction between self-organisation and selection can be investigated empirically. To this end, we investigate how the self-organising thermoregulatory huddling behaviours displayed by rodents might influence natural selection of the genetic components of metabolism. By applying a simple evolutionary algorithm to a simplistic description of self-organising thermoregulation huddling, we arrive at a clear albeit counterintuitive prediction: Animals able to huddle together in cold environments should evolve an increased thermal conductance at a faster rate than animals reared in isolation. According to the model, within-lifetime adaptation (self organising huddling) is able to guide the evolution of complementary between-lifetime adaptation (natural selection of thermoregulatory genes). Confirmation of these predictions in future experiments would constitute strong evidence of a mechanism by which self-organisation can guide natural selection.

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Contents

Chapter 1

Introduction

1.1 Self-Organisation

Self-organisation is a spontaneous process that generates order within an initially disordered system. Self-organising processes are ubiquitous across the natural world in both physical and biological systems, and the study of such systems has relevance to many fields of study such as economy, sociology, and technology. Examples of self-organisation range can be non-organic, such as sand dunes(1.1a) and chemical oscillation (1.1b), or organic such as ant colonies (1.1c), and neural structures(1.1d).

Self-organising processes are described as spontaneous because they fundamentally rely on interactions internal to the system, with no external influences required to generate order and structure. Camazine et. al (2001) provide the following succinct definition of self-organisation:

(a) Sand dunes (b) Belousov-Zhabotinsky reaction

(c) A bridge of ants (d) Ocular dominance stripes

Figure 1.1: Examples of self-organisation in natural systems.

> “ Self-organization is a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the system’s components are executed using only local information, without reference to the global pattern[1]. ”
>
> (Camazine et al., 2001)

In contrast to self-organisation, order may also be achieved through external influences upon a system, such as through direction of a supervisory leader, a blueprint, recipe, or pre-existing pattern within the environment (i.e., a template). The important distinction between self-organisation and other forms of pattern generation is that in a self-organising system the pattern does not pre-exist in one form or another – such as the goal of the leader, or within the instructions of a recipe – and instead the pattern is an emergent property of the system. A self-organising pattern cannot be ‘seen’ by simply inspecting the individual components of the system; instead we must also take into account the interactions that occur within the system.

1.1.1 Characteristics of Self-Organisation

Self-organising systems are typically comprised of many simple, often homogeneous, elements: from grains of sand (Bak, 1996), to ants (Hölldobler, B., Wilson, 1990), to neurons (von der Malsburg, 1987; Wolf, 2005). And when we describe these elements as being simple, we are speaking relative to the global system:

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[1] ‘Pattern’ refers to a particular, organised arrangement of objects in space or time.

while a neuron may be far more complicated than a grain of sand, it is still simple in comparison to the mind.

1.1.1.1 Emergence and Complexity

Intuitively, we can probably agree that the mind is a more complex object than the neurons that comrpise it. If nothing else, it seems clear that it should be no less complex. However, putting a definition to complexity is a difficult task. Why is the sand dune more complex than a grain of sand?

> “ Take a look in many dictionaries, and you will find Complexity defined along the lines of ‘The behavior shown by a Complex System’. Then look up ‘Complex System’, and you will probably see ‘A system whose behavior exhibits Complexity’. ” (Neil Johnson)

To understand complexity we must first understand *emergence.* Within a self-organising system, a property at the macro-level is described as being emergent if it cannot be understood simply by inspection of the micro-level components. These novel properties of the system are surprising because they cannot be predicted based on knowledge of the individual components. Thus emergent properties are described as being ‘greater than the sum of the parts’. They are instead the sum of the parts *and their interactions* (either with other components or with the environment). A system that exhibits emergent properties is described as being complex.

Complexity solves (or at least tackles) one of the greatest puzzles in biology: the amount of information stored within the the genes is much smaller than the amount of information needed to describe the structure of an adult individual. The solution is self-organisation. Rather than encode all the information required to describe the final structure, genes can instead encode information about the rules that generate the final structure (Maruyama, 1963).

An important question in the field of complexity science is how complex must the components of a self-organising system be in order to generate the complexity observed at the group level (Camazine et al., 2001). How far can this economisation of information be pushed? This question has important evolutionary implications.

1.1.1.2 Stability, Bifurcation, and Multi-Stability

The patterns and behaviours that are produced by self-organisation depend upon the initial conditions of the system, as well as parameters of the individual components and the environment. Evolution might exploit self-organisation for the economy it affords in terms of encoding information. This in turn creates another opportunity for evolution: natural selection can tinker with the parameters; the initial conditions from which order emerges.

One characteristic of self-organisation is that it often promotes stability, where an emergent property or pattern will be robust to changes over a range of initial conditions and parameters. Such patterns are described as being an *attractor* of the system. This has important consequences in biological systems, where behaviours are often adaptive, and where it is vital that they are consistently produced. In such cases, we would expect natural selection to tune the parameters of the system so that the behaviours occur across the range of conditions that are likely to be encountered.

Another characteristic of self-organising systems is the existence of bifurcations. A bifurcation describes a *qualitative* change in the pattern or behaviour of a system due to a *quantitative* change in the system parameters. Evolution may take advantage of this by tuning biological systems close to a bifurcation point. Systems poised at a bifurcation point are flexible, with the ability to switch between two different behaviours in response to the current external forces acting upon the system.

In some cases self-organising systems exhibit multi-stability, where there exist multiple stable possible patterns that could be produced or selected between. Environmental parameters, for example the distribution of food, play a key role in determining which pattern will be produced.

1.2 Self Organisation and Natural Selection

How does self-organisation fit alongside natural selection? In recent years, a major struggle has been the integration of self-organisation into the modern evolutionary synthesis (Depew and Weber, 1996; Kauffman, 1993; Weber, 1998), and the relationship between self-organisation and natural selection has been debated (Kauffman, 1993; Deacon, 2003). Indeed a common misconception has been that self-organisation and natural selection are alternative theories of evolution.

> "Perhaps, therefore, the most important misconception to dispel is the notion that mechanisms of pattern formation based on self-organization somehow minimize the importance of natural selection. "
>
> (Camazine et al., 2001)

Rather than competing theories, many in the field of complexity science see self-organisation and natural selection as two complimentary processes; perhaps with self-organisation acting as the driving force behind *form generation* and natural selection serving *form selection*.

> "Thus the natural marriage of self-organization and selection first discovers the powerful order inherent in complex systems . . . and then appeals to selection to achieve and sustain membership in this ensemble " (Kauffman, 1993)

1.2.1 Visions of Evolution

In their book, *Darwinism Evolving: System Dynamics and the Genealogy of Natural Selection*, Depew and Weber (1996) discuss the possible relationships that could exist between self-organisation and natural selection. The 'visions of evolution' that they propose are as follows:

Vision 1. **Natural selection and self-organisation are *unrelated.*** It is only recently that self-organisation has been associated with biological systems (see Kauffman, 1993; Camazine et al., 2001), prior to this theories of self-organisation were confined to non-living systems. Thus, the conventional wisdom was that natural selection and self-organisation were unrelated.

Vision 2. **Self-organisation is *auxiliary* to natural selection.** Natural selection occupies a central position in evolutionary theory. Only when natural selection cannot be used to explain a phenomena do proponents then look to other mechanisms, such as self-organisation, for an explanation. Self-organisation then serves as an additional force, much like genetic drift or mutation pressure.

Vision 3. **Self-organisation *constrains* natural selection, which drives evolution.** Self-organisation acts as a generating force, constraining the possible set of forms that appear. Natural selection then sifts through and refines this set of forms.

Vision 4. **Natural selection *constrains* self-organisation, which drives evolution.** Natural selection restricts the forms that persist, and so selection constrains the possible materials that could compose self-organising systems.

Vision 5. **Natural selection *instantiates* self-organisation.** Natural selection is a consequence of a self-organasing system in which the components replicate.

Vision 6. **Natural selection *generates* self-organisation.** Natural selection acts as the creative force, and generates systems that self-organise.

Vision 7. **Natural selection and self-organisation are *aspects of a single process.*** Natural selection and self-organisation work in tandem to generate ever increasingly more complex forms.

In a review of these seven visions, Batten et al. (2008) suggest that there are three underlying 'stages' of evolution. The relationship between self-organisation and natural selection changes depending on what stage of evolution they occupy. Thus, Depew and Weber's visions of evolution are not contradicting stances on the relationship between self-organisation and natural selection, but instead each vision is relevant based on the level of organisation under inspection.

Stage 1. **Natural selection drives evolution:** Organisation is a prerequisite of natural selection. In the first stage of evolution, forms are initially generated spontaneously by self-organisation (i.e, *self-organisation constrains natural selection*). Natural selection then drives evolution by refining the forms that self-organisation has generated. *'[O]rganization proposes what selection might dispose.'*

Stage 2. **Self-organisation drives evolution.** Products of self-organisation that are selected for in the first stage provide material for further complexity to emerge through self-organisation. *'[N]atural selection provides a form of constraints on self-organisation.'*

Stage 3. **Natural selection and self-organisation are complementary aspects of a single process.** Ever increasingly complex forms of organisation are produced, to the point that natural selection and self-organisation become complementary aspects of a single process.

1.2.2 The Baldwin Effect

A characteristic of self-organisation is that it promotes stable patterns. In biological systems, this is seen by the production of behaviours that allow organisms to adapt within their lifetime to variations in the environment (Camazine et al., 2001). A first step towards investigating interactions between natural selection and self-organisation is to look at interactions between natural selection and within lifetime adaptations. The relationships between selection and within lifetime adaptations were first discussed independently in the late 19th Century by Conway Lloyd Morgan, J. Mark Baldwin, and Henry Fairfield Osborn. The *Baldwin Effect*, as it came to be known, describes an interaction between selection and phenotypic plasticity, whereby traits acquired during an organism's lifetime can influence the evolutionary trajectory of a population.

The Baldwin effect is likely to occur when a change in the environment puts stress on a population. In this new environment, phenotypic plasticity is evolutionary beneficial and so individuals that are able to adapt within their lifetimes will be favoured. Eventually mutations will occur that produce hereditary traits that are similar in function to the acquired traits. Because there is typically a cost associated with the acquired traits (Baldwin, 1896; Simpson, 1953), and so selection will favour the genetic variant and it will spread through the population. The key aspect of the Baldwin effect is that there is no direct inheritance of the acquired traits, such as in Larmarkian evolution. Instead, the acquired traits act as an ‘in life’ crutch, holding the stress until mutation discovers a heritable trait to replace it. Therefore the Baldwin effect is understood to occur in three stages:

Stage 1 When a population is introduced to a novel environment, new selection pressures favour animals that are able to adapt within their lifetimes. The amount of plasticity within the population increases.

Stage 2 Eventually random mutations occur within the population that produce a hereditary trait that is similar in function to within lifetime adaptations.

Stage 3 The genetic trait eventually replaces the acquired trait, under conditions in which acquiring the trait within the lifetime incurs a cost.

Discussion of the Baldwin effect has often dealt with its theoretical plausibility, with researchers being described as either Baldwin Boosters or Baldwin Sceptics. Indeed, there has been great difficulty in identifying unequivocally the presence a Baldwin effect in biological systems (Waddington, 1942). Using artificial selection, Mery and Kawecki (2004) looked at the evolution of food preference in *Drosophila melanogaster*. It was shown that learning facilitated the evolution of innate preference for pineapple, but hindered it under selection for the preference to orange.

Numerous theoretical studies have used computational models in order to investigate the theoretical plausibility of the Baldwin effect. The general approach of these studies is to measure the rate of evolution of a genetically determined trait, while varying the amount of phenotypic plasticity built into the individuals.

Where studies have provided evidence that plasticity accelerates evolution (Hinton and Nowlan, 1987; Fontanari and Meir, 1990; Mayley, 1997; Ancel, 1999; Lande, 2009), while others have shown a decelerating rate on genetic evolution (Anderson, 1995; Ancel, 1999; Borenstein et al., 2006; Dopazo et al., 2001; Papaj, 1994; Simpson, 1953; Zollman and Smead, 2009).

1.2.3 The Hinton and Nowlan Model

Hinton and Nowlan (1987) presented an extremely simple evolutionary model, which claims to present an example the Baldwin effect. In this model each individual is represented by a string of 20 characters (or alleles), where each character is randomly set to either 1, 0 or ?. The ? character is how the authors incorporated a learning mechanism within the model. This learning mechanism is simply trial and error, where the ? can be flipped between 1 and 0 over an individuals' lifetime.

The authors define a single good solution, the string with all characters set to 1. An individual that matches this string is assigned a fitness of 20, while an individual that does not discover it is assigned a fitness of 1. Individuals that discover the correct solution through lifetime trial and error are assigned a fitness proportional to how quickly they are able to discover the solution. Given an initial population of 1000 individual strings, each successive generation is created by random crossover among the fitter organisms.

When learning is not present, i.e., all alleles are set to either 1 or 0, the problem was never solved. However, when alleles are set to ? with probability 0.5, and 1 or 0 with probability 0.25, the problem becomes tractable. The correct solution is discovered after roughly 10 generations, and within 20 generations the majority of ? alleles have been replaced by 1s.

This model provides a demonstration of how within-lifetime adaptations can effect the rate of evolution. The underlying mechanism behind this improvement is a smoothing of the fitness landscape.

1.3 Summary

Investigation of the possible interaction between natural selection and within-lifetime adaptation has been advanced through the application of computational modelling. However, models such as that developed by Hinton and Nowlan to explore the Baldwin Effect, have been abstract in nature, and as such have fallen short of generating specific testable predictions that could be used to further build the underlying theory. Moreover, investigations in which within-lifetime adaptability is achieved via self-organising processes are lacking. Hence, the aim of this thesis is to identify a system that can allow the possible interaction between self-organisation and selection to be tested empirically. The first step, which we turn to in Chapter 2, is to identify a system in which self-organisation and selection can be expressed in terms of a common (metabolic) currency.

Chapter 2 identifies thermoregulatory huddling as an adaptive self-organising system that could potentially interact with natural selection. Chapter 3 develops a computational model of self-organising thermoregulatory huddling behaviours. Chapter 4 exposes a simplistic description of thermoregulatory huddling to an evolutionary algorithm. Chapter 5 investigates the Baldwin effect in the context of thermoregulatory huddling behaviours. In Chapter 6 we highlight a number of specific predictions derived from the computational models that can be used falsify the theory that thermoregulatory huddling can guide the evolution of physiological thermoregulation as a Baldwin effect.

Chapter 2

Endothermic Homeothermy

> Irrespective of form, complexity,
> time or place, all known organisms
> are alike in that they must
> capture, transduce, store and use
> energy in order to live.
>
> (Haynie, 2001)

2.1 Introduction

A fundamental characteristic of all organisms is whether or not they regulate their body temperature. At one extreme there are animals that allow their body temperatures to conform to the environmental temperature, while at the other extreme there are animals who maintain a precise control over their internal body temperature. Tattersall et al. (2012) has described temperature as "...one of the most pervasive physical parameters affecting the fitness of an organism", primarily because of the temperature dependence of biochemical reactions rates. Consequently, temperature holds influence over the ability of all biological systems to function and thus every aspect of biological function is dictated by the thermodynamic context that an organism occupies (see Haynie, 2001; Careau et al., 2015; Mathot and Dingemanse, 2015).

Animals rarely exist within a constant thermal environment, and so they must evolve strategies to maintain functionality. There are two fundamental strategies for maintaining functionality: (1) adopting and evolving a tolerance for a varied thermal environment (*poikilothermy*), and (2) adopting and evolving thermoregulatory mechanisms that allow an animal to maintain an internal temperature independent of the environment (*homeothermy*)(Tattersall et al., 2012). Mammals and birds have independently evolved the capacity for *endothermic homeothermy*: the ability to maintain a high and constant body temperature .

Endotherms have evolved a diverse set of compensatory mechanisms that allow them to maintain a constant core body temperature across a range of environmental temperatures. For example, an endotherm in a cold environment may increase its capacity to produce heat (Else and Hulbert, 1981), or it may reduce its thermal conductance by increasing insulation (Hart, 1956). The first response to a changing environment is usually behavioural, such as the selection of a micro-climate or a change in posture (McNab, 1974; Gordon, 2012). When such a response is not suitable an organism will instead make a physiological response, for example by shivering to produce heat. If changes in thermal conditions are constant over sufficient number of generations, for example due to a shift in the climate, then the appropriate response may be a genetic adaptation. Slobodkin (1964) suggested that such genetic adaptations restore and maintain the flexibility of short-term behavioural and physiological adjustments. Hence, themoregulation is a composite of responses that occur across a variety of timescales; both within, and across lifetimes. Tattersall et al. (2012) describes three categories of response, based on the timescales over which they occur: (1) responses that occur between generations (genetic adaptation, see Fangue et al., 2009); (2) responses occurring during development (developmental plasticity); and (3) responses that occur throughout an organism's lifetime (reversible plasticity).

There are significant metabolic costs associated with endothermy, primarily because the main source of body heat comes from internal processes . Indeed, the energy requirements of an endotherm are typically in the range of five to ten times that of a comparable ectotherm, and it is estimated that $80 - 90\%$ of the total energy intake of a rodent under natural conditions is used for thermoregulation (Bennett and Ruben, 1979). Consequently the thermal challenges of an environment exert strong selection pressures on the morphological, physiological, and behavioural traits of an endotherm.

2.2 The Energetics of Endothermy

In this chapter we will be discussing the energetics of endothermy, starting with the fundamental processes of heat exchange between an organism and its environment. We will then discuss the metabolic cost of endothermic thermoregulation, and consider how within lifetime adaptations might affect the metabolic cost of thermoregulation. Finally, we will identify thermoregulatory huddling as a mechanism for within lifetime adaptation and present some of the current evidence that thermoregulatory huddling emerges from simple interactions between animals (i.e., by self-organisation). The review herein suggests that thermoregulatory huddling constitutes a system in which the interactions between self-organisation and evolution by natural selection can be expressed in terms of a common currency: metabolism.

The review follows closely the presentation by McNab (1974), with a focus on aspects of energetics that will serve as building blocks for computational models developed in Chapters 3, 4 and 5.

2.2.1 Thermal Exchange

All organisms are complex systems consisting of matter and energy, and the exchange of matter and energy between an organism and its environment is described by physical laws. *Diffusion* is the physical process by which matter or heat moves from a region of high concentration to one of low concentration. The simplest description of diffusion is given by *Fick's law*:

$$\dot{u} = -AD\frac{d\psi}{dX}, \tag{2.1}$$

where $\dot{u}$ is the flux between two mediums, $\frac{d\psi}{dX}$ is the concentration gradient between these mediums, and A is the surface area at the interface between the two mediums. The diffusion coefficient D modulates the rate of diffusion; it is specific to the matter diffusing, as well as the mediums in which diffusion occurs. Fick's law is used as the basis of many models, including the thermal exchange between an organism and its environment. However the process of thermal exchange is complicated, and must first be broken down in to the four basic components through which heat exchange occurs: radiation, conduction, convection, and evaporation (McNab and Brown, 2002; Brown, 2010).

Radiation

Solar radiation is a significant source of heat for terrestrial organisms. Some species of birds for example, modify the heat load of solar radiation by adjusting the angle of their body with the sun, and by selectively exposing dark and light surfaces to the sun (Lustick et al., 1980).

Heat radiates from all bodies that have a temperature above $0K$ in the form of electromagnetic waves. The *Stefan-Boltzmann law* describes how radiation emitted from a body increases with the body temperature:

$$\dot{Q} = \sigma A T^4, \tag{2.2}$$

where $\sigma = 2.04 \times 10^{-8} \mathrm{J}/(\mathrm{cm}^2 \mathrm{hK}^4)$ is the Stefan-Boltzmann constant, A is the surface area of the body, and T is its surface temperature. Any body conforming to Equation 2.2 is called a *black body*, however in reality many objects emit less energy than that described by the Stefan-Boltzmann equation. To capture this, a dimensionless constant describing the *emissivity* (ϵ) of a body can be used to augment Equation 2.2:

$$\dot{Q} = \epsilon \sigma A T^4. \tag{2.3}$$

The emissivity term varies between 0.0 and 1.0 with black body objects radiating maximally, i.e., emissivity $\sigma = 1.0$, while objects that do not radiate any energy will have an emissivity of $\sigma = 0.0$. Emissivity values are specific to the wavelength of radiation, however *Kirchoff's law of thermal radiation* states that a good emitter is also a good absorber, with emissivity being equal to absorptivity when an object is in thermodynamic equilibrium. As such the net thermal radiation exchange between a body and the environment (or another body) is given by

$$\dot{Q}_{\mathrm{rad}} = \bar{\epsilon} \sigma A (T_s^4 - T_a^4), \tag{2.4}$$

where $\bar{\epsilon}$ describes the mean emissivity over a band of radiation, A is the surface area, T_s is the surface temperature of the body, and T_a is the ambient temperature.

Conduction

The second basic component of thermal exchange is *conduction*, where heat is transferred between two bodies that are in contact. Conduction does occur between a body and the environment, however the amount of heat transferred is attributed to the movement of molecules within the fluid (atmosphere) and thus it is modelling as convective heat transfer (see *Convection*).

Fourier's law of thermal conduction states that the rate of heat exchange via conduction is proportional to the negative thermal gradient between the two mediums:

$$\dot{Q}_{\text{cond}} = -kA\left(\frac{T_2 - T_1}{X_2 - X_1}\right), \tag{2.5}$$

where $\frac{T_2-T_1}{X_2-X_1}$ is the thermal gradient across positions X_1 and X_2. The thermal conductivity (k) is a quantity that describes the ease of thermal transfer, and reflects the molecular structure of the materials in question. Water has a conductivity approximately 23 times greater than that of air; fat has a conductivity which is 8 times that of air; and fur pelts typically have a conductivity within the range of 0.9 to 2.4 times that of air (Gates, 1980).

Convection

Convection refers to the thermal exchange that occurs between a body and a fluid (gas or liquid). This exchange occurs at the interface between the body and fluid, and similar to conduction it is a result of molecular collisions. It differs from conduction however because the fluid moves. This movement may be a consequence of the heat exchange, but it may also have other causes. Thermal exchange through convection is again modelled by Fick's law, being a function of both surface area and the temperature gradient between the fluid and the surface of the body:

$$\dot{Q}_{\mathrm{conv}} = h_c A(T_s - T_a). \tag{2.6}$$

This model is however deceptively simple. While the thermal conductance parameter in Equation 2.5 is constant for any given material, the *convective coefficient* (h_c) is a complicated parameter taking one of three different forms based on the physical conditions (see Gates, 1968, 1980).

Wind velocity is an example of 'forced convection', and has important consequences for the rate of heat loss in mammals and birds – see Robinson et al. (1976) for sparrows, Wathen et al. (1971) for rabbits, and Marder (1973) for ravens.

Evaporation

Evaporation is the process by which heat energy is lost when fluid on the surface of the body (usually perspiration) is converted to a gas. While other forms of thermal exchange can either increase or decrease body temperature, evaporation differs because it leads only to a loss of body heat. Heat is lost because it requires energy, referred to as the latent heat of vaporisation, to change from a liquid to a gas. The rate of heat loss is given by

$$\dot{Q}_{\mathrm{evap}} = L\dot{E}, \tag{2.7}$$

where L is the latent heat of vaporisation, and $\dot{E}$ is the rate at which water is vaporised. The rate at which water evaporates depends upon the surface temperature, the surface area, and the differential in water vapor pressure of the boundary layer and the ambient air.

Net Thermal Exchange

The net thermal exchange between a resting animal and its environment is the sum of thermal exchanges by radiation, conduction, convection, and evaporation:

$$\begin{aligned} \dot{Q}_{\text{net}} &= \dot{Q}_{\text{rad}} + \dot{Q}_{\text{cond}} + \dot{Q}_{\text{conv}} + \dot{Q}_{\text{evap}}, \\ &= \epsilon\sigma A_1(T_s^4 - T_a^4) - k_1 A_2(T_s - T_a) + h_c A_3(T_s - T_a) + L\dot{E}, \end{aligned} \qquad (2.8)$$

where A_1, A_2, and A_3 are the effective surface areas for radiation, conduction, and convection respectively. While Equation 2.8 is valuable as a conceptual framework, there are several difficulties associated with its use as a practical model of heat exchange.

