Energetics in wild female Assamese macaques (*Macaca assamensis*): a behavioral and physiological approach

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To my family, and particularly to Ismaël and Victor.

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CHAPTER 1

General introduction

1. The close link between energy and fitness

1.1. Energy: a cornerstone in life history

In the same way money fuels trading and economic strategies, energy is the key currency of life and metabolic functions. Energy originally comes from plants that transform solar energy into chemical energy through photosynthesis. This chemical energy is transferred between all living organisms (e.g. from plants to plant-eater animals, and from plant-eater animals to carnivorous animals). Energy is a major requirement for life since living cells need it to perform their biological functions. For that reason, energy lies at the heart of major evolutionary theories such as life history.

Life history theory provides an evolutionary analytical framework connecting a set of individual adaptive traits such as age at first reproduction, interbirth intervals, body size at birth or lifespan (Stearns, 1976). Energy is the underlying connection between life history traits and supports major biological processes that can be ordered in four categories: growth, body maintenance, reproduction and storage (Gadgil and Bossert, 1970; Perrin and Sibly, 1993). Energy is involved in major life components determining fitness (Perrin and Sibly, 1993). On the one hand, energy is a determinant of survival. Oxidation of fat stores in adipose tissue is, for example, an important source of energy on which individuals rely in order to maintain body functions and sustain life (Young, 1976). In addition, female reproductive success is largely dependent upon energy (Wade and Schneider, 1992; Della Torre et al., 2014; Ellison, 2003; Bentley, 1999). For instance, female fertility is promoted by energy and is adjusted according to various metabolic cues of energetic condition (Schneider, 2004; Hill et al., 2008; Ellison, 1990). Finally, a case in point regarding the link between energy and fitness relies in the comparison of life history traits between wild and captive species: the enhanced energetic condition (i.e. readily energy available and energy stored) in the latter typically induces fitness benefits relative to their wild counterparts (Tidière et al., 2016).

By applying the first law of thermodynamics, energy can be gained, lost or stored but cannot be destroyed or created (Haynie, 2001). Consequently, at a given moment organisms have at their disposal a finite amount of energy to support the numerous bodily functions involved in survival and reproduction. From this energy constraint stems the principal component of life history theory: trade-offs in energy allocation (energy partitioning). A fitness cost will be associated with allocating energy to the support of one adaptive function insofar as it will be at the expense of another (Stearns, 1989; Roff and Fairbairn, 2007). In order to maximize fitness, energy has to be strategically allocated according to an age-dependent set of priorities, ensuring first immediate body maintenance and survival and only then processes promoting growth, reproduction or storage (Perrin and Sibly, 1993). For example, a major trade-off exists between female survival and reproduction, since energy investment in reproductive effort lowers energy allocation to other adaptive traits involved in female survival (Gadgil and Bossert, 1970; Hamel et al., 2010).

Energy is therefore a limiting resource playing a paramount role in fitness as it acts both as fuel for life history traits and as determinant of allocation strategies. Importantly, energy is not static as both energy supply and demands vary, which can lead to challenging situations and bear fitness consequences.

1.2. Energetic challenges

Over its lifetime, an individual has different energy requirements according to a myriad of internal factors that impact its metabolic state (such as growth, health, reproductive state; Hou et al., 2008; Devevey et al., 2008; Gittleman and Thompson, 1988). In addition, environment is not stable in most habitats. External factors (such as rainfall, ambient temperature, food availability) fluctuate through distinct seasons inducing changes in energy availability in the environment and in energy demands to survive under different climatic conditions. Internal and external factors can influence energy intake (i.e. energy ingestion in the form of calories extracted from food resources in the environment) and energy expenditure (i.e. energy use to support metabolic needs, which typically increase with body size; Key and Ross, 1999). Energy balance is the net difference between energy intake and energy expenditure (Hall et al., 2012), with a positive energy balance when energy surplus is stored (in the form of glycogen or fat) and a negative energy balance when energy stores are mobilized. An energetic challenge represents any factor that would lead to a negative energy balance and therefore trigger shifts in energy allocation with fitness consequences. Specifically, an energetic challenge can occur through situations associated with a decrease in energy intake, an increase in energy expenditure or both. I will present such challenging situations below.

1.2.1. Decrease in energy intake

One clear factor inducing a decrease in energy intake is a decline in the amount of food in the environment (Knott, 1998). Food availability and quality affect fitness in mammals as both survival and reproduction are dependent upon them (Bronson, 1985; Knott, 1998; Knott et al., 2009; Watts and Holekamp, 2009; Mduma et al., 1999; Bronson and Marsteller, 1985; Dobson, 1995; Koenig et al., 1997 ; Altmann and Alberts, 2003). For example, food shortage and the ensuing decrease in energy intake can drive a decline in body weight (Goldizen et al., 1988), an increase in infection risk (Gardner et al., 2011) or reproductive impairment in females and males (Emery Thompson and Wrangham, 2008; Gesquiere et al., 2011).