The first of these problems is due to the use of surface temperatures rather than core body temperature. Surface temperatures are difficult to measure, and typically the temperature is not uniform across the surface of an animal (Doncaster et al., 1990). Further, when temperature regulation occurs it is not the surface temperature that is being regulated. Instead, it is far more useful to consider the temperature gradient between the body and the environment ($T_b - T_a$). Veghte and Herreid (1965) found that the differential $T_s - T_a$ is independent of T_a in several species of birds, and in large species of birds (such as the raven, C. *corax*) they found that $T_s \approx T_a$. Therefore, a common simplification of Equation 2.8 is to use $T_b - T_a$ in place of $T_s - T_a$.

Another problem with Equation 2.8 as a practical model of thermal exchange for animals is that it is complicated. In practice the surface areas A_1, A_2, and A_3 will vary considerably with the behaviour of an animal, and will be influenced by factors such as posture. Further complications are introduced with the coefficients k_1 and h_c, as well as the rate of water vaporisation ($\dot{E}$). Therefore, biologists have made considerable effort towards producing simpler models of net thermal exchange between the organism and its environment.

Burton (1934) proposed one such simplification of Equation 2.8, reducing the four components of heat exchange into two terms:

$$\dot{Q}_{\text{net}} = C'(T_b - T_a) + L\dot{E} \tag{2.9}$$

The first term of Equation 2.9 encompasses thermal exchange due to radiation, conduction and convection, while the second term describes the rate of evaporative heat loss. The diffusion coefficient C' is referred to as the coefficient of ‘dry’ thermal exchange (also called the *thermal conductance*).

The *Burton model* is applicable over all biologically relevant temperatures, however it has some limitations. It is assumed that there is no significant external source of radiant heat load, such as that due to basking, and it is not accurate when forced convection (e.g., wind velocity) influences the rate of heat exchange (see Tracy, 1972).

Equation 2.9 can be further simplified if evaporative heat loss is negligible, for example at low environmental temperatures. In this case, the model of net thermal exchange can be simplified to

$$\dot{Q}_{\mathrm{net}} = C(T_b - T_a), \tag{2.10}$$

where the coefficient C (*wet* thermal conductance) now incorporates both evaporative and non-evaporative forms of thermal exchange. This model is often referred to as *Newton's law of cooling* (Scholander et al., 1950a; McNab, 1974, 1980).

2.2.2 Endothermic Homeothermy

Changes in an organism's body temperature reflect the total heat exchanged with the environment in addition to any heat that is generated through metabolism. We can describe these changes by the following equation:

$$\frac{dT_b}{dt} = -\dot{Q}_{\mathrm{net}} + G, \tag{2.11}$$

where G is the rate of internal heat generation through metabolism. Homeotherms strive to maintain a constant internal body temperature by balancing rates of heat gain and loss (i.e., $G = \dot{Q}_{\mathrm{net}}$). It follows from Equation 2.11 that an organism may exert control over its internal temperature in one of two ways: either (1) by manipulating the rate that heat is exchanged with the environment, or (2) by increasing or decreasing the rate of heat generation through metabolism. Such mechanisms are collectively referred to as *thermoeffectors*.

To compensate for increased rates of heat loss at lower ambient temperatures, endotherms respond by raising their rate of metabolism. Metabolic rate may be raised either through muscle contractions – such as during activity or shivering – or by non-shivering thermogenesis. Shivering is an important response to low ambient temperatures for both birds and mammals, and the extent of shivering has been shown to increase approximately linearly with reductions in ambient temperature (For birds see Steen and Enger, 1957; Hart, 1962; West, 1965; West et al., 1968 and for mammals see Pohl and Hart, 1965; Pohl, 1965). Non-shivering thermogenesis refers to any form of heat production that does not involve shivering. While many organ systems can be used to produce heat (e.g., muscles and liver), brown adipose tissue (BAT) is a tissue specialised for heat production (Cannon and Al, 1978). Non-shivering thermogenesis is especially important to young mammals and adults of small species (Janský, 1973): this can be seen in the prevalence of brown fat in such animals (Cannon and Al, 1978; Blumberg, 2001; Hull, 1973; Smith, 1964).

Over moderate to cool temperatures, Newton's law of cooling (Equation 2.10) can be used to model the rate of heat exchange at different ambient temperatures. For an endotherm maintaining a preferred body temperature ($T_b = T_p$), it follows from Equation 2.11 that its metabolic rate must equal the rate of heat exchange with the environment:

$$\mathrm{MR} = C(T_p - T_a), \tag{2.12}$$

which states that in moderate to cool temperatures, the required metabolic rate of endotherm is proportional to the temperature gradient that is to be maintained.

2.2.3 The Thermoneutral Zone

In a classic study of thermoregulation, Herrington (1940) looked at the effects of environmental temperature on the metabolic response in small mammals; the study found that there is a region of ambient temperatures for which metabolic rate remains at resting levels. Metabolic rates increased for ambient temperatures outside of this region (See Figure 2.1). Figure 2.2 shows a schematic of the thermoregulatory profile of an endothermic homeotherm; within this profile there is a range of ambient temperatures over which the metabolic rate remains at a minimum level (basal metabolic rate, BMR). Across this range of temperatures, referred to as the *thermoneutral zone* (TNZ), thermoregulation is achieved through adjustments in insulation, posture and skin blood flow (Gordon, 2012).

As ambient temperature is reduced, an endotherm will make adjustments to minimise its thermal conductance. When all physical impediments to heat loss are maximised, an animal must increase its metabolic rate in order to maintain thermal balance. This point marks the lower bound of the thermoneutral zone, and is referred to as the *lower critical temperature*. The lower critical temperature represents an important threshold in the thermoregulatory profile of an endotherm, and it is a key predictor of an animal's sensitivity to cold stress (Gordon, 2012). In a seminal piece of work on the thermoneutral zone, Scholander et al. (1950b) compared the metabolic rates of arctic and tropical mammals. Arctic mammals were

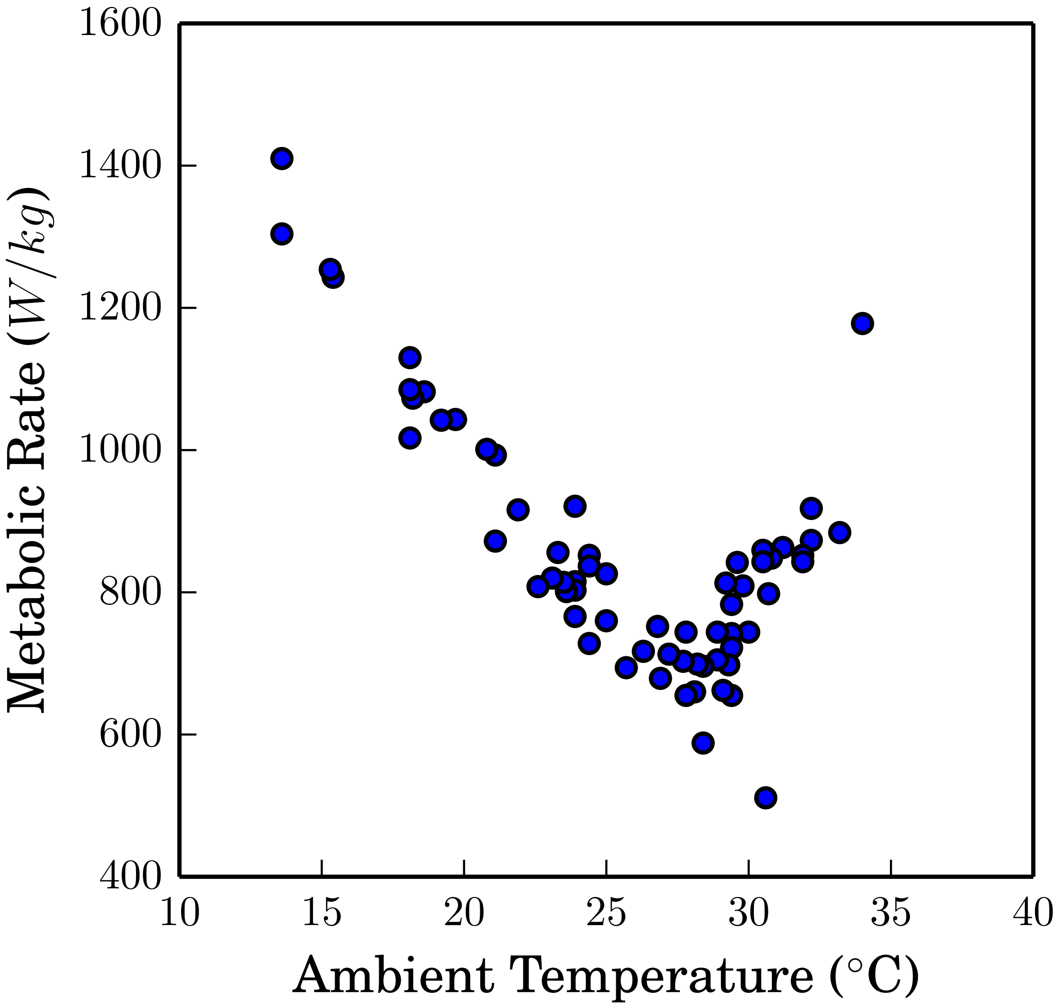

FIGURE 2.1: Metabolic rate of albino rats as a response to different ambient temperatures. For a region of ambient temperatures the metabolic rate remains at resting levels. Within this *thermoneutral zone* adjustments in insulation, posture, and blood flow are sufficient to maintain thermal homeostasis. At lower ambient temperatures, heat is generated through metabolic processes, while at higher ambient temperature metabolism increases as the animals attempt to actively increase thermal exchange with the environment (e.g., sweating, panting). Data from Herrington (1940).

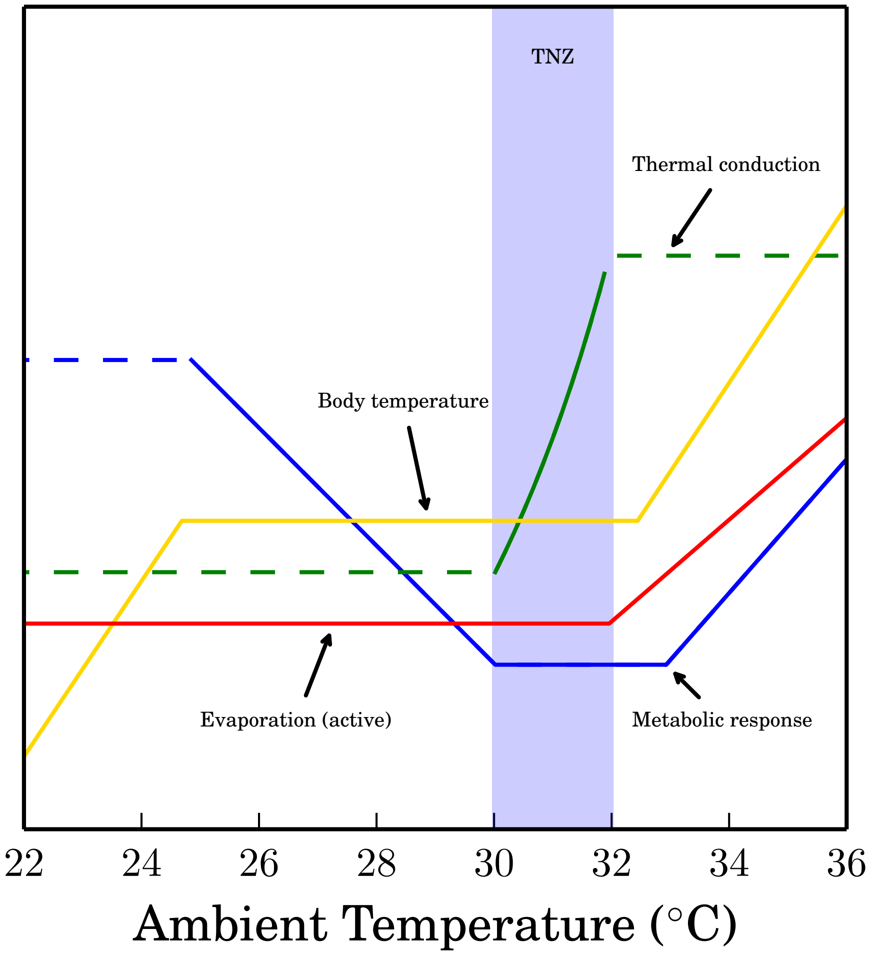

Figure 2.2: Schematic representation of the thermoregulatory profile of an endothermic homeotherm. (1) The blue shaded region indicates the thermoneutral zone, the range of ambient temperatures for which metabolic responses remain at basal levels. (2) As ambient temperatures increase above the upper critical temperature, active mechanisms of heat loss are employed (e.g. panting, sweating). As the ambient temperature decreases, physical adjustments are first made to increase insulation (e.g. posture, blood flow). When these adjustments reach their maximal effectiveness (at the lower bound of the TNZ), endogenous processes of heat production must be used to compensate for higher rates of heat loss. (3) Thermal homeostasis is maintained over a broad range of temperatures, including the thermoneutral zone. Limitations on both metabolic heat production, and active mechanisms of heat dispersion, mean that thermoregulation cannot be maintained at extreme temperatures, at which point body temperature is no longer independent of the environment. Figure modified from Gordon (2012)

found to have higher insulation (i.e., lower thermal conductance), very low lower critical temperatures, and significantly wider thermoneutral zones. A summary of some of the data from the Scholander study is presented in Figure 2.3.

2.2.4 Behavioural Thermoregulation

Behavioural temperature regulation is defined as ‘any coordinated movement of an organism ultimately tending to establish a thermal environment that represents a preferred condition for heat exchange of the organism with its environment’ (Bligh and Johnson, 2001). Such responses can range from the relatively simple, such as movement within a temperature gradient, to the more complex, such as the creation of a micro-climate through nest building. Studies have shown that, when given a choice, endotherms will preferentially choose to use behavioural responses over autonomic responses to maintain thermal balance (Gordon, 1983; Gordon and Refinetti, 1993; Gaskill et al., 2012). So we might assume that such behaviours are preferred because they afford reductions in the metabolic costs of endothermy (Gordon, 2012; McNab, 1974).

Studies of behavioural thermoregulation began with the use of a thermocline (a controlled thermal gradient across the environment) and the observation that animals move to a specific location on the thermocline, indicating a preferred ambient temperature (for a review of early literature, see Hart, 1972). Simple thermotaxic behaviours bring animals to a temperature that minimises their metabolic rate (Huffman et al., 1999; Kleitman and Satinoff, 1982; Malik and Fewell, 2003). Morphological and physiological changes that occur during development affect the

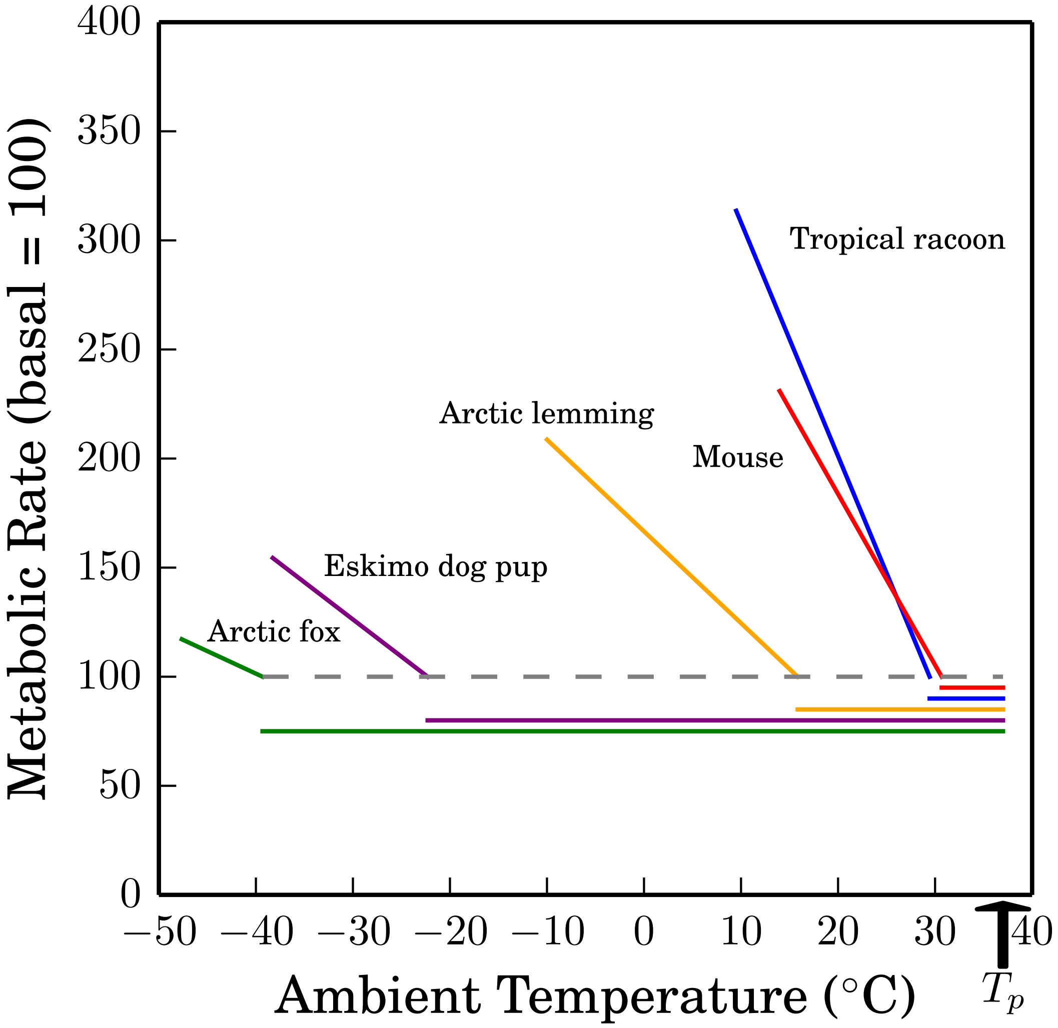

Figure 2.3: A comparison of the metabolic responses to varying ambient temperatures in arctic and tropical mammals. Horizontal lines denote the critical gradient, the difference between an animal's normal body temperature and its lower critical temperature. Within this range of ambient temperatures, adjustments are made to an animal's insulation, posture and skin blood flow. As the ambient temperature drops below the lower critical temperature, metabolic rates increase to balance heat loss. Graph reproduced from Gordon (2012), based on a selection of data from Scholander et al. (1950b)

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thermodynamic properties of an endotherm; consequently animals adjust their preferred ambient temperature as they develop (Ogilvie and Stinson, 1966). Farrell and Alberts (2007) showed that 7-day–old rats are able to adjust their preferred ambient temperature in response to artificial manipulation of their physiological heat production (increased BAT thermogenesis by injection of norepinephrine). The inability of 2-day–old pups to adjust implies that the integration of behavioural and physiological thermoregulation develops during the first week of a rats life.

2.3 Huddling Behaviour

The aspects of *Endothermic Homeothermy* presented so far derive from considerations of the animal in isolation from any social context. However for rodents, from which most of the evidence reviewed has been obtained, interaction with group members is a significant factor in early development.

Many species of mammals (Alberts, 1978b; Hayes et al., 1992; Haim et al., 1992), and birds (Fowler and Kellogg, 1975; Gordon, 1990), engage in social grouping behaviours as a response to cold temperatures. *Huddling* behaviours in rats begin at birth, when the mother dam gathers her litter of newborns into a clump. While the dam is nearly always present during the first few days after birth (Grota and Ader, 1969), she increasingly makes excursions from the litter (Thiels et al., 1990) and during this time the huddle aggregation is seen to be actively maintained by the actions of individual pups (Schank and Alberts, 1997; Alberts, 1978a, 2007).

Thermoregulatory huddling is an adaptive behaviour (Richter, 1927; Sealander, 1952; Alberts, 1978b), with important consequences for both energy expenditure (Alberts, 1978b), and survival (Sealander, 1952). Huddling is particularly important for altricial newborns, who lack the thermal physiology to achieve and maintain high body temperatures (Hull, 1973; Kaul et al., 1985; Kleitman and Satinoff, 1982).

> “ [H]uddling is of broad biological, ecological, and developmental significance, serving essential biological functions for the individual, which either cannot be achieved or only partially achieved by an individual on its own. ” (Schank and Alberts, 1997)

2.3.1 Energetic Consequences of Huddling

Canals et al. (1989) highlighted three important consequences of thermoregulatory huddling behaviours: (1) low metabolic rates (Alberts, 1978b, see Figure 2.4), (2) low rates of food ingestion (Prychodko, 1958, see Figure 2.5), and (3) improved survival rates at low temperatures (Sealander, 1952, see Figure 2.6). These benefits have primarily been attributed to reductions in the exposed surface area of an individual during huddling (Contreras, 1984; Sealander, 1952; Canals et al., 1989).

Looking at the geometrical aspects of huddling, and accounting for species specific differences in morphology, Canals et al. (1989) proposed a general mathematical expression to describe how the exposed surface area of an individual decreases

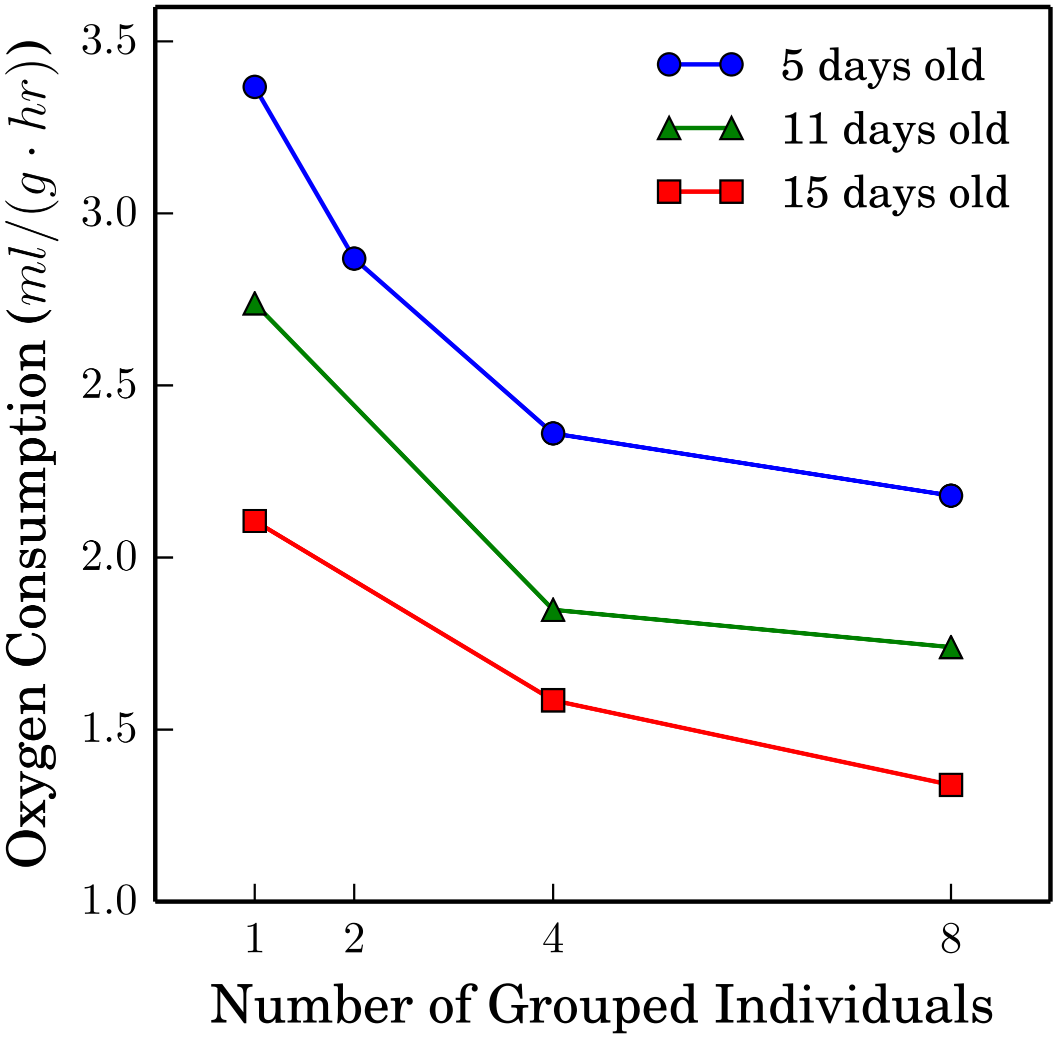

FIGURE 2.4: Mass specific rate of metabolism, as measured by oxygen consumption, is seen to reduce as a function of the number of grouped individuals increases. Data taken from Alberts (1978b).