In addition to availability, food access is also a factor constraining energy intake. It is common that competition occurs between groups for access to a limiting food resource (i.e. low food abundance; Isbell, 1991; Kurihara and Hanya, 2015; Harris, 2006). Intra-group feeding competition can also occur and is particularly driven by food distribution (Isbell, 1991). When a food resource is clumped, hierarchical structure among foragers drives food access with high-ranking individuals getting priority of access and fitness benefits ('contest' competition; Barrette and Vandal, 1986; Appleby, 1980; Janson, 1985; Majolo et al., 2012; Holand et al., 2004; Hofer and East, 2003). When food is dispersed, group size is the diver of intra-group feeding competition, with large group size inducing rapid food resource depletion, low energy intake per individual and fitness costs ('scramble' competition; Borries et al., 2008; Snaith and Chapman, 2005; Chapman et al., 2007).

1.2.2. Increase in energy expenditure

Metabolism encompasses all life-sustaining chemical reactions occurring in an organism and involves large molecule breakdown (catabolism) and biosynthesis (anabolism; Cox, 2005). Metabolic rate determines the amount of energy necessary for the metabolism's function. A fast metabolic rate is associated with high energy expenditure in mammals (Ricklefs et al., 1996). Basal metabolic rate represents the rate of energy metabolism (i.e. energy flow in the body, comprising intake, expenditure and storage) necessary to maintain critical biological processes such as major organ function, heart pumping and breathing; in an individual who is at rest, in a post-absorptive condition (fasting state where food has been fully digested, absorbed and stored) and undergoing neither heat or cold environmental constraints (Ricklefs et al., 1996; Hulbert and Else, 2004). The ubiquitous need for energy to fuel body maintenance in such a resting state illustrates its fundamental role in life and the energetic cost of living (Hulbert and Else, 2000). Some factor can result in a need to speed metabolism up as basal metabolic rate becomes inadequate in releasing enough energy to support energetic demands. These factors could potentially lead to challenging and fitness-threatening situations since they induce an increase in energy expenditure. Some of the most important factors, i.e. immune function, thermoregulation, physical activity and reproduction, will be presented below.

Factors generating an immune response, e.g. infections, trigger a rise in energy expenditure due to the hypermetabolic state necessary to up-regulate the host's immune system (Garza, 2005; Lochmiller and Deerenberg, 2000). The energetic costs associated with immune defense could consequently have fitness repercussions by shifting energy away from reproduction or growth (Burns et al., 2005; Careau et al., 2010). As illustrated by symptoms such as fever during extreme episodes of infection (Baracos et al., 1987), energy expends as heat. Metabolic rate and the associated energy expenditure has therefore a fundamental role to play in thermoregulation.

Thermoregulation is a process involved in maintaining core body temperature within a narrow viable window in homeotherm species, regardless of environmental conditions (Ivanov, 2006). Within a range of ambient temperatures called the thermoneutral zone, heat dispersion (energy expenditure) from basal metabolic rate is enough to maintain body temperature. When facing ambient temperature above or below thermoneutrality, thermoregulatory mechanisms involving modulation in metabolic rate and heat dissipation will be needed. For example, cold exposure increases energy expenditure and thus, heat production (Ocobock, 2016). This thermoregulatory expense could ultimately induce fitness costs (Xu et al., 2018).

Another important parameter increasing energy expenditure is physical activity as it is associated with a rise in metabolic rate (Sjödin et al., 1996; Taylor et al., 1982). Locomotion is a fundamental physical expense in the wild since animals need to move in their home range in order to reach food resources. Therefore, it is common for locomotion patterns to be closely linked to seasonal changes in environmental conditions (Wallace, 2006). In some species, low food availability can induce high foraging effort (Goodson et al., 1991), long travel distances (Harris et al., 2009; Hill and Agetsuma, 1995) and high energy expenditure. Additionally, feeding competition may also affect foraging-induced energy expenditure. Large groups and lower-ranking individuals often travel more as a result of scramble and contest feeding competition, respectively (Saj and Sicotte, 2007; van Schaik and Noordwijk, 1988). Finally, the energetic costs induced by physical activities can impair energy allocation to reproduction and consequently can bear fitness costs (Jasienska, 2003).