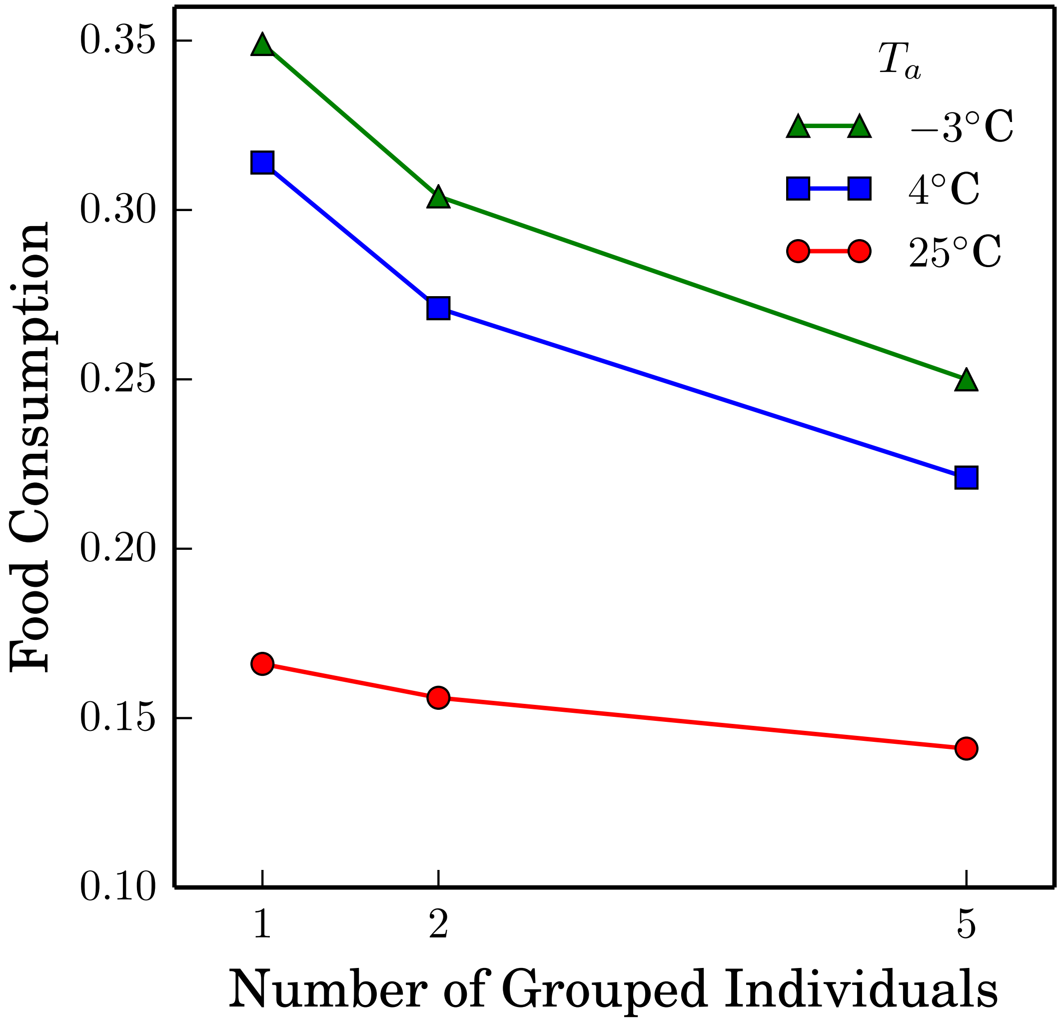

FIGURE 2.5: Relationship between food consumption of male mice and the number of animals per cage at different ambient temperatures. Food consumption was normalised for weight, and can be used as an indicator of the thermal stress experienced by individuals. Animals that were grouped consumed less, implying that the metabolic demands of low ambient temperature were reduced. Data taken from Prychodko (1958).

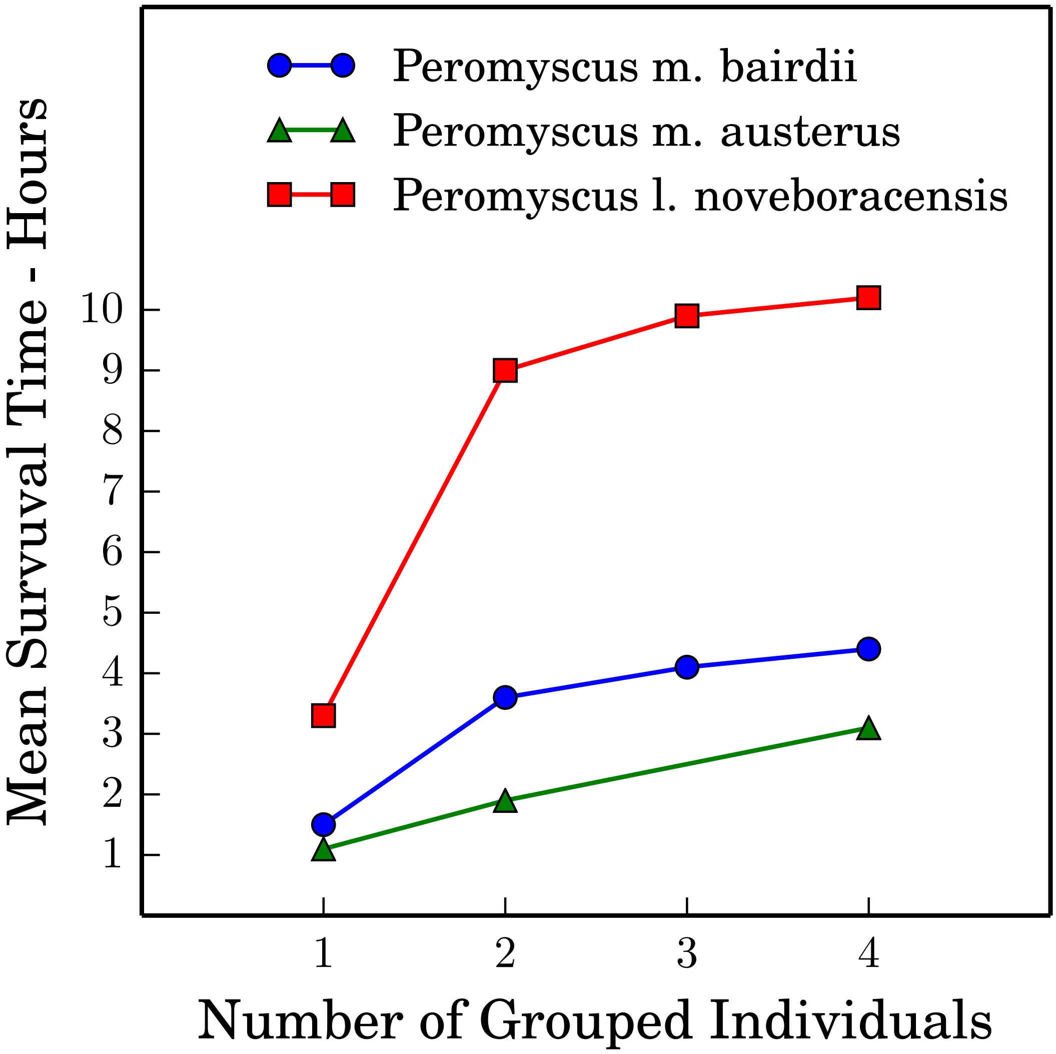

Figure 2.6: The survival rates of wild deer mice at very low temperatures (−30°C) improve as the number of grouped individuals increased. Data taken from Sealander (1952).

with the number of grouped individuals. The derivation of this model began by looking at the relationship between an individual's metabolic rate and its exposed surface area (Kleiber, 1961):

$$M = mA^v, \tag{2.13}$$

where m is related to the temperature gradient $(T_b - T_a)$, and v is an empirical exponent. Similarly, the metabolic rate of an individual engaged in huddling (MR_h) is proportional to its exposed surface area during to huddling (A_h):

$$\mathrm{MR}_h = m_h A_h^v, \tag{2.14}$$

The energetic benefits of huddling can be quantified by the metabolic ratio (R_m) of huddling to non-huddling animals:

$$R_m = \frac{M_h}{M} = \frac{m_h}{m}\left(\frac{A_h}{A}\right)^v = f(n)R_a^v, \tag{2.15}$$

where $f(n) = \frac{m_h}{m}$, and $R_a = \frac{A_h}{A}$. The function, $f(n)$, encompasses factors such as the number of huddling individuals, as well as changes in the temperature differential $T_b - T_a$ due to the effects of micro-climates in grouped individuals (Hayes et al., 1992).

To explore how the area ratio (R_a) changes with respect to the number of grouped individuals, Canals et al. (1989) modelled individual animals as deformable spheres. They found that the area ratio of n grouped individuals is given by the formula:

$$R_a = \frac{\phi}{n} + (1 - \phi), \tag{2.16}$$

where ϕ is the ‘deformation coefficient’, a value dependent on how closely individuals are able to group together. Finally, combining both Equations 2.15 and 2.16 gives the following model of metabolic ratio:

$$R_m = f(n)\left(\frac{\phi}{n} + (1-\phi)\right)^v \tag{2.17}$$

Based on allometric relationships between thermal conductance and body mass, an exponent value of $v = 0.735$ was derived (Herreid and Kessel, 1967). For simplicity, the authors set $f(n) = 1$:

$$R_m = \left(\frac{\phi}{n} + (1-\phi)\right)^{0.735} \tag{2.18}$$

In order to validate this model, the metabolic ratios of four species of small rodents were studied for a variety of group sizes. Linear regression techniques were used to fit Equation 2.18, which gave species specific values of ϕ ranging from 0.575 to 0.783. A selection of these results can be seen in Figure 2.7. For the studied four species, the average energy savings from huddling was 42% of an animals metabolic budget, and Canals et al. (1989) determined that reductions in exposed surface area were the principle source of these savings.

2.3.2 The Self-Organising Huddle

Several authors have suggested that rodent huddling is a self-organising system (e.g., Alberts, 1978b; Schank and Alberts, 1997; Canals and Bozinovic, 2011). This

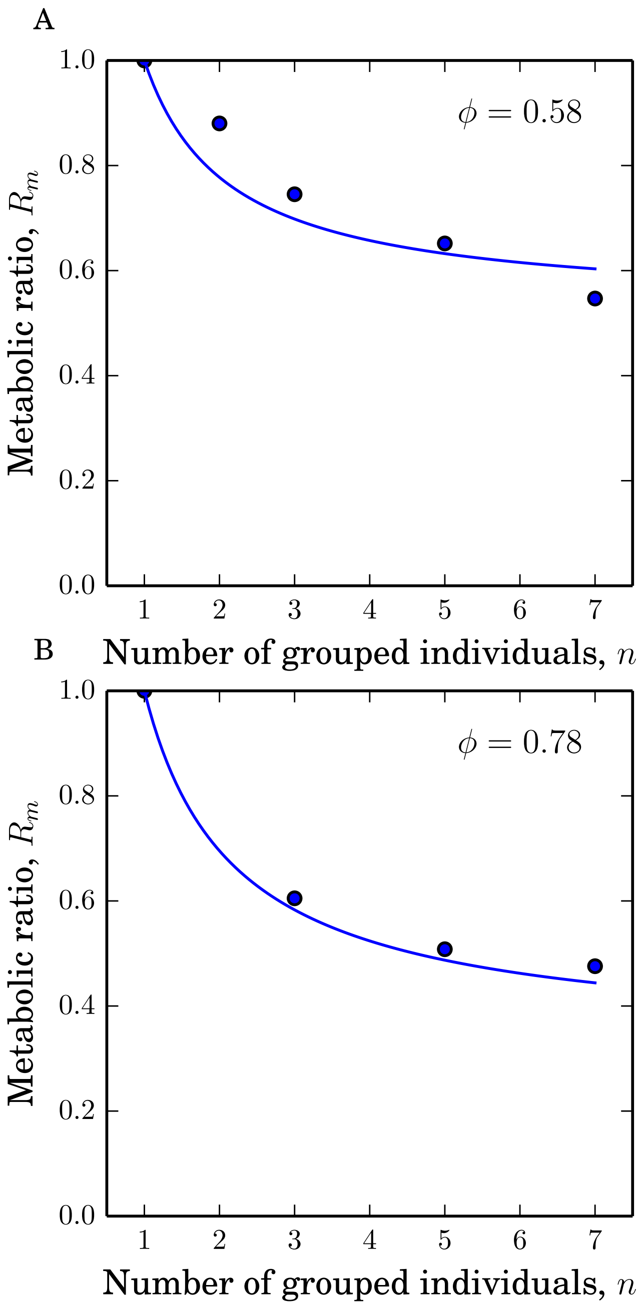

FIGURE 2.7: Looking at the metabolic ratio in two species of rodents as a function of the number of grouped individuals (n): *Mus musculus* (Panel A) and *Thylamys elegans* (Panel B). As the number of individuals in a group increases the metabolic ratio decays. Linear regression was used to fit a model of metabolic ratio (Equation 2.18). Coefficients of deformation, ϕ, were found for each species.

suggestion was originally based on two sets of observations. First, in a series of experiments reported in Alberts (1978a), a multitude of sensory cues were shown to govern the behaviours of rat pups at the individual level. Second, in a series of experiments reported in (Alberts, 1978b), a variety of group level properties not existing at the individual level were identified. Together, these observations have given rise to an informal description of the huddle as a 'super-organism' (Schank and Alberts, 1997; Canals and Bozinovic, 2011).

Group Thermoregulation

The huddle forms in response to cold environments, and disperses at high ambient temperature (Alberts, 1978b; Canals and Bozinovic, 2011). This behaviour provides an energy saving mechanism which allows energy to be diverted towards growth and maturation (Alberts, 1978b; Alberts and Gubernick, 1983). What is not clear from this observation alone is that huddling behaviours also provide a means of *group thermoregulation*. When viewed as a single entity, the exposed surface area of the huddle is seen to adaptively vary in direct response to the ambient temperature (Alberts, 1978b; Canals and Bozinovic, 2011; Alberts, 2007).

At low ambient temperatures individuals form tightly packed huddles with a relatively small exposed surface area. As the ambient temperature rises, looser aggregations begin to form until individuals eventually disperse (see Figure 2.8). This directly controls the rate of thermal exchange with the environment, and has the

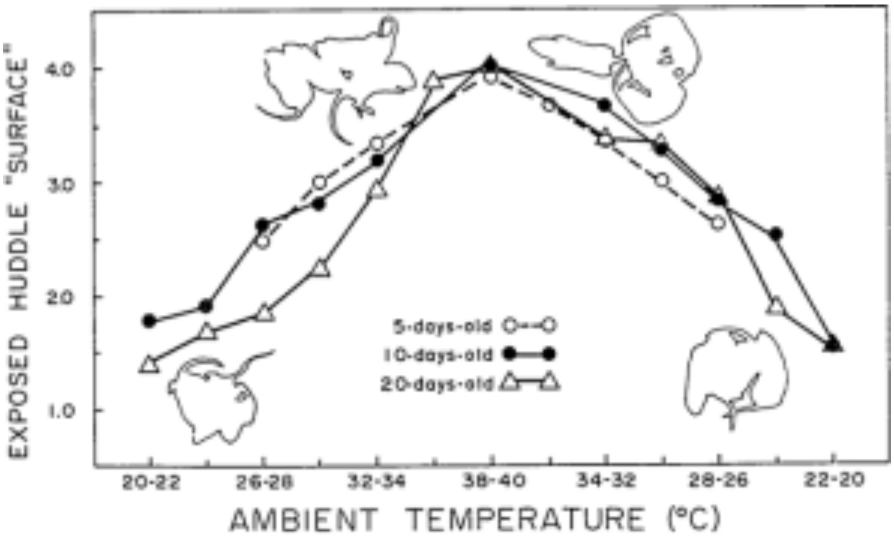

FIGURE 2.8: **Group Regulation:** Figurative and quatitative depictions of the 'phase transition' seen in thermoregulatory huddling. At low ambient temperature, the aggregation of pups is more closely packed together, and has a smaller exposed surface area. Graph from Alberts (1978b).

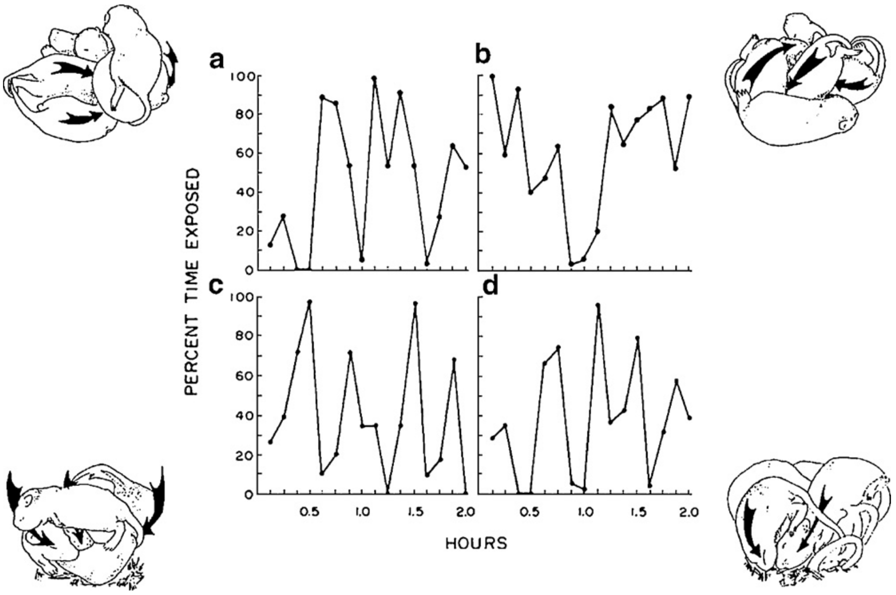

Figure 2.9: **Individual Regulation:** Figurative and quantitative depictions of 'pup flow', an emergent property of thermoregulatory huddling. Arrows superimposed on the drawings of pups indicate the direction of a pups movement within the huddle. Graph from Alberts (1978b).

effect of regulating the amount of heat energy within the group. Canals and Bozinovic (2011) have quantified this emergent behaviour as a second-order critical *phase transition*, i.e., an abrupt but continuous change in the degree of huddling.

Individual Thermoregulation

By controlling the amount of cold-exposed surface area of the group, huddling behaviours are able to regulate the amount of thermal energy within the group as a whole. However, locations within a huddle do not offer the same degree of protection; the amount of exposure experienced by a pup on the periphery of a huddle is significantly greater than a pup who occupies a central position (Alberts, 1978b; Waters et al., 2012).

Observations of the internal dynamics of a huddle have revealed that individuals do not maintain a fixed location within the group, and instead pups are seen to continuously exchange positions (Alberts, 1978b, see Figure 2.9). At low ambient temperatures, there is an inward flow as pups actively seek to reach the warm central locations, while at warmer temperatures this behaviour reverses, and instead pups flow outwards as they become too hot (Alberts, 2007). ‘Pup flow’, as it has been named, potentially allows the benefits of the huddle to be shared among all individuals (Alberts, 1978b; Schank and Alberts, 1997).

> “ The huddle, as an emergent entity regulates “downward” to the level of the individual ” (Alberts, 2007)

2.3.3 Computational Models of Huddling

Informal descriptions of huddling as a self-organising system have been complimented by formal descriptions of huddling in the form of computational models.

The Grid World Model of Schank and Alberts

Schank and Alberts (1997) found that a small set of simple rules, governing individual behaviours, were sufficient to synthesise group behaviours similar to the natural huddle. According to their model, individual rats are represented as occupying discrete cells within a grid world (see Figure 2.10). Movement of individuals from one cell to the next is determined probabilistically, based on whether adjacent cells are occupied by conspecifics or walls. The parameters of the model were optimised to generated patterns of aggregation that were quantitatively similar to observed patterns.

Schank and Albert's model shows how huddle-like patterns can emerge from simple, local interactions between individual agents. While this model serves as an existence proof that huddle-like behaviours can be the product of self-organisation, the model is limited in its application as a model of thermoregulatory huddling. The model makes no explicit reference to temperature and so it cannot account for influences of the ambient temperature, nor can it model the internal thermodynamic properties of the huddle.

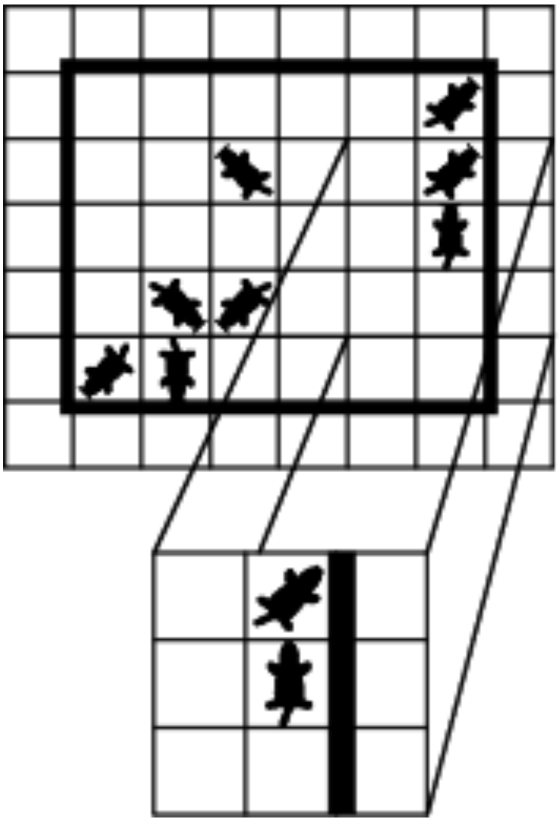

Figure 2.10: Schank and Alberts (1997) designed a computational model of huddling behaviours. In this ‘Grid World’, the movements of individual agents are determined probabilistically. Aggregation patterns spontaneously appear, and through optimisation of the model parameters, these aggregation patterns can be tuned so that they match the natural system. Graph from Schank and Alberts (1997).

Waters' Model of Huddling Penguins

Waters et al. (2012) developed a computational model of huddling penguins, with an explicit description of the ambient temperature. This model implements a single rule at the individual level, in which each penguin seeks only to reduce its own heat loss. Consequently, penguins located within the central regions have a thermal advantage and so remain stationary, whereas penguins on the periphery that are exposed to the wind will seek to move to a more sheltered location.

This model shows how a co-operative group-level behaviour can emerge from purely competitive interactions between individuals. However, the model relies on a global supervisory mechanism to identify both the coldest individuals and the warmest locations for them to find shelter. Therefore, while this model provides evidence of the thermodynamics at play within a huddle, it does not support the hypothesis that they emerge purely as a consequence of simple, local interactions.

2.4 Summary

In this chapter we have discussed the importance of temperature, and its influence on the fitness of an organism. Endothermic homeothermy is a an adaptive strategy to survive in a changing environment; a high and constant body temperature is maintained through both physiological and behavioural mechanisms. However, the metabolic requirements of endothermy are significant and so energy saving mechanisms are an important evolutionary response to cold challenge.

Huddling behaviours have been identified as a within lifetime adaptation that afford two key benefits: (1) huddling reduces the metabolic demands of cold environments (energy saving); and (2) huddling adaptively regulates an individual's body temperature (behavioural thermoregulation). Further, both empirical and computational studies have provided evidence that huddling behaviours may emerge from simple, local interactions between individual animals (i.e., self-organisation). However, a model in which displays both genuine self-organisation (i.e., relying on no global supervisor) *and* captures the thermoregulatory properties of the huddle, is currently lacking. Therefore, while thermoregulatory huddling constitutes an excellent system through which to investigate interactions between self-organisation and natural selection, the first step is to construct such a model.

In the next chapter we will use the theories that have been developed here to construct a model of thermoregulatory huddling by self-organisation. In particular, this model will address the limitations that we have identified in previously existing models of huddling behaviours:

1. A need for explicit representation of temperature, which will allow us to explore the internal thermodynamics of huddling.
2. Interactions based on simple, local information, and in the absense of a global supervisor.

In Chapters 4 and 5 we will use this model of huddling to address the overall question of this thesis: How can self-organisation (huddling) guide evolution (of physiological components of homeothermy)?

Chapter 3

A Self-Organising Model of Thermoregulatory Huddling

The work presented in this chapter appears, with minor modifications, as:

Glancy, J., Gross, R., J., S., & Wilson, S. P. (2015). A self-organising model of thermoregulatory huddling. PLoS Computational Biology.

3.1 Introduction

Many species of mammals (Alberts, 1978b; Hayes et al., 1992; Haim et al., 1992), and birds (Fowler and Kellogg, 1975; Gordon, 1990), spend a large proportion of their lives in direct contact with conspecifics, engaging in a synergistic pushing, climbing, wriggling, and burrowing behaviour referred to as 'huddling' (Alberts, 1978b). Huddling begins at birth, when the dam first gathers her litter of around a dozen pups into a single aggregation, and it persists as the frequency and duration of her excursions from the nest increase (Thiels et al., 1990). Pups aged between 2 and 10 postnatal days reliably orient themselves in the direction of contact with a littermate (Grant et al., 2012), and pups that are displaced from the huddle center orient themselves back towards its center (Alberts, 1978b), suggesting that individual behaviours actively help to maintain the integrity of the huddle (Alberts, 1978a; Canals and Bozinovic, 2011).

In turn, the huddle is thought to help individuals to maintain their body temperatures (Richter, 1927; Sealander, 1952). Compared with the adult, the metabolism of the neonate generates less heat, its lack of insulative fur and subcutaneous fat increases the rate of heat loss, and a higher surface area to volume ratio further limits the ability of the individual pup to thermoregulate (Hull, 1973; Conklin and Heggeness, 1971; Malik and Fewell, 2003), to the extent that pups are often considered to be *ectothermic* (Fowler and Kellogg, 1975) (i.e., dependent on environmental heat sources). However, the metabolic rate of individual pups decreases as the number of huddling littermates increases (Alberts, 1978a; Canals et al., 1989), and huddling slows the rate of heat loss from individuals by reducing their cold-exposed surface areas. Moreover, the exposed surface area of the entire litter has been observed to increase or decrease to adapt to the ambient temperature (Alberts, 1978b). Hence it has been suggested that the litter of huddling neonates together behave like a single organism, which displays an *endothermic* thermoregulatory profile comparable to that of the adult (Schank and Alberts, 1997).

Behavioural experiments with rats and mice have identified two characteristic patterns in the dynamics of the huddle that could further improve thermoregulation. First, as the ambient temperature drops below a critical value, the dynamics of the huddle undergo what has been described as a second-order critical *phase transition* (Canals and Bozinovic, 2011), i.e., an abrupt but continuous change in the degree of huddling. At high ambient temperatures the group dissipates, whereas at low ambient temperatures large aggregations of pups tend to form. Second, around the critical ambient temperature, huddling pups have been observed to continually exchange positions relative to the centre of mass of the huddle, in dynamics referred to as *pup flow* (Alberts, 1978b), which ensure that cooler pups at the periphery replace warmer pups at the centre (Alberts, 1978a), and which minimises the overall metabolic cost to all littermates (Canals et al., 1989; Canals and Bozinovic, 2011). An illustration of the phase transition and the pup flow is provided in Figure 3.1.

Observations of the phase transition and pup flow have led many to consider the huddle to be a self-organising system, with adaptive thermoregulatory properties that emerge spontaneously from simple, local interactions between individuals, in the absence of any global supervisory mechanism (e.g., (Alberts, 1978b; Schank and Alberts, 1997; Canals and Bozinovic, 2011)). This view is supported by evidence from computational modelling studies showing how groups of agents evaluating only local rules of interaction can form and maintain a single aggregation. For example, the seminal model of Schank and Alberts (1997) (Schank and

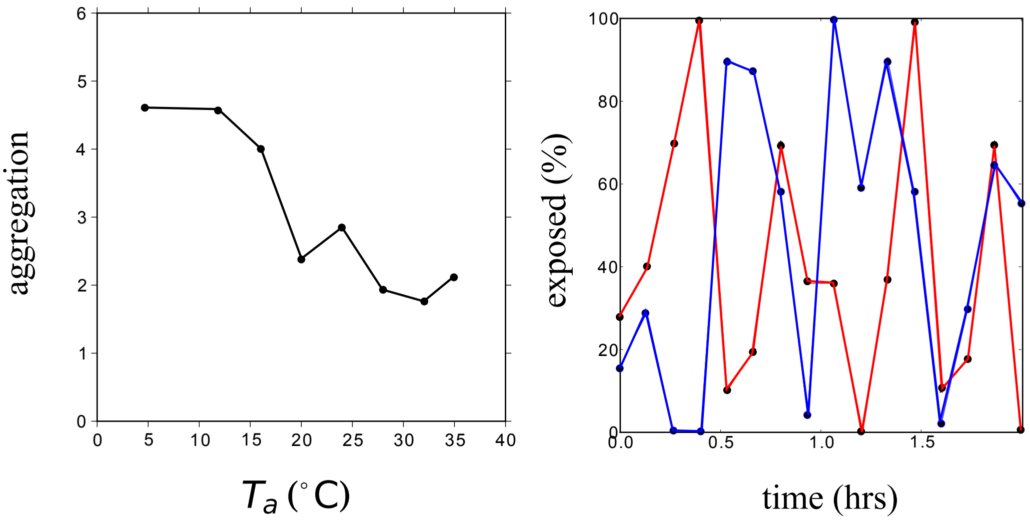

FIGURE 3.1: **Huddling dynamics revealed by previous animal behavioural experiments.** *Left*: Phase transition. Aggregation patterns in juvenile mouse litters were measured in experiments in which the ambient temperature T_a was experimentally manipulated (Canals and Bozinovic, 2011). 'Aggregation' was defined as the mean-variance coefficient of the number of individuals occupying cells of a grid overlaid on video frames from recordings of mouse litters (note that by this metric, an aggregation score of 1 is baseline; see (Canals and Bozinovic, 2011)). The data reveal what has been termed a second-order phase transition into huddling at low ambient temperatures, such that the litter huddle together when it is cold and disperse in a large arena when it is warm, with a smooth transition around a critical temperature in the range 15–25°C. *Right*: Pup flow. The proportion of time spent exposed at the periphery of an aggregation is shown for two focal pups from the same huddle, and varies periodically as individuals continually exchange positions between the cool periphery and the warm center. Data are reproduced, respectively, from (Canals and Bozinovic, 2011) (original error bars removed and axes relabelled), and (Alberts, 2007) (data from two pups collected into the same figure for convenience).

Alberts, 1997) (see also (Alberts, 2007)) shows how group-level aggregation patterns can be formed by simple agents making probabilistic decisions to navigate a grid-world, based on responding to obstacles detected in adjacent grid locations (Schank and Alberts, 1997). However, this model does not explicitly represent the heat exchanged between individuals and so was not designed to explore potential relationships between self-organisation of aggregate movement patterns and self-organisation of collective thermoregulatory dynamics. Conversely, a model proposed recently by Waters, Blanchette & Kim (2012) (Waters et al., 2012) provides a parsimonious account of thermoregulation via huddling, but this model represents the assumption that global supervisory mechanisms are in place to identify amongst the group both the coolest individual and the warmest location. Hence, to the best of our knowledge, no previous model of huddling has used only simple local interactions to govern individual behaviour *and* has explicitly represented the exchange of heat between individuals, and therefore previous models have not addressed either the emergence of a temperature-mediated phase transition or the emergence of a thermoregulatory pup flow.

The aim of the current chapter is to determine whether the observed patterns of group contact and the group-level dynamics of heat exchange, could in principle both emerge via self-organisation. We present a simple self-organising model of thermoregulatory huddling that can explain each of these observations as emergent properties of the collective interactions of individuals. From the model we derive specific predictions that can be used to test self-organisation as a theory of thermoregulatory huddling.

3.2 Results

3.2.1 Thermotaxic Individuals

We set out to test whether the thermoregulatory properties of huddling observed in juvenile rodents could be explained as a product of self-organisation via simple, local interactions between individuals, in the absence of global supervisory mechanisms. We constructed an agent-based model, in which each pup is represented as a circle with 1000 thermal sensors (henceforth 'thermometers') evenly spaced around its circumference, that moves under simple thermotaxic control, orienting and moving towards sources of heat in a two-dimensional arena (see Figure 3.2). We hypothesised that this simple thermotaxic controller could be sufficient to reproduce the phase transition into huddling at low ambient temperatures, as observed in experiments (Canals and Bozinovic, 2011; Alberts, 1978b) in which litters were, in independent conditions, exposed to a range of constant ambient temperatures. See Section 3.4 for a more in depth discussion of the methods used.

In the following sections we present a series of incremental modifications to our basic model of the pup as a thermotaxic 'vehicle' (Braitenberg, 1984) to investigate the interplay between behavioural and physiological thermoregulation and the contribution of each to the collective behaviour. As we are modelling the litter as a (potentially) self-organising system, involving only individual-level rules of interaction, our approach necessarily involves modifying the description of the behaviour and physiology of the individual before simulating interactions between

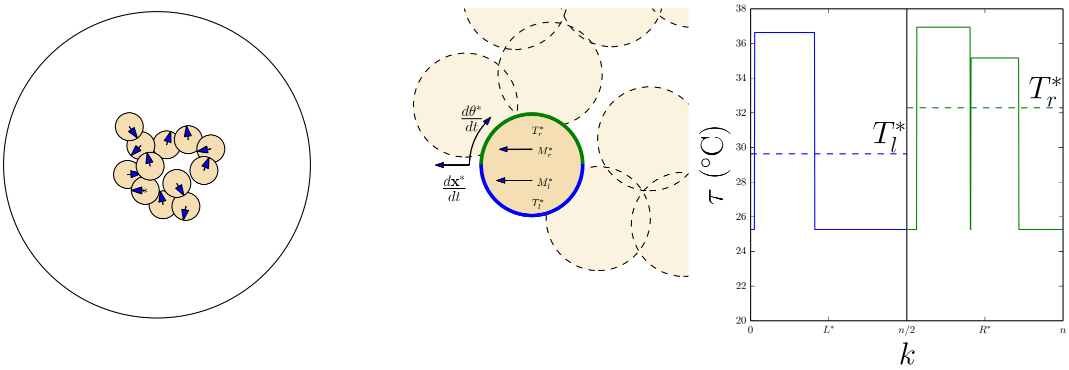

FIGURE 3.2: **Modelling thermotaxic individuals.** *Left:* A snapshot of the model, showing twelve simulated pups (small circles) in a circular arena (large circle), with orientations indicated by arrows. In this snapshot, pups are shown aggregated, often overlapping. *Center:* The same snapshot is shown, zoomed in on the focal pup indicated by *. The left and right sides of its body are coloured green and blue respectively, to indicate the regions of the body surface over which average temperatures constitute the left and right sensor values T_l^* and T_r^*. To implement thermotaxic control, these sensor values set the drive speed of contralateral motors M_l^* and M_r^*, which change the position $\mathbf{x}$ and orientation θ of the pup. *Right:* For the focal pup, the temperature (τ) registered at discrete positions around the body circumference (indexed by k) is shown. For the focal pup T_r^* is greater than T_l^*, indicating that it is warmer on the right than the left, hence at this point in time $M_l^* > M_r^*$ and therefore the pup will orient clockwise. See *Models* for precise definitions of these terms.

a litter of many individuals and analysing the group-level effects (see (Alberts, 2012)).

In our basic thermotaxic simulation, each pup is modelled as a moving circular body with all thermometers on a given half of the circular body surface projecting to one of two 'sensors' (left or right). On each iteration of the simulation, the movement and orientation of each pup in a large arena with a circular boundary is computed following five steps; i) the left and right sensor values are determined by averaging the temperature registered by thermometers on either half of the body surface; ii) to generate thermotaxic orienting behaviours, the two resulting sensor values for each pup are used to determine the speed of a motor driving the opposite side of the body (Braitenberg, 1984); iii) the orientation and position of each pup is updated based on the motor speeds; iv) collisions between pups are resolved by making contacting pups spring away from each other with a force that increases with the degree of overlap between them; and v) the body temperature of each pup is updated based on the temperature and proportion of thermometers that are either exposed to the ambient temperature or in contact with another pup. Equations describing these steps in full are provided in *Models*. Note that we allow no distal sensing of either proximity or temperature, hence our modelling approach is to assume that information is exchanged only locally, between contacting pups.

3.2.2 Endothermic Individuals

The key assumption represented by our first and simplest model is that individual pups are able to maintain a constant body temperature of $T_b = 37°\text{C}$. Hence in this model, step v of the algorithm described above is redundant. Accordingly, at each step of the simulation, each thermometer of each pup detects either the ambient environmental temperature or the 37°C body temperature of any pup with which it makes contact. Reflecting the perfect capability of each individual to maintain a constant body temperature, we refer to this as the endothermic individuals (or just the endothermic) model. This model represents the minimal set of constraints that we anticipated *a priori* could account for the phase transition reported by Canals et al., (2011) (Canals and Bozinovic, 2011). Some preliminary experiments with this model are presented in (Glancy et al., 2013).

By analogy with the experiment of (Canals and Bozinovic, 2011) we simulated the endothermic model at twenty ambient temperatures T_a ranging from 5°C to 50°C at regular intervals. Each simulation consisted of 8,000 time-steps (iterations of steps i-v, as described above), and analyses were carried out with respect to data averaged over ten replications, with the initial positions of each of twelve pups distributed uniform randomly within a distance of one pup radius from the center of the arena (pups are therefore close together at the onset of each simulation; see *Discussion* for justification).

We observed that at ambient temperatures above approximately 37°C, simulated pups oriented away from contacts and dissipated from their initial positions, whereas at lower ambient temperatures pups tended to quickly collect together into aggregations in which multiple pups continue to maintain contact for the duration of the simulation. This group-level behaviour is reasonably straightforward to intuit, because at low ambient temperatures pups will sense a higher average temperature on the side of the body where most contacts occur, which increases the relative drive speed of the contralateral motor, and results in the pup orienting towards contacts. Conversely, at ambient temperatures greater than 37°C the side with least contact will register the greater sensor value, and so pups will orient away from contact.

A simple thermotaxic scheme is therefore sufficient to reproduce the phase transition into huddling at low ambient temperatures observed experimentally, at least in terms of our group-level metric of huddling, which we define to be one minus the proportion of exposed thermometers ($1-\eta$; see *Models*), averaged across pups and simulation time-steps. Ambient temperatures above 37°C lead to values of $1-\eta \approx 0.2$ (i.e., 80% thermometers exposed), whereas ambient temperatures below 37°C lead to $1-\eta \approx 0.5$, either side of a steep transition at the critical 37°C body temperature. The overall trend in aggregation patterns predicted by this model is comparable to that measured by Canals et al. (2011; (Canals and Bozinovic, 2011); see Figure 3.1).

However, closer inspection of the simulation and animal data reveals two important differences. First the critical temperature at which huddling 'switches on' is around 20°C for the animals, which is lower than the prediction of the model that the critical temperature should be the 37°C body temperature. Second, the form of the transition predicted by the model is more similar to a Heaviside step function than to the smoother sigmoidal shape of the transition in the animal data. It is simple to manipulate the model to account for these differences. For example, we can lower the critical temperature of the transition by setting the heat registered by each thermometer to be an arbitrary fraction of the body temperature of contacting pups, and we can likewise add noise to all thermometers at each simulation timestep to smooth the transition. Figure 3.3 shows how these manipulations can be used to create a good fit of the model to the experimental data. However, these improvements in terms of our group-level huddling metric mask a more important weakness of the endothermic individuals model.

Whilst the endothermic model quantitatively reproduces the phase transition at the macro-level, visual inspection of the aggregation patterns formed in each simulation revealed a strong tendency for the initial aggregation of pups to fracture into several smaller isolated groups, rather than to maintain one global cluster comprising all pups. We refer to the small isolated clusters as ‘micro-huddles’, and to the global aggregation typically observed in animal experiments as a ‘macro-huddle’. Although micro-huddles have been observed experimentally, they are not typical at low ambient temperatures (Alberts, 2007; Canals and Bozinovic, 2011); hence the endothermic model is unable to account for the maintenance of naturalistic aggregation patterns.

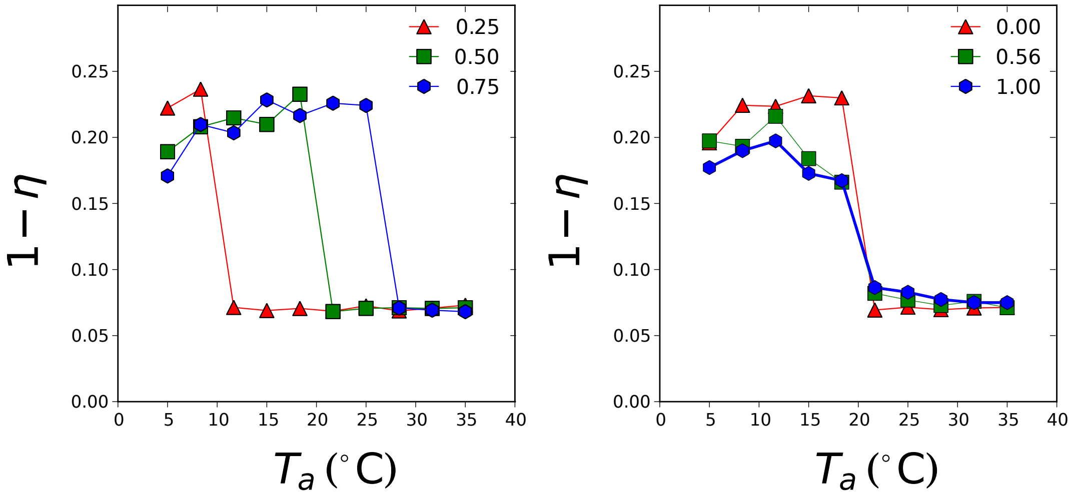

Figure 3.3: **A phase transition emerges in simulations of the endothermic individuals model.** Simulation of the experiment of (Canals and Bozinovic, 2011), in which each pup simply turns in the direction of heat sources. The ordinate axis represents the mean proportion of pups' body surfaces that are in contact with another pup, $(1-\eta)$ averaged across pups and time-steps within a simulation and across 10 repeated experiments with random initial conditions. *Left*: The critical temperature of the phase transition can be increased by arbitrarily scaling the temperature registered at each point of the pup body surface to be 0.25, 0.5, and 0.75 of the ambient temperature (legend denotes scaling factor). *Right*: With the temperature scaling set to 0.5, the slope of the phase transition can be smoothed to better match the form of the experimental data presented in Figure 1, by adding normally distributed noise to the temperature sensed at each point on the pup body, with variances 0.0, 0.56 and 1°C (indicated by the legend) increasing the smoothness of the transition. Tuning the endothermic model in this way can give a reasonable match to the experimental data but it generates qualitatively poor huddling, as explained in the main text.

3.2.3 Ectothermic Individuals

In the endothermic model, all pups were assumed to be capable of maintaining a constant body temperature, $T_b = 37°\text{C}$. We observed that a single pre-formed large macro-huddle fractured into small micro-huddles. Hence we interpret micro-huddles as stable local maxima and macro-huddling as an unstable global maximum solution to the collective thermotaxic dynamics of the system. We reasoned that the global solution could be stabilised if individuals could be attracted towards heat propagating from more distal pups via a chain of intermediaries. Supporting the propagation of heat along a chain of contacting pups requires the body temperature of each pup to be capable of changing over time.

In contrast to the assumption of the endothermic model, and in contrast to the thermoregulatory capacity of mature rodents, juveniles have only a weak capacity to regulate their body temperature, to the extent that pups are often described as ectothermic (Alberts, 2007). Hence, in what we call the ectothermic model, we allow the body temperature T_b^i of each pup (indexed by i) to change over time. The following equation captures three key dynamics that we assume govern the change of the body temperature of the individual pup ($\frac{dT_b^i}{dt}$); i) heat decay, ii) heat exchange, and iii) heat generation:

$$\frac{dT_b^i}{dt} = -k_1\eta_i(T_b^i - T_a) - k_2(1-\eta_i)(T_b^i - T_c^i) + G \tag{3.1}$$

The first term on the right of Equation 3.1 represents our assumption that pups continually lose heat to the environment, mediated by factors such as the amount of insulative fur and subcutaneous fat, which we collect together in the thermal conductance constant k_1, and which we scale by the proportion η of thermometers that are exposed. The second term describes how heat is exchanged between pups that are in contact, mediated by a second thermal conductance constant k_2. T_c^i is the contact-mediated surface temperature; i.e., the sum temperature registered by the thermometers of pup i that are in contact with a littermate (see *Models* for a precise definition). The final term of Equation 3.1 represents the generation of a small, constant rate of heat by each pup via internal physiological processes, namely via the brown adipose tissue (BAT) thermogenesis system ((Sokoloff and Blumberg, 2001); see *Discussion*). Note that according to this model, for an isolated pup at thermal equilibrium (i.e., $\eta = 1$, and $\frac{dT_b^i}{dt} = 0$), Equation 3.1 yields the *endothermic* relation often used to describe the metabolic rate of an individual, $G = k_1\eta(T_b - T_a)$ ((McNab, 1980); see also (Canals et al., 1997, 1998; Canals and Bozinovic, 2011)).

We simulated the model as before, now iterating the ectothermic equation (Equation 3.1) at each time-step, and we found two important differences in the group-level behaviour.

First, we were able to confirm that the new thermodynamics are sufficient to perturb the system into reliably maintaining a macro-huddle. This observation was supported by high values of our huddling metric; around 0.6 in the majority of simulations. We observed that the emergent macro-huddles maintain a core of warmer pups surrounded by a periphery of cooler pups, which is consistent with the experimental observations of (Gilbert et al., 2012), for example. Moreover, we observed that individual pups tend to move constantly with respect to the center of mass of the huddle. These group-level dynamics suggest that a continual ‘pup flow’ as described by (Alberts, 1978b) might emerge from a model of this form, although we delay a formal analysis until the penultimate results section.

The second important difference is that in the ectothermic model the phase transition into huddling at low ambient temperatures ceases. Instead, stable macro-huddles emerge and persist for the duration of the majority of simulations, irrespective of the ambient temperature. The loss of the phase transition in the ectothermic model can be explained in terms of the thermogenesis term $G > 0$ in Equation 3.1, which ensures that the temperature of the body is always at least that of the environment in the steady state ($T_b \geq T_a + \frac{G}{k_1 \eta}$), and which therefore determines that our simple thermotaxic pups will always orient towards another pup.

3.2.4 Homeothermotaxic Individuals

To achieve a system capable of maintaining stable global huddles that dissipate at high ambient temperatures, we require a model in which each pup is able to display a preference for higher contact-meditated temperatures at cooler ambient temperatures, and for lower contact-mediated temperatures at warmer ambient temperatures. To this end, we note that when isolated on a thermocline (i.e., an approximately linear temperature gradient) rat pups will not climb the temperature gradient indefinitely towards the highest temperature, an implicit prediction of our ectothermic model, but instead they will move through the temperature gradient to a point that allows them to maintain a body temperature of 37°C with minimal metabolic cost (Malik and Fewell, 2003). Importantly, isolated pups show an ability to navigate both up and down a temperature gradient as required to achieve thermal homeostasis (Farrell and Alberts, 2007).

Naively, we can introduce a preferred temperature T_p into the model simply by changing the linear mapping of temperatures sensed at the body surface into motor drives (see *Models*) to instead be a non-monotonic function, e.g., a Gaussian, $e^{-\frac{(T-T_p)^2}{\sigma}}$, where $T = T_l + T_r$ is the sum of the temperature measured on the left and right of the body. Such a mapping would ensure that individuals display a temperature preference when isolated on a thermocline. However a model of this form cannot account for data showing that the temperature at which an individual pup will settle on a thermocline adapts to changes in its ability to generate heat. Farrell and Alberts (2007) pharmaceutically manipulated thermogenesis in seven-day old rat pups using norepinephrine and found that they will move to a position on a thermocline that compensates for the resulting physiological change; pups generating more heat will settle at a (proportionately) cooler location than controls to maintain a constant 37°C body temperature.

Thus we introduce into the model not an explicit preferred environmental temperature, but rather a drive to move so as to reduce the discrepancy between the actual body temperature and T_p as a target body temperature, i.e., by introducing a function of the form,

$$f(T) = (T_p - T_b)T. \tag{3.2}$$

We implement the assumption represented by Equation 3.2 by adding to the drive of the left and right 'motors' of each pup, the sum of the body temperatures of the contacting pup that is nearest to each contralateral thermometer, before squashing the result with a steep (effectively linear) sigmoid to ensure that all motor drives are positive (see *Models*). The result of this modification is that the orienting of each pup brings T_b towards T_p by a form of gradient descent that allows for the body temperature of the individual to achieve homeostasis. Consequently, simulated pups isolated on a thermocline will settle to a location that maintains the body temperature at T_p, so as to compensate for any variation in the rate of thermogenesis, G. We therefore refer to this as the homeothermotaxic individuals model.

When we subject the homeothermotaxic model to the experimental protocol of (Canals and Bozinovic, 2011) we observe that the phase transition reappears, and that macro-huddles emerge at low ambient temperatures. See Figure 3.4.

A key question that we have not yet addressed is to what extent can the emergent aggregation patterns benefit the individuals that collectively give rise to them? We therefore examined the average body temperature of the litter as a function of the ambient temperature, and identified three distinct regions that correspond with three distinct regions of the phase transition. As expected, for simulations at high ambient temperatures where pups tend to dissipate, and thus tend not to be in contact, the average body temperature of the litter varies precisely with the ambient temperature. However, for simulations at low ambient temperatures the

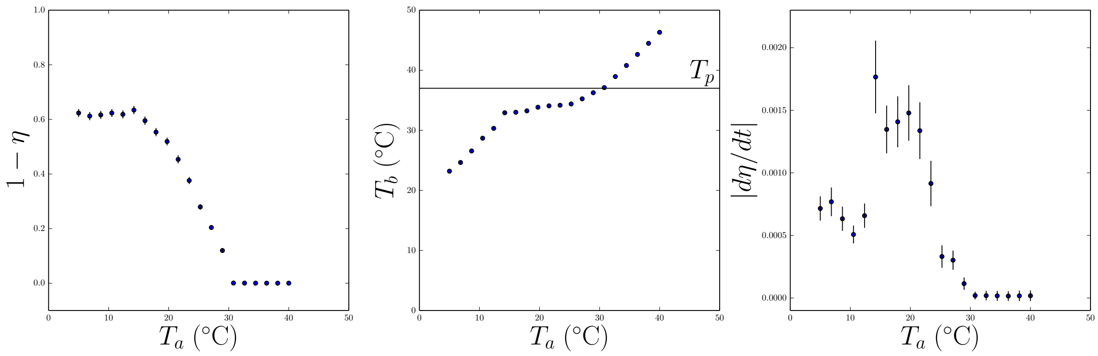

FIGURE 3.4: **Thermoregulatory huddling in the homeothermotaxic individuals model.** *Left*: The phase transition returns in the collective huddling behaviour $(1-\eta)$ of the full model. Here individual pups are ectothermic, generating their own heat which is dynamically exchanged between individuals and decays towards the ambient temperature T_a, and orienting responses direct pups towards heat sources with which they make contact that bring them closer to their preferred 37°C body temperature T_b. *Center*: The average body temperature is shown as a function of the ambient temperature, which reveals that for a range of temperatures the huddle is able to adaptively maintain a stable 37°C temperature (shown as a solid line). Hence, huddling in the model is thermoregulatory, enabling endothermic dynamics to emerge from local interactions within a group of ectothermic individuals. *Right*: Pup flow was quantified as the time-averaged absolute time-derivative of the exposed surface areas of the pups. The rate of pup flow was small at low and high ambient temperatures, but was large during the sloping region of the phase transition, where pups were observed to continually exchange positions between the center and periphery of macro-huddles or between micro-huddles. Data are averages of ten randomly seeded simulations in which the rate of thermogenesis $G = 6.32$ was chosen to give an approximate fit between the left panel and the data presented in Figure 1. Error bars show standard error, calculated for 120 observations (ten simulations, each with twelve pups).

average temperature of the litter becomes much higher than the ambient temperature, as individuals cluster to maintain the heat that they collectively generate. Hence, huddling at low ambient temperatures increases the average temperature of the litter, and confirms a group-level advantage to huddling at low ambient temperatures. Interestingly, for a range of ambient temperatures that corresponds to the slope of the huddling phase transition, the average body temperature remains approximately constant, which suggests that beyond simply warming the litter when it is cold, huddling helps to regulate body temperatures over a range of intermediate ambient temperatures.

3.2.5 The Emergence of Pup Flow

We observed in our simulations of the homeothermotaxic model that for a range of ambient temperatures, around the critical temperature for the phase transition, pups appeared to continually exchange positions with respect to the centre of the macro-huddle. Pups in the center of the huddle will remain there until their body temperature rises above the preferred temperature, at which point they will move to the periphery. Similar dynamics observed in real litters at low ambient temperatures have been termed ‘pup flow’ by (Alberts, 1978b).

We objectively quantify the degree of pup flow in terms of the average absolute value of the time derivative of the proportion of exposed surface area, i.e., $\frac{1}{n_t-1}\sum_{t=2}^{n_t}|\eta(t)-\eta(t-1)|$ for n_t simulation time-steps. This metric reflects the overall rate at which pups exchange positions with respect to the aggregations that they belong to. As a pup changes from being at the center of the huddle to being at the periphery it will contribute a positive time-difference in exposure, and when a pup changes from periphery to center it will contribute a negative difference, hence the absolute value indicates the total rate of flow. Pups that remain in the center or periphery of a huddle, or remain isolated, will have a constant degree of exposure and hence will not increase the pup flow metric.

Figure 3.4 (right panel) shows how the pup flow varies across a range of ambient temperatures. Like the corresponding plots of huddling and average body temperature in Figure 3.4, pup flow varies in three distinct regions. At low ambient temperatures, when we observe that macro-huddles tend to be maintained, the mean absolute time derivative of η remains at around 6.5×10^{-4}, reflecting a small but constant change in the configuration of the macro-huddle as it swells and contorts under the movement of the litter. As the ambient temperature is raised, and the slope of the huddling phase transition begins, there is a sharp rise in flow peaking at around $T_a = 16°\text{C}$ where we observe that pups comprising a macro-huddle will constantly flow between the center and periphery. Based on observing the aggregation patterns as they unfold we identify the group dynamics in this initial peak to be qualitatively similar to the pup flow characterised by (Alberts, 1978b). Simulations at higher ambient temperatures yield a reduction in pup flow, and here we observe that the flow is not maintained in a macro-huddle but instead reflects the exchange of pups between nearby micro-huddles. As the ambient temperature is raised further and the pups start to disperse, the peak in flow drops rapidly, approaching a zero baseline for $T_a > 30°\text{C}$ where all pups tend to remain isolated.

3.2.6 The Huddle as a Single Organism

We have seen that the homeothermotaxic individuals model allows the configuration of the group to adapt to temperature changes in the environment, such that at lower ambient temperatures a lower overall exposed surface area enables the group to conserve the heat generated by each pup, leading some authors to think of the huddle as a single organism (e.g., (Alberts, 1978a)). We therefore ask; if the group behaves as a single entity, optimising its overall exposed surface area, how would its dynamics compare to those of the full agent-based self-organising system? We answer analytically, by adapting our description of the individual into a description of an entire litter, as a single organism capable of modifying its exposed surface area. To this end we first remove the heat exchange term from Equation 3.1. Then to highlight the change in interpretation from an individual-level description to a group-level description we substitute the individual exposed surface area η from Equation 3.1 with a similar parameter A representing the overall exposed surface area of the huddle. As we are interested in the settled temperature of the huddle we define $0 = k_1 A(T_a - T_b) + G$, and to represent the assumption that the huddle is able to maintain a preferred temperature, we set $T_b = T_p$. The result can be rearranged to determine how the surface area of the huddle should adapt so as to maintain thermal homeostasis: $A = \frac{G}{k_1(T_p - T_a)}$. Finally we obtain $A_{\text{min}} = 0.36$ and $A_{\text{max}} = 1.0$ as the minimum and maximum values measured over all agent-based simulations with the homeothermotaxic model, and impose these same limits on the exposed surface area of our huddle:

$$A(T_a) = \begin{cases} A_{\min} & T_a \leq T_p - \frac{G}{k_1 A_{\min}} \\ A_{\max} & T_a \geq T_p - \frac{G}{k_1 A_{\max}} \\ \frac{G}{k_1(T_p - T_a)} & \text{else} \end{cases} \tag{3.3}$$

For a direct comparison with the behaviour of the full agent-based model we define the huddling metric as $1-A(T_a)$. By the same logic we can derive a prediction from the mathematical description of the huddle for how the mean body temperature B should vary with the ambient temperature:

$$B(T_a) = \begin{cases} T_a + \frac{G}{k_1 A_{\min}} & T_a \leq T_p - \frac{G}{k_1 A_{\min}} \\ T_a + \frac{G}{k_1 A_{\max}} & T_a \geq T_p - \frac{G}{k_1 A_{\max}} \\ T_p & \text{else} \end{cases} \tag{3.4}$$

Figure 3.5 shows that the behaviour of the huddle, when considered as a single organism that adapts its exposed surface area to changes in the ambient temperature, is remarkably similar to that predicted by the agent-based (homeothermotaxic) model, with a notable exception when thermogenesis is absent. When $G = 0$ all agent-based simulations result in a dispersion of pups, irrespective of the ambient temperature, whereas the huddle model predicts that strong huddling should persist until the environment is warmer than the target 37°C body temperature. In this case it is interesting that both the simulation and analytical models predict a linear relationship between the ambient and body temperatures, neither fully able to achieve thermal homeostasis, suggesting that huddling and non-huddling are to be considered equally valid thermoregulatory solutions in the absence of thermogenesis. We will return to this point in the *Discussion*.

Otherwise, a strong agreement between the results of the agent-based model and the model of group-level adaptation motivates an interpretation of the agent-based model as a unitary system that uses collective thermotaxis to adaptively control its overall exposed surface area in order to regulate its temperature. Hence these results support a view of the huddle as the collective expression of thermotaxis amongst individuals, from which a huddle emerges with a thermoregulatory capability superior to that of the individual.

We can see from the group-level model (Equation 3.4) that the region in which huddling behaviours keep body temperatures constant, which corresponds to the slope of the huddling phase transition and the plateau in Figure 3.5, extends across a range of ambient temperatures $\Delta T_a = \frac{G}{k_1}\left(\frac{1}{A_{\text{min}}} - \frac{1}{A_{\text{max}}}\right)$, that is centred on $T_a = T_p - \frac{G}{2k_1}\left(\frac{1}{A_{\text{min}}} + \frac{1}{A_{\text{max}}}\right)$. See the annotated sketch in Figure 3.6 for an illustration. Hence the central testable prediction of our model is that either pharmaceutically increasing thermogenesis G or insulating pups to reduce the thermal decay k_1 will increase the set point and the range of temperatures over which body temperatures will be regulated via huddling behaviour. Failure to confirm these two hypotheses would falsify the theory represented by the model, that adaptive thermoregulatory huddling self-organises from simple local homeothermotaxic interactions between individuals.

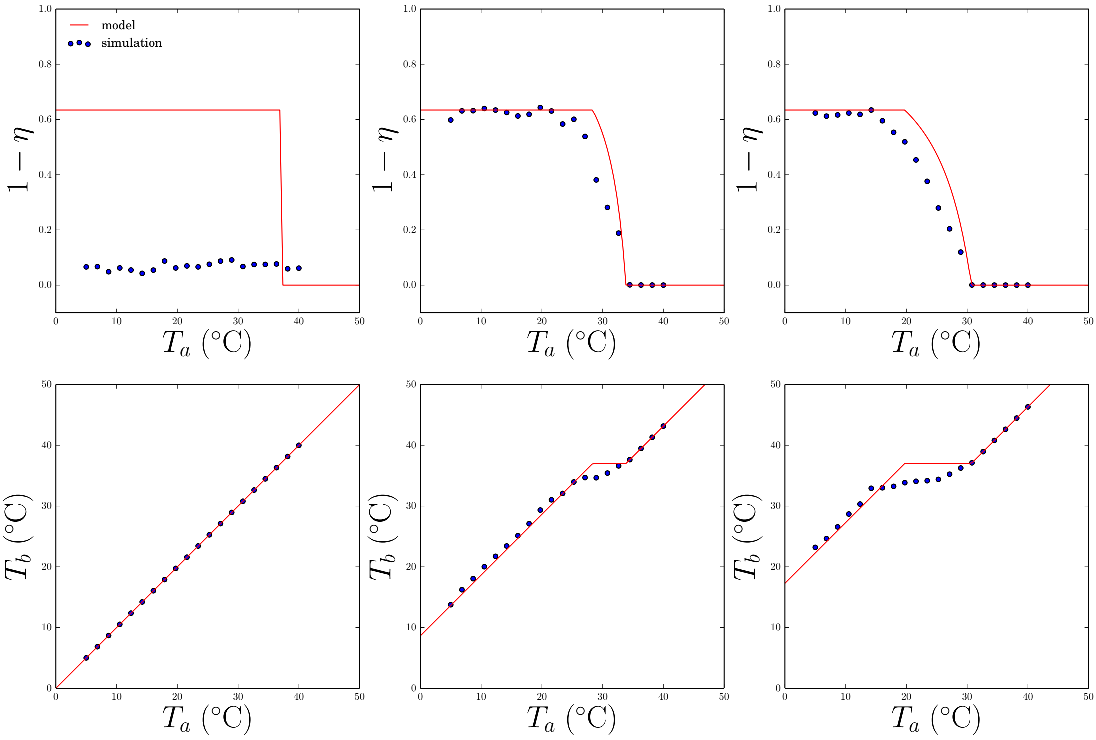

FIGURE 3.5: **The huddle as a single entity.** The homeothermotaxic model was simulated for a range of rates of thermogenesis G. Plots of huddling are shown in the top row and corresponding plots of the average body temperature are shown in the bottom row. Increasing G smooths the huddling phase transition and increases the critical ambient temperature at which the transition occurs. The critical region of the phase transition corresponds to the range of ambient temperatures over which the average temperature of the litter is maintained at the preferred 37°C. We found a close agreement between the simulation data (filled circles) and that predicted by an analytical model (solid lines) that we derived by considering the huddle as a single organism with thermodynamics based on our ectothermic individuals model, with the additional capacity to adapt the overall exposed surface area of the group to maintain thermal homeostasis. The simulation and model data agree closely for all conditions, except where $G = 0$, where the model incorrectly predicts a sharp phase transition at the preferred temperature.

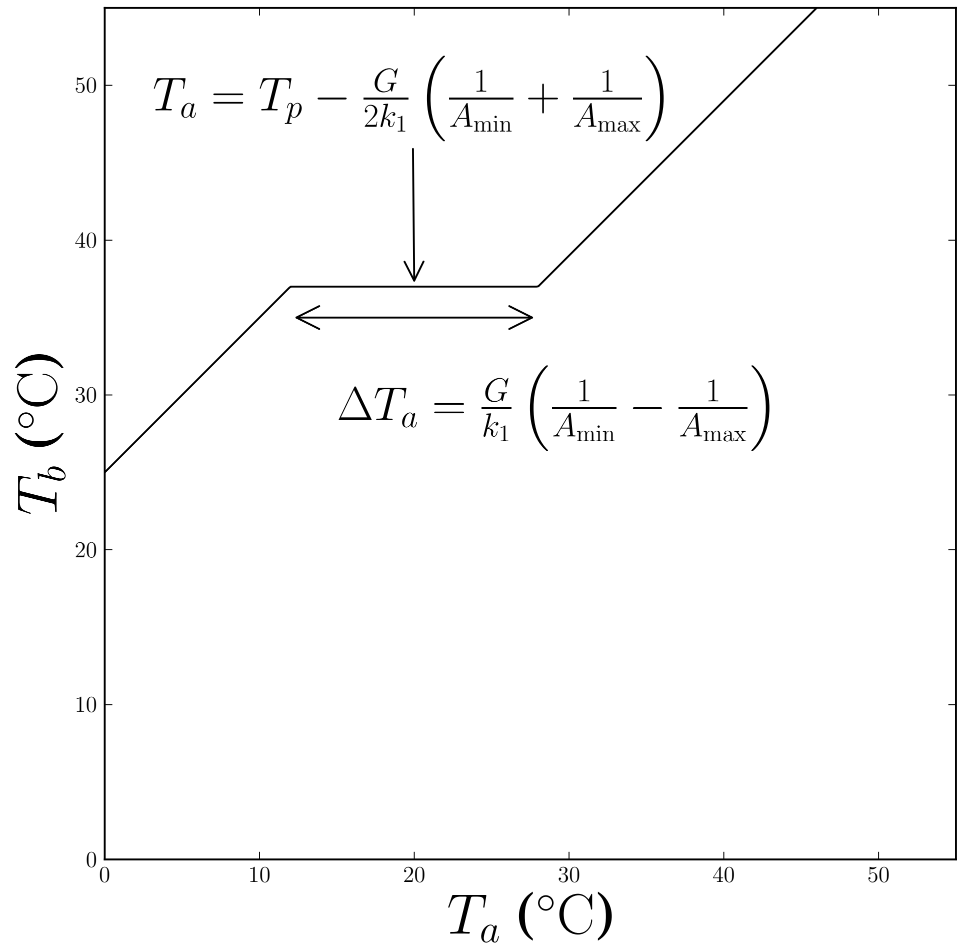

FIGURE 3.6: **Testable predictions of the model.** By approximating the huddle as a single organism, we are able to derive the following prediction from our theory of thermoregulatory huddling as the self-organising product of simple local interactions between pups. Accordingly the key parameter is the term $\frac{G}{k_1}$, where G is the rate of thermogenesis and k_1 is the thermal conductance of each pup. The model predicts that either increasing thermogenesis (e.g., by pharmaceutically enhancing the action of brown adipose tissue) or decreasing the thermal conductance (e.g., by insulating each pup) will increase both the critical ambient temperature (single-headed arrow) and the range of ambient temperatures (double-headed arrow) over which the temperature of the huddle is stable. Confirming this prediction in future experiments would provide strong support for our description of the huddle as a self-organising system.

3.3 Discussion

We have presented an agent-based model of thermoregulatory huddling behaviours in juvenile rodents as a self-organising system, according to which individuals behave like the simple vehicles of Braitenberg's thought experiments (Braitenberg, 1984), orienting in the direction of heat sources. Our model adds support for the theory that both the aggregate patterns of group contact and the thermoregulatory properties of huddling can emerge via self-organisation from simple local interactions between animals.

According to the model, there are two requirements for the emergence of thermoregulatory huddling. First, the body heat of each pup needs to be dynamic, such that it continually decays to the ambient temperature, is exchanged with contacting pups, and is generated by each littermate. Second, each individual should orient towards sources of heat more similar to its preferred temperature than its current temperature. When these two mechanisms are in place, a sufficiently low ambient temperature will naturally trigger the emergence of an aggregation pattern. We identify this collective behaviour as thermoregulatory huddling on the grounds that it adaptively maintains the body temperatures of all individuals and produces a phase transition under experimental manipulation of the ambient temperature, and such that pups continually flow from the cool periphery to the warm center. These phenomena have been observed in real litters of rodents. The key feature of the model, that distinguishes it from other models of thermoregulatory huddling, is that these collective behaviours emerge from only local interactions between individual animals, in the absence of a global supervisor that accesses information about the state of multiple animals. We therefore interpret the results as evidence that thermoregulatory huddling in young rodents is the product of self-organisation.

Our model represents an extreme version of this theory, where thermo-tactile information is exchanged only when pups make contact. Hence the model serves as an existence-proof for the plausibility of the hypothesis that the known thermoregulatory properties of the huddle emerge via self-organisation, in addition to the self-organisation of aggregate patterns of group contact established by the model of (Schank and Alberts, 1997). We presented our model as a progression through a series of refinements to the underlying assumption that pups orient towards heat sources (thermotaxis), with the addition of heat generation, decay, and exchange accounting for the emergence of large stable huddles, and with the decay of individuals' heat towards a target temperature accounting for the continuous pup flow (Figures 3.4 and 3.5).

According to the model, at low ambient temperatures agents orient towards littermates, which increases contacts and thus increases the exchange of heat between littermates. In simulations where body temperatures are held constant at 37°C this leads to weak huddling, sustaining only relatively small aggregates of $N \leq 4$ pups. When the ambient temperature increases, the behaviour of the individuals effectively switches, and the same underlying mechanism instead causes littermates to orient away from contacts, causing the huddle to dissipate, and thus accounting for the phase transition measured by Canals et al. (Canals and Bozinovic, 2011).

The addition of body heat decay stabilises the dynamics and thus enables a much larger huddle of $N > 6$ pups to be maintained. In larger huddles, pups closer to the centre have less exposed surface area than those at the periphery, which leads to a more dynamic exchange of positions. During strong huddling we observe the relative positions of the littermates to be fluid, with individuals cycling between the periphery and the center. In contrast, during weak huddling, we noted that while the distance of each individual from the center of the huddle remained fairly constant, there was a tendency for the overall center of mass of the huddle to drift and for its shape to skew.

Although our simulations show how the huddle, once formed, can be maintained by local thermotaxic interactions, it is important to note that we essentially pre-formed macro-huddles at the beginning of each simulation to avoid the appearance of locally stable micro-huddles, and that this may be considered to be a crude form of the global supervisory mechanism that we have claimed that the model does not require. When agents instead begin randomly distributed across the entire arena, it becomes increasingly unlikely that a single huddle will emerge (data not shown). The endothermic model may be correct in predicting that micro-huddles are a more stable solution than the macro-huddle, which are unlikely to reform once the pups are dispersed, particularly in a large arena and in the absence of the dam who is otherwise known to herd isolated pups back towards to the huddle (Grota and Ader, 1969; Adels and Leon, 1986). An extension to the model that could increase the tendency for macro-huddles to reform once dispersed could allow pups to respond to thermotactile cues sensed more distally, perhaps by sensing a temperature gradient radiating from the position of each littermate. However we note that for the experiment of (Canals and Bozinovic, 2011), which first quantified the phase transition and first inspired our modelling approach, the arena was carefully ventilated so as to precisely control the ambient temperature and thus to minimise heat diffusion. We might similarly appeal to alternative forms of distal communication between pups, such as olfactory sensing or vision, however during early postnatal development pups are known not to respond to such cues (Alberts, 1978a). Note that adding noise to the movement of each pup might help overcome micro-huddling (simulation data not shown), but that we chose to avoid adding unnecessary non-linearities into the system, to avoid creating a smooth phase transition by arbitraily smoothing an underlying step-function (as demonstrated in Figure 3.3).

Our model predicts that increasing thermogenesis will increase the critical temperature for the emergence of huddling (see Figure 3.6). In line with this prediction, recent theories suggest that rather than constituting a separate mechanism to huddling, thermogenesis is a necessary prerequisite for the emergence of thermoregulatory huddling. This is evidenced by data from experiments with Syrian golden hamsters, who do not huddle before brown adipose tissue (BAT) thermogenesis comes online at around postnatal day 14 (Sokoloff and Blumberg, 2002), and with rats who cease to huddle when BAT is pharmaceutically blocked (Blumberg, 1997). Furthermore, groups of rats comprising more BAT-disabled individuals lose their heat more rapidly (Sokoloff and Blumberg, 2001), and when non-huddling hamsters are introduced into rat litters they begin to exhibit huddling behaviours

(Sokoloff and Blumberg, 2002). Hence individual thermogenesis appears to be an essential ingredient for thermoregulatory huddling to emerge. Consistent with this view, setting the thermogenesis term G to 0 in the model disables huddling altogether and causes body temperatures to decay rapidly to the ambient temperature. Figure 3.7 shows the results of varying G in the homeothermotaxic individuals model, and reveals how the model can account for each of these data points.

The model thus accounts for the integral role of thermogenesis in huddling, because a key requirement of the model is that each pup acts as a thermogenic heat source to direct the thermotaxic movement of its littermates. The model accounts for the role of thermogenesis as a crucial source of heterogeneity amongst individual body temperatures that is required for temperature-dependent dynamic group behaviours to emerge. Hence, thermogenesis provides the energy source and fulfils the symmetry-breaking requirements for the emergence of huddling. Our modelling results therefore suggest that thermogenesis does not cause huddling *per se*, but rather allows huddling to reveal itself in groups of individuals that orient towards preferred temperatures. We can thus describe the emergence of huddling as the natural expression of collective thermotaxis by thermogenic individuals.

3.4 Models

At a given simulation time the components that effect the body temperature of pup i are determined as follows. We index the littermates of pup i by $j \neq i$, and

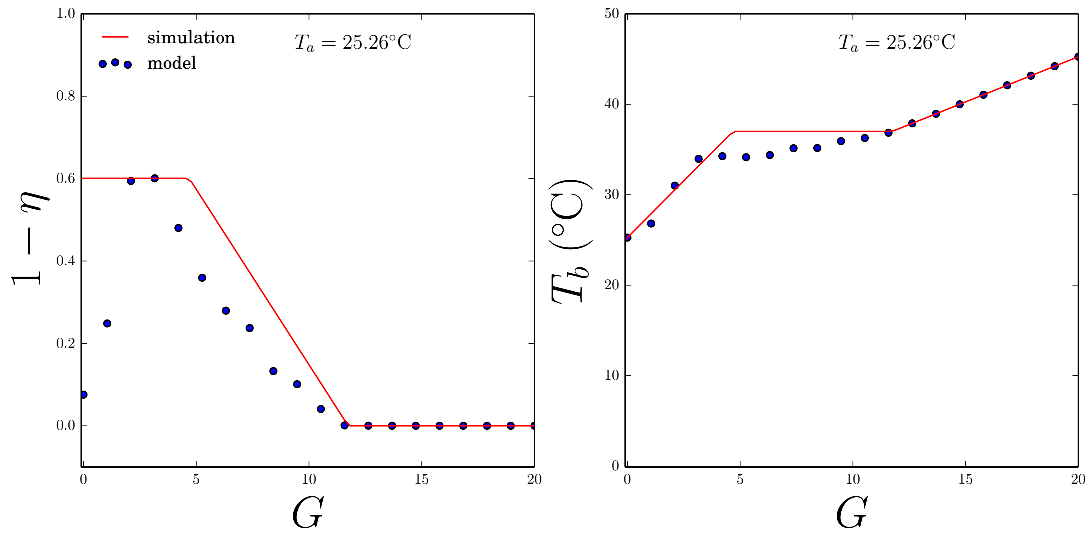

FIGURE 3.7: **The role of thermogenesis.** Intuitively, an animal that is able to produce more heat internally (e.g. through BAT-thermogenesis) could tolerate having a greater exposed surface area. Experiments have shown that when BAT-thermogenesis is pharmaceutically increased, rats will adapt to balance behavioural thermoregulation with the altered internal state(Farrell and Alberts, 2007). However, it has also been shown that animals without BAT-thermogenesis (Syrian golden hamsters (Sokoloff and Blumberg, 2002) and rats with BAT-thermogenesis pharmaceutically inhibited (Sokoloff and Blumberg, 2001)) will not display huddling behaviour. We tested the effects of varying the thermogenesis term G in the model and found the same pattern. *Left:* At very low values of G contacts cannot be reliably maintained and huddling ceases (at $T_a = 0$). As G increases, body temperatures become larger than the ambient temperature and macro huddling occurs (rising phase). As G further increases huddling is maximum within geometrical constraints (plateau phase). Increasing G further reduces the degree of huddling such that the collective behaviour maintains the group at their preferred body temperature T_p (falling phase). *Right:* Self-organised huddling is able to maintain the average body temperature of the group across a wide range of thermogenic rates.

we index $n = 1000$ thermometers tiling the circumference of its circular body by k. Thermometers are located at coordinates $(x_{ik} = x_i + r\cos\left(\frac{2\pi k}{n} + \theta_i\right),\ y_{ik} = y_i + r\sin\left(\frac{2\pi k}{n} + \theta_i\right))$, where r is the radius of all pups. To determine the heat transfered via surface contacts between pups we first register at each thermometer

$$\alpha_{jk} = \begin{cases} 1, & d_j^2 \leq 4r^2 \wedge \left[k\frac{2\pi}{n} + \theta_i - \phi_j\right] < \cos^{-1}\frac{d_j}{2r} \\ 0, & \text{else} \end{cases}, \tag{3.5}$$

where $\phi_j = \text{arctan2}(y_j - y_i, x_j - x_i)$ and $d_j^2 = (x_j - x_i)^2 + (y_j - y_i)^2$ give the angle and distance of pup j from pup i, and $[.] = \pi - |\pi - |.||$ denotes absolute distance around the circle. Using Equation 5 we can determine whether or not a thermometer is exposed $\epsilon_k = \prod_j(1 - \alpha_{jk})$, and thus define the proportion of the surface area of the pup that is exposed to be $\eta = \frac{1}{n}\sum_k \epsilon_k$. The temperature at a thermometer in contact with other pups is $\chi_k = \alpha_{jk}T_b^{j'}$, where $j' = \arg\min_j((x_{ik} - x_j)^2 + (y_{ik} - y_j)^2)$ indexes the littermate that is closest to thermometer k, and we thus define the contact-mediated surface temperature to be $T_c = \frac{1-\eta}{n}\sum_k \chi_k$. The terms η and T_c are used for the body temperature update equation, reproduced here for completeness,

$$\frac{dT_b^i}{dt} = -k_1\eta_i(T_b^i - T_a) - k_2(1 - \eta_i)(T_b^i - T_c^i) + G, \tag{3.6}$$

where k_1 and k_2 are thermal conductance constants for exposed and contact regions respectively, and G is the rate of thermogenesis.

The kinematics of each pup is driven by the difference between the average surface temperature on its left and right. The temperature at each thermometer is $\tau_k = T_a\epsilon_k + \chi_k$, and for a pup with orientation θ the surface temperature on its left and right can be defined as,

$$T_l = \frac{1}{2n} \sum_{L=0}^{n/2} \tau_L, \quad T_r = \frac{1}{2n} \sum_{R=0}^{n/2} \tau_R. \tag{3.7}$$

For the homeothermotaxic model only we redefine T_l as $\left(1 + e^{-\frac{1}{\sigma}\left(T_p - T_b^i\right)T_l}\right)^{-1}$ and likewise squash T_r using an equivalent sigmoid.

Thermotaxic orienting is based on the difference between T_l and T_r. These sensor values determine motor speeds ($M_l = \frac{T_r}{T_l+T_r}$ and $M_r = \frac{T_l}{T_l+T_r}$), which in turn are used to determine the rate of change in orientation. On each timestep, each pup is rotated at velocity v_1 by,

$$\frac{d\theta_i}{dt} = v_1 \tan^{-1}\left(\frac{1}{M_l^i - M_r^i}\right), \tag{3.8}$$

and translated at velocity v_2 by,

$$\frac{d\mathbf{x}_i}{dt} = v_2 \begin{pmatrix} \cos\theta_i \\ \\ \sin\theta_i \end{pmatrix} + \beta_i \frac{\mathbf{x}_i}{|\mathbf{x}_i|} + \sum_{j \forall d_{ij}^2 \leq 4r^2} \left(r - \frac{d_{ij}}{2}\right) \frac{\mathbf{x}_i - \mathbf{x}_j}{|\mathbf{x}_i - \mathbf{x}_j|}, \tag{3.9}$$

where a circular arena boundary of radius $r_{\text{arena}} = 10r$ centered at the origin is enforced by defining $\beta_i = (r_{\text{arena}} - |\mathbf{x}_i| - r)$ if $|\mathbf{x}_i| + r \geq r_{\text{arena}}$, else $\beta_i = 0$.

Pups are initialised at uniform random locations in a circle of radius r, with random orientations θ, and an initial $T_b = T_p$ is allowed to settle for 100 timesteps before kinematics are enabled. Unless otherwise stated, the following parameters were used for all simulations reported: $k_1 = \frac{1}{2\pi r}$, $k_2 = \frac{2.5}{2\pi r}$, $v_1 = 200$, $v_2 = 0.3$, $G = 6.32$, $T_{\text{p}} = 37°\text{C}$, $\sigma = 100$, and $dt = 0.05$.

Chapter 4

How Self-Organisation can Guide Evolution

The work presented in this chapter appears, with minor modifications, as:

Glancy, J., Stone, J. V, & Wilson, S. P. (2016). How self-organization can guide evolution. Royal Society Open Science.

4.1 Introduction

In a self-organising system a complex group behaviour emerges from local interactions between individuals behaving without plan or instruction (see Camazine et al., 2001). Huddling behaviours displayed by mice (Canals and Bozinovic, 2011), rats (Schank and Alberts, 1997), and other social rodents (Sanchez et al., 2015), as well as penguins (Waters et al., 2012) and social insects (Ocko and Mahadevan, 2014), have been described formally as examples of self-organisation.

Agent-based computer modelling has demonstrated how group aggregation patterns can emerge, based on simple interactions between individuals. One such model (Glancy et al., 2015, see Chapter 3) reveals how aggregation patterns observed in rodents exposed to different temperatures can emerge spontaneously when cold or warm ('homeothermotaxic') individuals simply turn towards warmer or colder littermates, respectively.

The aim of the present study is to investigate the effects that self-organising thermoregulatory huddling behaviours displayed by many mammals, birds, and other social animals might have on the evolution of genetic components of thermoregulation. Thermoregulatory huddling is a self-organising system with the advantage of being both simple to experimentally manipulate, and well-described by established theoretical and computational models.

Despite this, the potential for behavioural thermoregulation to affect evolution by reducing the metabolic costs of thermoregulation have been expressed only informally (e.g., see Haig, 2008). When evolutionary algorithms have been applied to formal models of huddling, they have concentrated on fitting parameters to empirical data rather than formalizing evolutionary theory (e.g., see Schank and Alberts, 2000).

Here, a simple evolutionary algorithm is challenged to minimize metabolic cost by evolving two model genes, which specify physiological and morphological components of thermoregulation, respectively. We show that evolution occurs only when within-lifetime adaptability is introduced, i.e., when huddling is possible. Specifically, the model predicts that increasing within-lifetime adaptability by increasing the number of available huddlers should accelerate the evolution of physiological thermoregulation. The main result of this paper is the counter-intuitive finding that cold-exposed animals which are allowed to huddle should evolve insulative fur and/or subcutaneous fat at a faster rate than animals reared in isolation.

We normally think of evolution by natural selection as a direct response to selection pressure. However, the model suggests that the evolution of thermal physiology may actually be improved when selection pressure on the growth of fat and fur is relaxed due to huddling.

4.2 Model

Thermoregulation is a complex emergent property of interactions between many factors affecting the metabolism of an organism. These can be broadly categorised as, i) environmental factors including the climate and temperature around an organism, ii) physiological factors regulating the capacity of the organism to generate heat, iii) morphological factors determining the rate at which heat is lost from the body to the environment, and, iv) behavioural factors by which an organism may relocate or adapt its exposed surface area to regulate heat loss. Given the importance of thermoregulation for all biological processes (Kleiber, 1961), and the energetic costs of metabolism (Brown et al., 2004), we should expect interactions between environment, physiology, morphology, and behaviour to play a central role in the evolution of species by natural selection (McNab, 1978).

In mammals, the amount of fat or fur impose physiological and morphological limits on heat generation and heat loss. The relationships between these factors have been well-characterised for endotherms, in particular via experiments with rodents such as rats and mice, from which we derive the majority of our modelling assumptions. Newton's law of cooling (Scholander et al., 1950a; McNab, 1974, 1980) (see also Heldmaier, 1975) can be used to derive an expression for metabolic rate M:

$$M = AC(T_b - T_a). \tag{4.1}$$

where T_b is the body temperature and T_a is the environment (or ambient) temperature; C is the whole body thermal conductance, which modulates the rate at which the body exchanges heat with the environment; and A is the proportion of the body surface area that is exposed to the ambient temperature. Equation 4.1 therefore formalizes the intuition that metabolic costs are greatest when a highly exposed body conducts heat rapidly to a cold environment.

The metabolic costs of prolonged cold exposure can be reduced by insulating the body to reduce the morphological factor C, or by moving or morphing the body to reduce A. Changes to both C and A can occur through several mechanisms (depending on the species and the environment) and on multiple timescales, as explained in the *Discussion* (see McNab and Brown (2002) for a comprehensive review). A simplifying assumption represented by the present model is that a change in A corresponds to an immediate behavioural change, whereas a change in C would occur predominantly on an inter-generational timescale. When the option is available, rodents are expected to respond to environmental change by adapting their behaviour rather than their physiology or morphology (Gordon, 2012).

In cold environments, huddling allows each huddler to exploit the heat generation of others, to increase T_a in its local microclimate, and to reduce A (Sealander, 1952; Alberts, 1978b; Canals et al., 1989; Alberts, 2007). Huddling allows an individual to reduce the proportion of its surface area that is exposed up to a limit that depends on the number n of aggregated animals. Derived from geometrical considerations, it has been found that A has a lower limit which varies with n, specifically,

$$n^{-\frac{1}{4}} \leq A \leq 1. \tag{4.2}$$

According to Equation 4.2, the proportion of the surface area that is exposed has an upper bound of 1 (i.e., when the entire body is exposed), and a lower bound of $n^{-\frac{1}{4}}$ (i.e., as the number of available huddlers n increases, the minimum exposed surface area that they can acheive, on average, by huddling together, decreases exponentially).

The degree to which increases in n can reduce the exposed surface area of the group varies depending on the geometry and morphology of the species. Estimates of the exponent $-\frac{1}{4}$ vary depending on the underlying geometrical assumptions about animal aggregation patterns (Canals and Bozinovic, 2011). In practice, an exponentially decaying function of n, such that metabolic savings asymptote for larger n, is supported by several investigations of aggregation in small mammals (Heldmaier (1975); Martin et al. (1980); Canals et al. (1989, 1997, 1998); see also Gilbert et al. (2010)).

In a self-organising model of rodent huddling (Glancy et al., 2015), the thermoregulatory capacity of simulated huddles was shown to be greater than that of the individuals, and self-organisation was found to yield adaptations of A in the average huddler consistent with a mathematical description of the huddle as a single organism able to thermoregulate by shifting its overall shape.

Accordingly, self-organising behavioural interactions allow the litter to adapt the average area $A(n)$ to extend the range of T_a over which T_b can be maintained at the preferred temperature, T_{pref}, while M and C remain constant within a generation. The geometrical constraints defined by Equation 4.2, combined with the ability of the huddle to adapt its surface area $A(n)$ by self-organisation according to the derivation of (Glancy et al., 2015), yields the following relation:

$$A(n) = \begin{cases} 1 & \text{if } 1 \leq A_{\text{pref}} \\ A_{\text{pref}} & \text{if } n^{-\frac{1}{4}} < A_{\text{pref}} < 1 \\ n^{-\frac{1}{4}} & \text{if } A_{\text{pref}} \leq n^{-\frac{1}{4}} \end{cases}, \tag{4.3}$$

where $A_{\text{pref}} = \frac{M}{C(T_{\text{pref}} - T_a)}$ is the exposed surface area required to maintain the body temperature at the preferred temperature.

The adaptable surface area defined by Equation 4.3 can be substituted back into Equation 4.1 to define the average body temperature for a litter of size n:

$$T_b(n) = \frac{M}{CA(n)} + T_a \tag{4.4}$$

This allows a simple fitness function to be defined,

$$F = \begin{cases} \dfrac{M_{\max} - M}{M_{\max}} & \text{if } T_b(n) = T_{\text{pref}} \\ 0 & \text{if } T_b(n) \neq T_{\text{pref}} \end{cases}, \tag{4.5}$$

where $M_{\max}$ sets an upper bound on the metabolic rate. Litters able to maintain the average body temperature at the preferred temperature have a fitness which decreases with metabolic rate, and litters unable to maintain the average body temperature at the preferred temperature have a fitness of zero. In summary, Equation 4.3 states how the size of the litter determines the extent to which the exposed surface area can be adapted by huddling, Equation 4.4 specifies the resulting body temperature, and Equation 4.5 incorporates the body temperature into the definition of a fitness function that promotes homeothermy and penalizes higher metabolic rates.

To investigate how the capacity for behavioural thermoregulation could affect selection of genes determining the limits of physiological and morphological thermoregulation, we can modify M and C using a simple evolutionary procedure.

This procedure is used to evolve a population comprising N litters, where each litter is represented as a pair of metabolic rate and thermal conductance values. For convenience, the population is maintained as N pairs of m and c values ranging 0 to 1, scaled to obtain $M = M_{\text{max}}m$ and $C = C_{\text{max}}c$ when Equation 4.5 is used to determine fitness (this allows a single parameter σ to specify comparable effects of mutation for both genes).

To make each child litter, two different parent litters (mum and dad) are chosen from the population at random with a probability proportional to their relative fitnesses. Each generation is populated by repeating the following process of recombination N times (hence each parent may seed multiple children). First, the metabolic rate of the child litter is chosen to fall randomly between bounds set by the two parent values:

$$m = r_1 m_{\text{mum}} + (1 - r_1) m_{\text{dad}}, \tag{4.6}$$

where r_1 is a random number from the uniform distribution $r_1 \in [0, 1]$. This value of m is then modified for mutated genes by setting $m = m + r_2$, where r_2 is a random number from a uniform distribution $r_2 \in [-\sigma, \sigma]$. The value of c for each child is determined in exactly the same way, from the same parents and with r_1 and r_2 generated anew, and the two genes are mutated (independently) with a fixed probability, set to $p = 0.1$ here.

The effect of mutation (for genes that are selected to mutate) was set to $\sigma = 0.1$, the ambient temperature was set to $T_a = 20$°C and the preferred temperature was set to $T_{\text{pref}} = 37°\text{C}$, the maximum metabolic rate was set to $M_{\text{max}} = 37$ kcal/day, the maximum thermal conductance was set to $C_{\text{max}} = 2$ kcal/day°C, and the population size was set to $N = 500$ litters. Note that the behaviour of the model is robust to changes in the value of T_a, for ambient temperatures below T_{pref}, and it is robust to variation of the population size. The value chosen for M_{max} represents the intuitive assumption that a mutation in metabolic rate which causes the body temperature to exceed T_{pref} (when fully exposed to ambient temperatures above 0°C) cannot be viable.

To help explain the behaviour of the model, it is useful to define the boundary conditions that separate litters with zero fitness from litters with non-zero fitness, as expressed in Equation 4.5. We can do this by substituting $T_b = T_{\text{pref}}$ into Equation 4.1;

$$M = (T_{\text{pref}} - T_a)CA(n). \tag{4.7}$$

In essence, this states that non-zero fitness is achievable when the genetically specified values of M and C allow $A(n)$ to be varied so as to keep the body temperature at T_{pref}.

Equation 4.7 effectively defines two boundaries, indicated in Figure 4.2. At one boundary, $A_{\text{pref}} \geq 1$, so $A(n) = 1$, and therefore $M = (T_{\text{pref}} - T_a)C$. At this boundary, the exposed surface area can increase no further because all pups in the litter are isolated, and any increase in ambient temperature will cause their body temperatures to exceed the preferred temperature.

At the other boundary, $A_{\text{pref}} \leq n^{-\frac{1}{4}}$, so $A(n) = n^{-\frac{1}{4}}$, and therefore $M = (T_{\text{pref}} - T_a)Cn^{-\frac{1}{4}}$. At this boundary, the exposed surface area can decrease no further because the litter is maximally huddled, and any further reduction in ambient temperature will cause the average body temperature to drop below the preferred temperature.

For the ‘no-huddling’ control condition, combinations of M and C that yield non-zero fitness are confined to the solution of Equation 4.7 when $n = 1$. To reveal the evolutionary dynamics it is therefore convenient to initialize populations with values of M and C such that some in the initial population have a chance of non-zero fitness. Populations of litters were thus initialized with uniformly distributed random values ranging $m \in [0.8 - \sigma/2, 0.8 + \sigma/2]$ and $c \in [0.8 - \sigma/2, 0.8 + \sigma/2]$.

4.3 Results

An evolutionary algorithm was used to test how natural selection for the morphological and physiological components of thermoregulation might be affected by a capacity for self-organising huddling behaviour to support within-lifetime adaptation to a cold environment. Populations of litters of various sizes were evolved under explicit pressure to, a) maintain the average body temperature of the litter at T_{pref} and, b) minimize the metabolic rate, and thus the metabolic cost of thermoregulation. The metabolic rate M and thermal conductance C were subjected to natural selection. Crucially, lower metabolic rates were explicitly associated with lower cost, but lower thermal conductances were not. Within each simulation, the litter size n was kept constant across litters, and the effects of increasing n were compared between simulations. Many randomly seeded populations through a full range of litter sizes were evolved for several thousand generations each, and the dynamics summarised next were observed to be highly robust.

Figure 4.1 shows how the average fitness in the population evolves over time for four example populations comprising litters of size $n = 1$, $n = 2$, $n = 4$, and $n = 8$, respectively. In the no-huddling control condition ($n = 1$), fitness did not increase over time. However, for litters able to adapt by huddling ($n > 1$), the population fitness increased steadily. Populations comprising larger litters evolved more quickly and reached higher asymptotic fitness.

To understand how self-organising thermoregulatory huddling can accelerate evolution, it is useful to study the trajectory of each population as it evolves through the two-dimensional (M, C) fitness landscape. Each panel in Figure 4.2 shows the trajectory of a single population, with the initial and final generations connected by a blue line depicting the change in the population average over time. Note that in each condition, including the $n = 1$ control, the distribution of the final population in the fitness landscape tends from an initial square shape to a cross shape, simply because the probability p^2 of both genes mutating in a given child litter is less than the probability $2(p - p^2)$ that only one gene mutates. Otherwise, any differences between the initial and final generations in the control condition merely reflect the random walk of the population through the fitness landscape.

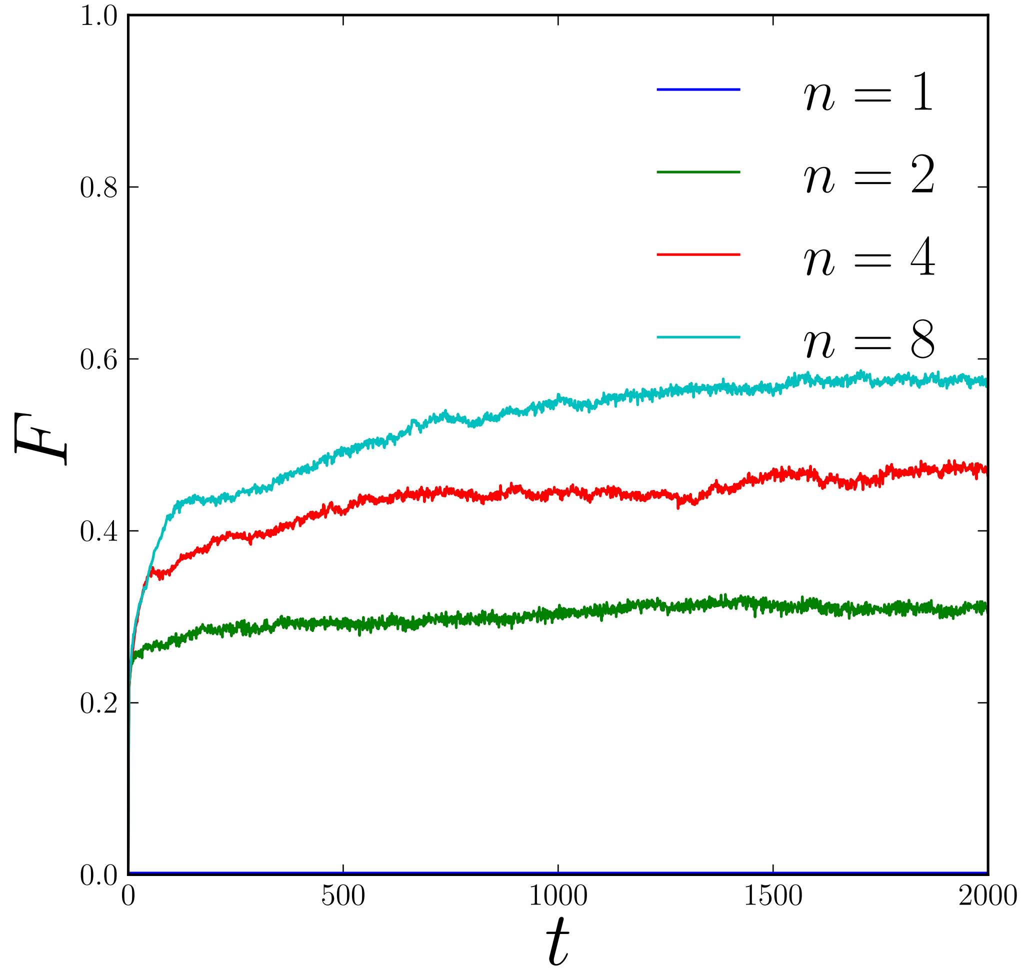

Figure 4.1: **Behavioural thermoregulation accelerates the evolution of physiological thermoregulation.** Populations of litters, each specified genetically as a combination of a metabolic rate and a thermal conductance, were evolved to minimise metabolic costs while maintaining a stable body temperature. Each line shows how thermoregulation evolves in populations comprising litters of a given size n. The average fitness F of the population is plotted against time t (in generations). In the no-huddling control condition ($n = 1$), fitness does not increase. However, for litters that can adapt to the environment by huddling ($n > 1$), fitness increases over time. The model predicts that as the capacity for adaptation by self-organising huddling increases (i.e., as litter size n increases) so too will the rate of evolution of genes specifying the physiological and morphological components of thermoregulation. See Figure 4.2 for a mechanistic account of these effects.

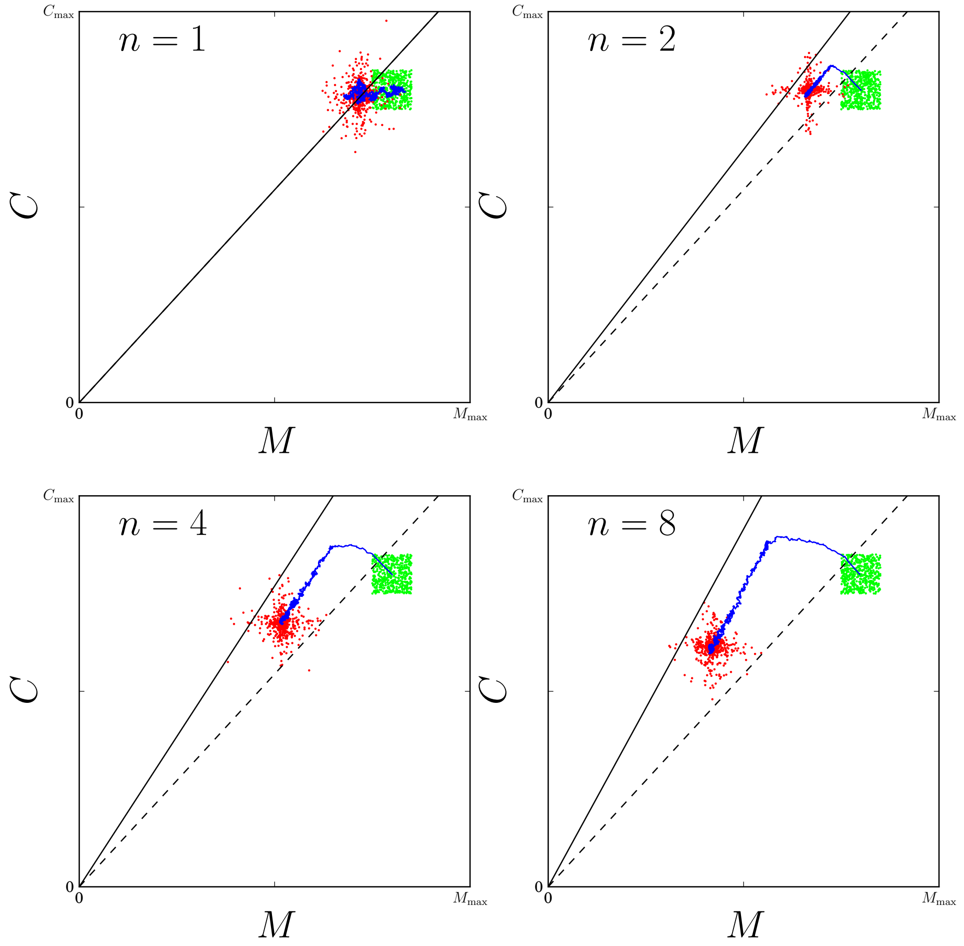

FIGURE 4.2: **Evolution of thermoregulation in the fitness landscape.** Results from the simulations reported in Figure 4.1 are shown. Each panel depicts the evolution of thermoregulation in a population comprising litters of a given size, n. Solid and dashed straight lines indicate the lower and upper boundaries of a 'zone of increased fitness', within which the litter is able to maintain the average body temperature at a preferred temperature by within-lifetime (behavioural) thermoregulation, i.e., by huddling. The initial population is shown as a square-shaped cluster of green dots, the trajectory of the population average is shown as a continuous blue line, and the final population after 2000 generations is shown as a cluster of red dots. In the control condition, where $n = 1$ and hence huddling is impossible, the zone of increased fitness is almost impossible to find by chance, hence the initial and final populations are indistinguishable except for the drift of a random walk and the effects of mutation. However, as n increases, the capacity for huddling makes the zone of increased fitness easy to find. When the population enters this zone, explicit selection pressure to minimize M pushes the population to the left of the landscape, and as the upper boundary is approached, indirect selection based on the failure of litters straying beyond it push the population down the landscape. Interestingly, the evolutionary dynamics also minimize the thermal conductance C despite no explicit metabolic cost or selection pressure being associated with this component of thermoregulation in the fitness function.

Two lines in each panel in Figure 4.2 represent solutions to Equation 4.7 for $A = 1$ (dashed line), below which litters overheat, and for the geometrical limit of huddling, $A = n^{-\frac{1}{4}}$ (solid line), above which litters are too cold to maintain the preferred body temperature. Between these boundaries, litters are able to maintain $T_b = T_{\text{pref}}$ by adapting A (i.e. by huddling), hence the region defined by $1 \leq C(T_{\text{pref}} - T_a)/M \leq n^{\frac{1}{4}}$ constitutes a 'zone of increased fitness' (Hinton and Nowlan, 1987).

Once the population enters this zone of increased fitness, it is subject to an explicit pressure to minimize M, and (as expected) the metabolic rate decreases. Note that the initial reduction in M occurs at the same rate for all $n > 1$, although it continues for longer in the wider zones of larger litters, thus accounting for the similar rates of initial fitness increase shown for each litter size in Figure 4.1. In each case, M drifts freely with respect to C, with which no metabolic cost or other selection pressure had been explicitly associated (see Equation 4.5). However, when the population encounters the lower bound on the metabolic rate for a given thermal conductance, the conductance also starts to fall, and the reduction of M and C becomes correlated. In Figure 4.2, the combination of M and C can be seen to evolve with a trajectory that runs parallel to the upper boundary of the zone of increased fitness.

Directed evolution of the thermal conductance, in the absence of an explicit selection pressure on C, is an interesting and surprising result, but Figure 4.2 reveals the underlying mechanism to be straightforward. At the upper boundary of the zone of increased fitness, litters that fail to maintain the preferred body temperature due to a low metabolic rate do not survive, preventing further reduction of M. Similarly, litters that (by chance mutation) have a high thermal conductance may stray outside the zone of increased fitness, biasing the population towards lower thermal conductances. At lower thermal conductances the potential for the explicit selection for low metabolic rates to reach still lower rates is greater, hence the reduction of M continues to be complemented by a reduction in C away from the upper boundary. Explicit selection for litters with lower metabolic rates M, due to the appearance of M in the fitness function (Equation 4.5), continually pushes the population towards the upper boundary, above which litters are too cold. At this boundary, selection based on the failure of high thermal conductances is implicit (because C does not appear as a term in the fitness function); this effectively pushes the population away from the boundary to regions in the fitness landscape where the *potential* for further reduction in the metabolic rate is greater. The net effect is that the population maintains a distance from the upper boundary, and this distance is determined by the rate and extent of mutation.

This continues as the zone of increased fitness narrows, until mutation pushes some litters in the population below the lower boundary where they overheat, at which point evolution effectively stops. Zones of increased fitness defined by larger n are wider, and therefore larger litters evolve lower values of M and C. This increased width of the zone of increased fitness associated with larger litters (n) accounts for the increased asymptotic fitness of larger litters (Figure 4.1).

4.4 Discussion

A simple evolutionary algorithm was challenged to discover a combination of genes to specify the physiological and morphological components of thermoregulation, and to optimize the former to reduce metabolic cost. The challenge was such that, in the case where individuals cannot huddle, and hence adaptation of the exposed surface area is not possible, solutions where homeothermy can be acheived were constrained to a very narrow region of the fitness landscape. A valid solution is combinatorially difficult to find by random search alone, like finding a needle in a haystack (see Hinton and Nowlan, 1987). Moreover, should a solution be found, reducing metabolic costs by random local search is difficult because any mutation in metabolic rate is catastrophic unless paired with a precise compensatory mutation in thermal conductance, so optimisation becomes like taking a random walk along a tightrope. Fitness landscapes defined with physiological and morphological tolerances in mammals may of course be more forgiving than in the model, but consideration of the most treacherous landscape used here is useful for exposing the full potential for within-lifetime adaptation to guide evolution.

According to the model, allowing the exposed surface area to adapt during the lifetime increases the range of thermal conductances over which a preferred body temperature can be maintained for each genetically specified metabolic rate. Crucially, as the population evolves, no information is directly communicated from phenotype to genotype, yet over generations the thermoregulatory effects afforded by within-lifetime adaptation of the exposed surface area becomes consolidated as a genetic adaptation in the thermal conductance. Evolution proceeds until the advantages of huddling are offset by the extent of mutation, hence the final population retains a degree of within-lifetime adaptability.

McNab (1978) considers that small endothermic mammals (with low thermal conductance and high mass-specific metabolic rates) were unlikely to have evolved directly from small ectothermic reptiles (with high conductances and low mass-specific metabolic rates) because intermediate stages would not have been viable; "... a small endotherm with reptilian conductance would squander heat in a hopeless attempt to maintain a constant body temperature." (McNab, 1978). Instead he proposed that reptiles ancestral to mammals first increased in body mass, gaining a degree of 'inertial homoiothermy', i.e., a resistance to changes in temperature due to a reduced surface-area to volume ratio, before developing a fur coat that further improved the constancy of body temperature. Homeothermy afforded nocturnal hunting and/or foraging (see also Jerison, 1976), and endothermic mammals subsequently emerged from an incremental (linear) reduction in thermal conductance and basal metabolic rate as body size reduced (and mass-specific metabolic rate increased). This account is corroborated by a transition from the lizard to mammalian lineages whereby metabolic rate and thermal conductance remain constant as intermediate species drifted with respect to body mass (compare Figure 4.2 in the present paper with Figure 1 in McNab (1978)). Interestingly, a model representing this proposal would be similar in form to that presented here, except that the adaptability parameter (i.e., the capacity for huddling, n) should instead be expressed in terms of the postulated inertia of pre-endothermic homeothermy. The common underlying mechanism is a relaxation of selection pressure on one parameter (i.e., thermal conductance) allowing another (i.e., metabolic rate) to drift freely, followed by an interaction with a boundary in the combined fitness landscape that correlates the subsequent evolution of both.

An alternative theory of the evolution of endothermy from ectothermy emphasizes the selective advantage of sustaining a high metabolic rate for aerobic exercise over thermogenesis, the latter providing only secondary benefits for thermoregulation that were exploited subsequently. Accordingly, direct selection for an increase in the maximal metabolic rate would reveal itself as an indirect selection for an increase in the resting metabolic rate (Bennett and Ruben, 1979). This ‘aerobic theory’ is supported by recent population genetic analyses confirming the central prediction that maximal and resting metabolic rates should be associated by a high genetic correlation (Hayes, 2010).

According to Bennett and Ruben (1979) selection for thermoregulation over aerobic capacity would have acted only to reduce thermal conductance by optimising the growth of insulative fat or fur, keeping the costs of sustaining a high resting metabolism to a minimum (Bennett and Ruben, 1979). It is therefore interesting that significantly high heritability and high additive genetic variance of thermal conductance have been reported in cold-acclimated mice, suggesting that thermal conductance is a potential target for natural selection in this species (Nespolo et al., 2003). Furthermore, in a follow up study with the same species, basal metabolic rate and maximum metabolic rate were found not to be significantly heritable (Nespolo et al., 2003, 2005). Instead, the authors reported a high (negative) genetic correlation between birth mass and non-shivering thermogenesis, i.e., brown adipose tissue (BAT) thermogenesis, more consistent with an inertial homeothermy than an aerobic account for these highly social (wild-caught) rodents. In their words "...this is an interesting outcome since it relates adult capacity for aerobic energy expenditure to a very different attribute, related to the quality of pups in a litter. [...] In other words, non-shivering thermogenesis could respond to indirect selection on birth mass." (Nespolo et al., 2005). Might huddling provide the basis for this indirect relationship?

BAT-thermogenesis is thought to be critical for effective huddling in rodents, as evidenced by experiments showing that rats move to cooler locations when BAT is pharmaceutically increased (Farrell and Alberts, 2007), and that huddling in rats ceases when BAT is pharmaceutically blocked (Sokoloff and Blumberg, 2001). Interestingly, Syrian golden hamsters, which are born without functional BAT (Blumberg, 1997), and do not huddle until BAT becomes functional at around postnatal day 14, have been shown to huddle when fostered into litters of weight-matched rats with functional BAT (Sokoloff and Blumberg, 2002). These data are consistent with the central role of BAT thermogenesis in the self-organisation of rodent thermoregulatory huddling behaviours, according to the model of (Glancy et al., 2015).

A recent study found no relationship between BAT-thermogenesis and birth weight in neonatal rabbits (García-Torres et al., 2015). However, pups born heavier are known to occupy the warmer central positions in the huddle, whereas lighter pups occupy the cooler peripheral positions (Bautista et al., 2010). Pups who spent more time at the periphery of the huddle responded to an acute cold challenge at postnatal day three with a greater reduction in BAT metabolism compared to pups that occupied the center of the huddle (García-Torres et al. (2015); see also Bautista et al. (2013)). Similar huddling patterns have been reported for lighter pups cross-fostered to be heavy relative to their surrogate littermates, with relatively heavy littermates occupying the warm huddle center. Hence any relationship between birth weight and adult thermogenesis may indeed be an indirect one, mediated by the thermotaxic struggle for position in the huddle. In circumstantial support, lighter (adult) rats move to higher ambient temperatures in a thermocline than heavier rats, where they are found to metabolise at higher rates (Gordon, 1988).

Furthermore, the effects of birth weight on many aspects of later development are similar to the effects of litter size; for example pre-weaning weight gain and the development of motor co-ordination are both improved in heavier pups (Muciño et al., 2009; Rödel et al., 2008), but they are also improved in pups raised in litters compared to those reared in isolation (Nicolás et al., 2011). We might speculate that since first exploiting the thermoregulatory benefits of huddling, evolution may have later exploited a variety of possible benefits of social thermoregulation for later development (Dimitsantos et al., 2007; Uriarte et al., 2009; Reyes-Meza et al., 2011; Hudson et al., 2011; Rödel and Meyer, 2011).

Huddling has been considered as an epigenetic factor in several other discussions. For example, Haig (Haig, 2008) explains that the genes encoding the potential for BAT-thermogenesis (Pref1/Dlk1 and Necdin) interact with a BAT-activating gene

(GNAS) either to promote thermogenesis when the maternal allele is expressed or to inhibit thermogenesis when the paternal allele is expressed, and therefore males and females have a differential genetic investment in the success of the huddle. In support, male rat pups, who generate less heat through BAT, have been described as heat sinks that drain the extra heat generated by female littermates (Harshaw et al., 2014). These authors also suggest that the ratio of males to females in a litter can affect BAT-thermogenesis directly via sex hormones, hence the adaptive capacity for huddling may be affected by the sex ratio within the huddle. Another potential epigenetic effect is suggested by the experiment of Yamauchi (Yamauchi et al., 1983), who bred from mice housed (in pairs) under two conditions; the first from parents housed at a fixed ambient temperature from 8 weeks that mated between 9 and 11 weeks, and the second from parents who were temperature controlled from 8 weeks and mated between 16-18 weeks. Mice maintained at ambient temperatures above 27^oC bore litters averaging around nine pups, whereas mice maintained at lower temperatures had litters averaging upwards of eleven. Remarkably, the animals housed below 27^oC for the longer period had litters averaging around fifteen pups. Thus prolonged cold-exposure in one generation can increase the litter size, and hence increase the capacity to adapt to the cold by huddling, in the next generation. It would be interesting in an extension of the model to establish the potential implications of these epigenetic effects for the evolution of endothermy.

We might have naively expected that cold-exposed animals with the opportunity to keep warm by huddling should evolve a reduced thermal conductance at a slower rate than animals reared in isolation. But the present model clearly makes the opposite prediction; by reducing selection pressure on the thermal conductance, huddling allows cold exposed populations to reduce thermal conductance at a faster rate compared with non-huddlers. The mechanism behind this effect therefore corresponds to what Deacon refers to as ‘relaxed selection’ (Deacon, 2010), whereby outsourcing selection pressure to the environment relaxes the selection pressure on the two genetic components of thermoregulation, freeing one to vary independently of the other.

The present study has been concerned with establishing the potential for self-organising behaviour within the lifetime to alter the course of evolution. The experimental test of the model would be to breed successive generations of rodents reared in cold environments; animals bred and reared in larger groups should evolve insulative fur and/or subcutaneous fat faster than those reared in smaller groups.

Self-organising thermoregulatory huddling is likely one of several within-lifetime factors that can help accelerate the evolution of endothermy by natural selection. Establishing the relative contribution of each factor in controlled experiments may help reveal in more general terms the extent to which self-organisation guides evolution.

Chapter 5

Huddling and the Baldwin Effect

5.1 Introduction

We have previously shown that huddle-like aggregations can be produced in a self-organising manner (see Chapter 3). Using agent-based modeling techniques, we developed a minimal model of thermoregulatory huddling and demonstrated how individual 'homeothermotaxic' behaviours were sufficient to synthesise group-level dynamics that qualitatively match experimentally observed huddling. While previous models of huddling (see Schank and Alberts, 1997) have also provided evidence in support of the self-organising huddle hypothesis, to the best of our knowledge we are the first to demonstrate the emergence of temperature mediated behaviours in the absence of a global supervisory mechanism. Namely (1) a critical phase transition into huddling at low ambient temperatures, and (2) a thermoregulatory 'pup flow'.

Building on our agent-based model of huddling, we next sought to find a mathematical description of the huddle (see Section 3.2.6). Consistent with the ideas of Schank and Alberts (1997), we began by considering the huddle as a single entity that adapts its exposed surface area in response to the ambient temperature (see Equation 3.3 and 3.4). When compared to the full agent-based model, we found that the behaviour predicted by this mathematical description was remarkably similar. Thus, our group-level model represents a simple mathematical description of a *within-lifetime adaptation* that emerges as a consequence of simple, local interactions, in the absence of a global supervisory mechanism (i.e., self-organisation).

In Chapter 4, we investigated how within-lifetime adaptations, such as thermoregulatory huddling, might alter the course of evolution. Using simplistic description of the self-organising behaviours, we challenged a simple evolutionary algorithm to optimise the genetic components of thermoregulation. We looked at the rate of evolution in populations of varying litter sizes, n, and found that rates of evolution improved as the size of litters increased. In the control case of no huddling, $n = 1$ we found that no optimisation occurred. Our understand of this result is that adaptive huddling behaviours relax the selection pressures on metabolism, and allow other traits (e.g., thermal conductance) to drift freely. Therefore our model makes the counter-intuitive prediction that animals under relaxed selection pressure may actually evolve faster.

In this chapter we will explore the possibility that huddling behaviours, as a example of within-lifetime adaptation, could elicit a Baldwin Effect. In Chapter 1 we identified the Baldwin Effect as a potential interaction that might occur between an adaptive (self-organising) behaviour, such as thermoregulatory huddling, and natural selection. Previously, the Baldwin Effect has been strongly associated with learning (Dennett and Mittwoch, 1996; Deacon, 2003), however learning is one particular case of ontogenetic adaptation and any form of ontogenetic adaptation is potentially suitable.

The Baldwin Effect can be broken down into three distinct aspects referred to as: 1) the Simpson-Baldwin effect, 2) the Baldwin expediting effect, and 3) the Baldwin optimising effect (Zollman and Smead, 2009). The Simpson-Baldwin effect focuses on the effect of evolution on plasticity. It predicts that, within certain scenarios, plasticity is first selected for and then selected against. The Baldwin expediting effect refers to the effect of plasticity on the rate of evolution. And finally, the Baldwin optimising effect relates to the influence of plastic individuals on the evolutionary trajectories of a population. The model presented in Chapter 4 demonstrated how the presence of huddling behaviours can increase the rate of evolution of physiological and morphological components of thermoregulation, akin to the Baldwin expediting effect. Therefore, in this study we will place emphasis on an investigation of the Simpson-Baldwin effect.

5.1.1 The Simpson-Baldwin Effect

The Simpson-Baldwin effect is concerned with how natural selection affects the presence of plasticity within a population. This effect is understood to occur in three stages:

Stage 1 A change in environment occurs and individuals that are capable of adapting within their lifetime are able to out-compete others.

Stage 2 Mutation(s) occur that produces a heritable trait that is functionally similar to the trait that plasticity acquired.

Stage 3 Natural selection favours the heritable trait, presumably because there is a cost related to plasticity.

A prediction of the Simpson-Baldwin effect is that the amount of plasticity present within the population will initially rise (Stage 1), until a point when mutations in physiology and/ or morphology begin to replace the adaptive behaviour (Stage 2), and then the amount of plasticity in the population would decline (Stage 3).

There are two main concerns with this narrative. The first concerns the assumed superiority of the heritable trait over the acquired trait. This assumption is based on the premise that there is a cost associated with plasticity. This cost could be caused by a delay in acquiring the trait (i.e., learning), or because the process of acquisition is prone to errors. The results in Chapter 3 have shown that our agent-based model of thermoregulatory huddling is a good solution for thermoregulation, but not a perfect one and so it does carry a cost when compared to an individual that does not need to huddle (because it has ideal physiological parameters).

The second concern is a little more difficult to resolve. Why should we expect that a plastic trait is discovered before the heritable trait? And if the heritable trait is found first, then there would be no rise in plasticity. Godfrey-Smith (2003) considers this problem, and concludes that the only plausible case is when plasticity actually creates the circumstances in which the heritable trait is superior. That is, the presence of plasticity within the population creates a new selection pressure on the individuals. In our previous study of the interactions between self-organisation and natural selection (Chapter 4), we were considering a population of litters that were entirely separate from one another. The presence of plasticity within one litter had no bearing on the fitness of others. Consequently, the setup of such a model is ill suited to the investigation of a Simpson-Baldwin effect. Therefore, in order to study the Simpson-Baldwin effect we will change our computational model to focus on the evolution of a single litter, where individuals are able to interact with each other, and are able to display varying degrees of plasticity.

5.2 Methods

Similar to our approach in Chapter 4, we will challenge an evolutionary algorithm to optimise the morphological and physiological components of thermoregulation. However, to investigate the Simpson-Baldwin effect we will modify our previous model to focus on the evolution of a single, heterogeneous litter. We will evolve litters of size $n = 12$, and compare the cases where individuals are grouped together, and when they are kept isolated. The agent-based model presented in Chapter 3 assumed that all agents within a litter had the same physiological and morphological properties, and so the model used here has been modified to simulate groups with heterogeneous thermal physiologies, initialised as uniform random values of $G \in (0, 14]$, and $C \in (0, 2]$. Huddles were simulated for 2500 time steps, and the first 500 time steps were ignored to allow dynamics of the system to settle.

Evolutionary Algorithm

The fitness of an individual within our litter is based on the intuition that a fit individual should be able to maintain a preferred body temperature, $T_p = 37°\text{C}$ at a low metabolic rate. Therefore our fitness metric is a function of the error value, $|T_p - T_b|$, and the metabolic rate, G:

$$F = K - (|\hat{T_b} - T_p| + G), \tag{5.1}$$

where $K = 25$ is a arbitrary constant that ensures that all fitness scores are positive, and $\hat{T_b}$ is the average body temperature that an individual achieves over the course of the simulation.

To evolve the physiological and morphological parameters of a litter, we apply a simple evolutionary algorithm based on one reported in Bak (1996). The algorithm is as follows:

1. Initialise a group of n individuals, each with a random physiology as defined by the parameters G (thermogenesis) and C (thermal conductances).
2. Simulate a huddle, as described in Chapter 3 for 2500 timesteps, ignoring the first 500 steps while the dynamics settle.
3. Evaluate the fitness of each individual based on the cost of metabolism and the ability to thermoregulate.
4. Select the weakest individual, and replace this with a new randomly generated individual.

5. Repeat steps 2 - 4 for 200 generations.

Huddlers, Non-Huddlers, and Exploiters

In the context of huddling and the Baldwin effect, the acquired trait is the exposed surface area of an individual, A, while the thermal conductance, C, is a heritable trait that is functionally equivalent to surface area. That is to say, they both modulate the rate of heat decay. We have shown in Chapter 3 that self-organising huddling behaviours allow individuals to manipulate their exposed surface area in an adaptive fashion in order to balance the amount of heat decay and heat generation. Effectively, huddling behaviours attempt to solve the following equation:

$$A_{\text{pref}} = \frac{G}{C(T_p - T_a)} \tag{5.2}$$

However, the exposed surface area is bounded due to geometrical limitations of huddling. An individual's exposed surface area is maximal ($A_{\text{max}} = 1$) when individuals are isolated, and minimal (A_{min}) when all agents are fully huddled. by the number of huddling littermates, n. Taking these bounds into consideration, we can predict the surface area of a huddling individual as:

$$A(n) = \begin{cases} 1 & \text{if } 1 \leq A_{\text{pref}} \\ A_{\text{pref}} & A_{\text{min}} < A_{\text{pref}} < 1 \\ A_{\text{min}} & \text{if } A_{\text{pref}} \leq A_{\text{min}} \end{cases}, \tag{5.3}$$

where A_{min} is based on the litter size and is determined by the minimal surface area achieved by the agent-based model.

These predictions of $A(n)$ are useful because they all us to label individuals in a litter as either *huddlers*, *non-huddlers*, or *exploiters* based on their thermodynamic properties. A *huddler* is defined as an individual with thermoregulatory properties that are sufficient to maintain a stable body temperature in a litter of size n, i.e., $A(n) = A_{\text{pref}}$. A *non-huddler* characterised by an expected surface area of $A(n) = 1$. The implication being that such an individual has a set of thermoregulatory properties that make it actively avoid contact with other individuals because it generates too much heat. An *exploiter* is defined as an individual that actively tries to avoid, but has thermoregulatory properties that are insufficient to maintain a preferred body temperature in a litter of size n, i.e., $A(n) = A_{\text{min}}$. Note that these labels are used to describe both the individuals that are grouped together, and those that are isolated. Hence, they describe the capacity of an individual to huddle rather than the observation of individuals huddling. These definitions are shown visually in Figure 5.1.

A Metric of Plasticity

A prediction of the Simpson-Baldwin effect is that, when presented with a novel environment, the degree of plasticity within a population will initially increase before returning to a baseline level. Therefore, it is necessary to quantify the presence of plasticity within a litter of agents. We define the following metric of

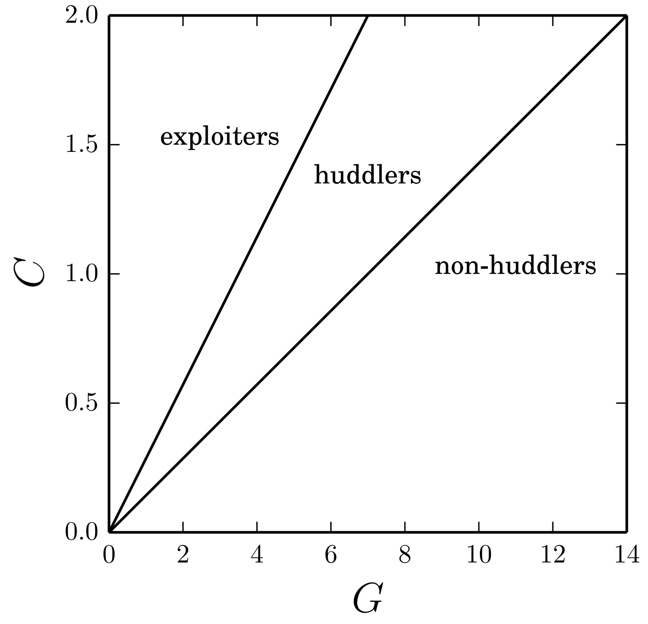

FIGURE 5.1: We define a *huddler* as an individual that engages in huddling behaviour to regulate its body temperature. An *exploiter* also engages in huddling behaviours, however it is physiologically unable to generate enough heat in order to be useful to the group. A group comprised entirely of exploiters will not successfully thermoregulate. A *non-huddler* generates more heat than is required, and so actively avoids huddling.

for an individual's plasticity based on its physiological parameters:

$$P = \frac{\arctan(\frac{C}{G}) - \arctan(\frac{1}{A_{\max}(T_p - T_a)})}{\arctan(\frac{1}{A_{\min}(T_p - T_a)}) - \arctan(\frac{1}{A_{\max}(T_p - T_a)})}. \tag{5.4}$$

For agents labeled as *on-huddlers*, we assign a plasticity of $P = 0$. This metric uses the angle between G and C, and is normalised about the boundaries that mark the 'zone of increased fitness'.

5.3 Results and Discussion

We set out to investigate what interactions might occur between natural selection and thermoregulatory huddling behaviours. We highlighted the Simpson-Baldwin effect as a priority for this investigation, and we deduced that in order to observe this effect we must necessarily model the interactions between individuals within the evolving population. Therefore, where previously we had used a mathematical description of thermoregulatory huddling in lieu of the agent-based model, in this study we returned to using the model of homeothermotaxic agents developed in Chapter 3.

The Baldwin effect is concerned with the evolutionary benefits that can be gained from phenotypic plasticity. In our model we considered two cases: two populations, each of twelve individuals, are either grouped together or kept isolated. We then evolve the litters, removing the least fit individual every generation and replacing it with a new individual with random parameters. When individuals are

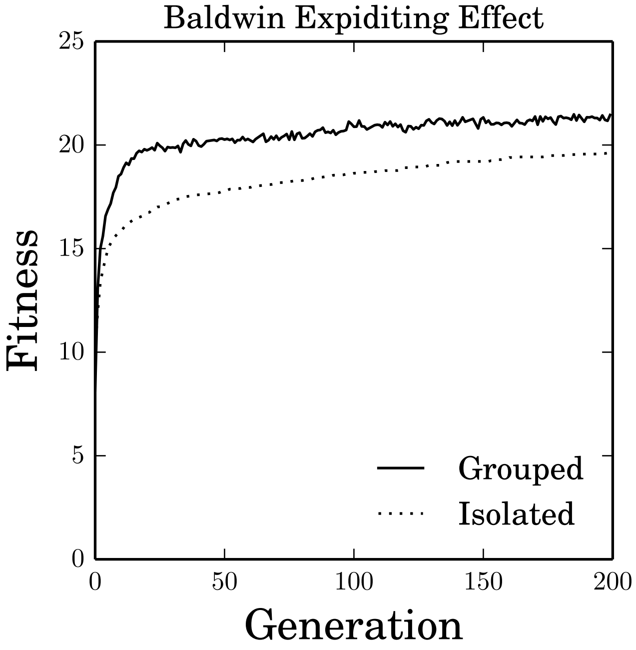

Figure 5.2: The fitness of the group for each generation, comparing the 'Grouped' and 'Isolated' cases. We see that in the 'Grouped' case fitness improves at an increased rate, and reaches a higher value than the 'Isolated' case. We take this as evidence for the existence of a Baldwin expiditing effect in the case when agents are able to huddle.

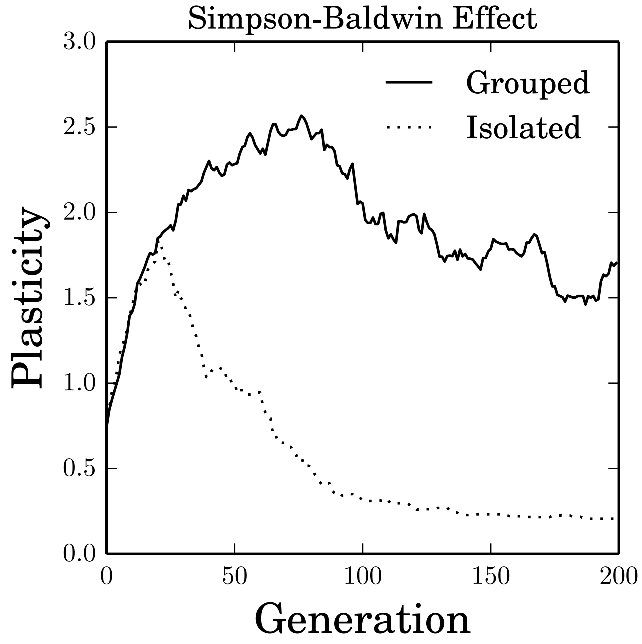

Figure 5.3: Showing average plasticity for individuals within the group for each generation, comparing the 'Grouped' and 'Isolated' cases. We see that in both cases there is a settling period over the first 20 generations, with no difference in behaviour. After this point, there is a drastic drop in the amount of plasticity seen in individuals in the Isolated case. However, in the Grouped case we initially see a growth in plasticity, followed by a decline. This is what the Simpson-Baldwin effect predicts.

grouped together they are able to employ homeothermotaxic behaviours over the course of their lifetime in an attempt to manipulate their exposed surface area. In the isolated case individuals are at the mercy of their genetically predetermined thermal properties, as within lifetime behaviours cannot be used to improve their fitness.

In both the isolated and grouped cases we found that the evolutionary algorithm was able to improve the fitness of an initial population randomly spread across the parameter space (see Figure 5.2). Figure 5.3 shows how the amount of plasticity present within the litter changes over the evolutionary algorithm. Up until generation 20 there is no difference between the evolutionary trajectory of individuals that are grouped and those that are isolated. This appears to be a settling period of the simulation. From generation 20 onwards we see that the prevalence of plasticity within the group follows a drastically different evolutionary trajectory to the isolated case. Our explanation for this is that prior to this point huddling dynamics were not fully established, and only once there is a critical mass of plastic individuals within the litter can huddling behaviours influence the evolutionary trajectory.

Huddling is a cooperative group behaviour, however each individual behaves in a selfish manner. In a group of non-huddlers, who each actively avoid contact, a single huddler (or exploiter) will struggle to huddle successfully. At best, the huddler will attach itself to a non-huddler who will continually try to escape his new friend and in this situation the huddler gains fitness at the expense of the non-huddler. For huddling behaviours to be beneficial to the population there needs to be multiple individuals engaging in the behaviour. Once a critical point is reached, we see that plasticity is selected for (generation 20) and then eventually selected against – as predicted by the Simpson-Baldwin effect.

Chapter 6

Discussion

The work presented in this thesis has been organised around three significant computational modelling studies. In study 1 (Chapter 3), a novel agent-based model was developed which demonstrates how rodent thermoregulatory huddling behaviours can emerge spontaneously via simple local interactions between individuals. In study 2 (Chapter 4), a simplified description of the full self-organising model was subjected to a simple evolutionary process to explore the possibility that self-organising huddling interactions that occur during the lifetime might interact with natural selection. In study 3 (Chapter 5) a modified evolutionary process was used to interrogate the full self-organising model, and the reported simulations generate several new insights and theoretical predictions concerning the Baldwin Effect. Together, these studies suggest that rodent thermoregulatory huddling behaviour offers a means of subjecting theoretical ideas about the potential interaction between self-organisation and natural selection to empirical testing.

The major contribution of the thesis is therefore to establish a set of testable predictions from which a full theory of the interaction between self-organisation and selection might emerge. The following sections condense the various testable predictions and novel insights contained in this thesis into a list intended to provide a clear guide to experimentalists and theoreticians about how progress towards building such a theory might be achieved. The chapter ends with a discussion of the role of computational modelling in the process of theory building, with specific reference to the process by which the huddling models in this thesis were developed.

6.1 Study 1 - A Self-Organising Model of Thermoregulatory Huddling

Chapter 1 set up the overall question of this thesis – 'How can self-organisation guide evolution?' – and ended with a list of requirements for a system that would facilitate the study of interactions between self-organisation and natural selection. Chapter 2 developed theories of endothermic homeothermy, and identified thermogulatory huddling as an excellent system through which to address the question 'How can self-organisation (huddling) guide evolution (of physiological components of homeothermy)?'. Chapter 3 presents a novel agent-based model that demonstrates how rodent thermoregulatory huddling behaviours can emerge spontaneously via simple local interactions between agents. The agent-based model was created in order to investigate interactions between self-organisation and natural selection (Chapters 4 and 5), however it also provides a baseline model for further research into group thermoregulatory behaviours.

Novel insights from study 1

1. **Thermoregulatory huddling can be described as an adaptive self-organising system.** The agent-based model presented in Chapter 3 shows that group thermoregulatory huddling behaviours can be explained by simple, local interactions between animals without the direction of a global supervisory mechanism. While this does not prove that observed behaviours of thermoregulatory huddling are indeed self-organising, the agent-based model serves as an existence-proof in support of this theory.

2. **Huddling-specific rules of individual behaviour are not necessary.** The synthetic rat pups that were created for the agent-based model follow a simple homeothermotaxic rule: orient towards heat when cold, and orient away when hot. This is a general behaviour of thermoregulation, and is not specifically tailored to ellicit huddling. Indeed, an isolated agent on a thermocline will navigate towards an optimal location that maintains a preferred body temperature. This suggests that the evolution of huddling does not require the evolution of novel individual behaviours, but instead can rely on existing behaviours of thermoregulation.

3. **Endothermy ellicts huddling behaviours.** In the agent-based model, thermogenesis is a necessary component for the emergence of huddling behaviours. When thermogenesis is disabled, i.e., $G = 0$, huddling behaviours

do not appear. This is consistent with the findings of Sokoloff et al. (2000), who proposed that endothermy has a modulating effect on (huddling) behaviours. A strength of computational modelling is that one aspect of the model (e.g., thermogenesis) can be disabled without compromising others (e.g., individual behaviour). In this case, the model shows that when thermogenesis is disabled the body temperature of each pup will decay to ambient temperatures. Therefore, conspecifics do not provide the stimuli required for an agent to maintain contacts. Hence, huddling behaviours do not appear in the absense of thermogenesis and we can describe the emergence of huddling as the natural expression of collective thermotaxis by endotherms.

4. **Huddle cohesion relies on heterogenity of body temperatures.** An assumption in early iterations of the agent-based model was that agents could maintain a constant body temperature. The litters created by this assumption were homogeneous in terms of body temperature and large huddles ($n > 4$) were seen to be unstable, inevitably fracturing into smaller ‘micro huddles’. It was hypothesised that an element of symmetry breaking was necessary, and so a model of thermal exchange was introduced into the agent-based model. Consequently, an agents body temperature became representative of an agents phsyiology (G), morphology (C), and behaviour (A), as well as the environment (T_a). In the context of the huddle, an agents body temperature is reflective of its relative location to the center of the huddle; in an otherwise homogeneous environment, the huddle creates a gradient of body temperatures with a warm core and a cooler periphery.

5. **The huddle behaves as a single organism.** A description of the huddle as a single-organism that manipulates its surface area to maintain thermal balance led to a mathematical description that captures the global behaviour of the agent-based model. Strong agreement between the results of the agent-based model and this top-down model motivates an interpreation of huddling as a unitary system that uses collective thermotaxis to adaptively control its overall exposed surface area in order to maintain thermal balance. In the case when these two models do not agree (low thermogenesis), it is the agent-based model of huddling that correctly predicts the behaviour observed in experimental studies. Further supporting the theory that huddling is a self-organising system.

Testifiable predictions for an experimentalist

i The critical temperature of the phase transition into huddling is dependent on both the physiology and morphology of an animal. Both the agent-based model, and the group-level model, predict that either pharmaceutically increasing BAT-thermogenesis or insulating pups to reduce the thermal decay will lower the critical temperature at which huddling appears.

ii The range of ambient temperatures over which a huddle can maintain thermal homeostasis is a function of the number of huddling animals, as well as the phsyiology and morphology of the huddlers. Pharmaceutically increasing BAT-thermogenesis, or insulating pups to reduce the thermal decay, will increase the range of ambient temperatures over which body temperature can be regulated via huddling behaviours.

iii The agent-based model predicts a peak in the amount of pup flow around the the critical temperature of the phase transition in to huddling.

Study 2 - How Can Self-Organisation Guide Evolution?

Chapter 4 challenged a simple evolutionary algorithm to optimise the morphological and physiological aspects of endothermic homeothermy. The fitness of an individual was assessed based on the assumption that an endotherm has two major concerns: (1) maintaining a preferred body temperature, and (2) minimising its metabolic expenditure (see Equation 4.5). In Chapter 2 thermoregulatory huddling was identified as a within-lifetime adaptation that both reduces the metabolic cost of endothermy, and provides a thermoregulatory mechanism. Therefore, it was expected that huddling constitutes a self-organising behaviour that could potentially interact with the evolution of genetic components of endothermy. The rate of evolution was measured in order to observe potential interactions.

Novel insights from study 2

6. **Behavioural thermoregulation accelerates the rate of evolution of physiological thermoregulation.** Populations of litters were evolved to minimise metabolic costs while maintaining a stable body temperature. The rate of evolution was seen to improve with the size of litters, n. In the

absense of huddling ($n = 1$), fitness did not increase. The model predicts that as the capacity for adaptation by self-organising huddling increases (i.e., as litter size increases) so too does the rate of evolution of genetically encoded phsyiological and morphological aspects thermoregulation.

7. **Adaptive behaviours relax selection pressures.** Adaptive behaviours, such as thermoregulatory huddling, can compensate for shortcomings of genetically encoded traits. For example, huddling can augment the thermal conductance of an animal to achieve a thermal balance between the rate of heat loss (proportional to $A \cdot C$) and the rate of heat gain (M). This compensatory mechanism provides a window of *relaxed selection* on the genetic trait, allowing it to drift without a drastic impact on fitness.

8. **Relaxed selection increases the rate of evolution.** A counter-intuitive prediction of the model is that the rate of evolution increases as selection pressures are reduced. This can be explained by inspection of the fitness landscape: in the case of no huddling ($n = 1$) the only combinations of morphological and physiological traits that have a none zero fitness are exactly the solutions to the equation $M = C(T_p - T_a)$. Consequently, any mutation in one trait is catastrophic unless it is accompanied by a precise compensatory mutation in the other. Relaxed selection changes the fitness landscape, and creates a ‘zone of increased fitness’ where mutations can occur freely without drastic consequences.

9. **Explicit selection on metabolic rate creates an implicit selection pressure on thermal conductance.** A surprising result of this model is a

directed evolution of the thermal conductance in the absence of an explicit selection presure on C, however this mechanism too can be explained by inspection of the fitness landscape. An explicit pressure on the metabolic rate, M, pushes the population to the edge of the 'zone of increased fitness' where reductions in metabolism cannot survive without first an increase in thermal conductance. At this edge of increased fitness mutations that decrease a litter's thermal conductance will be drastic (litters will be too cold), and so the average thermal conductance of the population actually increases. Therefore, the explicit selection pressure on metabolic rate creates an implicit selection pressure on the thermal conductance.

Testifiable predictions for an experimentalist

iv This model predicts (counter-intuitively) that phsyiological and/ or morphological components of thermoregulation will evolve faster when animals are able to exploit huddling behaviours to adapt during their lifetime. The experimental test of this model therefore, is to breed successive generations of rodents reared in cold environments. It is expected that animals bred and reared in larger groups will evolve insulative fur and/ or subcutaneous fat faster than those reared in smaller groups.

Study 3 - Huddling and the Baldwin Effect

In Chapter 1, the Baldwin effect was identified as a potential interaction between self-organisation and natural selection. Chapter 5 returned to a full description of self-organising thermoregulatory (as described in Chapter 3) and challenged an evolutionary algorithm to evolve the composition of a heterogeneous litter.

Novel insights from study 3

10. **Group plasticity can influence evolutionary trajectories.** A novel environment condition, such as a reduced ambient temperature, will cause the amount of plasticity within a group to increase because plasticity improves the fitness of the individual. However, once the amount of plasticity within the group reaches a critical mass, there is a bootstrap effect that is significant enough to alter the evolutionary trajectory of the population.

Testifiable predictions for an experimentalist

v Given a species of animals that has evolved within a constant thermal environment, we would expect to see a baseline degree of plasticity (huddling). If then success generations were bred at a lower ambient temperature, we would expect to see the degree of plasticity (huddling behaviours) to spike, before slowly return back to a baseline level.

6.2 The Role of Computational Models

In his short book *'Vehicles, Experiments in Synthetic Psychology'*, Valentino Braitenberg popularised the synthetic approach of model construction. Described in a series of thought experiments, Braitenberg showed that remarkably simple 'machines' have the potential to produce a plethora of complex and seemingly intelligent behaviours. This thesis not only builds on Braitenberg's principles of synthetic psychology, but the synthetic critters that are featured in Chapter 3 are based heavily on Braitenberg's very own vehicles.

Inspired by the writings of Camazine et al. (2001) and Alberts (2012), Chapter 3 tells the complete story of building a minimal model of thermoregulatory huddling. It is by choice that this model is incredibly simple, striving for the simplest possible description that can account for thermoregulation Therefore, it is my hope that another function of Chapter 3 is to serve as an example for good practices in the modelling of self-organisation in biological systems.

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