Lastly, a major factor involving an increase in metabolic demands and in energy expenditure in mammals is reproduction. Although some important energetic costs have been highlighted in males (Emery Thompson and Georgiev, 2014), female mammals bear the bulk of the energetic burden of reproduction. Females have to support the substantial demands of gestation and lactation, which cause an increase in energy requirements by 20 – 30 % and 35 – 149 %, respectively (Gittleman and Thompson, 1988). Lactation is the most expensive stage of the reproductive cycle since a tremendous energetic investment is necessary when producing milk and providing maternal care (Gittleman and Thompson, 1988; Prentice and Prentice, 1988; Pond, 1977). In some species, some of the costs of lactation can be alleviated by allomaternal care (Heldstab et al., 2017). The energetic costs of gestation are also substantial since energy has to be allocated to the support of the fetus and critical tissues (e.g. uterus, placenta, mammary gland; Gittleman and Thompson, 1988). Thus, reproducing females typically exhibit high metabolic rates and energy expenditure (Stephenson and Racey, 1993; Powell and Leonard, 1983; Rashid and Ulijaszek, 1999). The energetic costs of female reproduction can result in fat stores withdrawal (with extreme cases reported in grey seal (*Halicoerus grypus*): Fedak and Anderson, 1982; Oftedal, 2000; Wade et al., 1986), weight loss (Bercovitch, 1987), oxidative damage (Bergeron et al., 2011), immune deficiency (Festa-Bianchet, 1989; East et al., 2015; Archie et al., 2014) and faster aging (Jasienska, 2020). Ultimately, investing energy in reproduction may lead to severe fitness consequences in females, affecting future reproductive performance and survival (Festa-Bianchet et al., 2019; Koivula et al., 2003; Hamel et al., 2012).

Different energetic challenges, from both internal and external factors, are therefore likely to induce a decrease in energy intake and/or an increase in energy expenditure, leading to a negative energy balance and severe consequences on fitness. Several adaptations have evolved to overcome energetic challenges and their impact on energy balance.

2. Behavioral adaptations

Behavioral plasticity is a key mechanism involved in maintaining a viable energy balance in the face of energetic challenges. Behavioral adaptations have emerged since they enhance fitness by overcoming current or future fluctuations in energy supply and demands. Behaviorally counteracting the costs of energetic challenges particularly relies on adjustments with regards to activity budget and feeding behavior.

2.1. Modulation in activity budget

Environmental conditions such as climate or food availability are major factors inducing modulation in activity patterns. When conditions become harsh (e.g. in winter, typically characterized by food shortage and low ambient temperatures), and when species do not migrate to escape them, it becomes vital for individuals to reduce costly activities in order to keep energy expenditure to a minimal level (Riek et al., 2017; Arnold et al., 2006). For example, some species lower physical activity and increase resting time when facing cold ambient temperatures (Hanya, 2004). In addition, behavioral thermoregulation is common when overcoming ambient temperatures outside thermoneutrality. For example, when it is too cold, huddling behaviors limit heat dispersion and increase survival (Terrien et al., 2011; Sealander, 1952).

When coping with cold and energy shortages some species also suspend the maintenance of body temperature by entering a state of hypometabolism, i.e. lowering their metabolic rate, and thus their endogenous heat production, and by becoming more tolerant to low body temperatures (Arnold et al., 2006). In extreme cases, considerable reductions in basal metabolic rate have been reported, with a 65 % reduction during daily torpor (a torpid state characterized by a cold lethargy) and up to a 98 % reduction during hibernation (torpor bouts lasting several days; Ruf and Geiser, 2015; Jastroch et al., 2016). Substantial energy saving can therefore be achieved by entering a torpid state (Armitage et al., 2003; Kelm and Helversen, 2007). Torpor is also typically included in a set of behavioral adaptations. For example, food hoarding or activities promoting fat accumulation prior to environmental harshness can be essential for some species to provide an energy supply during periodic arousals in the course of hibernation (Lyman, 1954; Speakman and Rowland, 1999).

Besides environmental constraints, energetic challenges relative to internal factors have also induced behavioral adaptations. Gestating or lactating females can reduce their physical activity and increase their resting time as an energy-saving mechanism to cope with the energetic requirements of reproduction (Goldberg et al., 1991; Melzer et al., 2009; Dias et al., 2011; Rose, 1994; Barrett et al., 2006; Miller et al., 2006; Gamo et al., 2013). Such behavioral coping mechanisms enhance female reproductive performance (Roberts et al., 1982).

Behavioral adaptations in response to energetic challenges involve some activities being expressed more or less extensively (e.g. resting) and some emerging only during challenging time (e.g. in torpid state). Another fundamental activity likely to change in the face of energetic challenges is feeding as it determines energy intake and therefore represents in itself a major component of energy balance.

2.2. Feeding behavior

2.2.1. Nutrient extraction from the environment

Food is the one and only external source of energy for animals and food ingestion is therefore an indispensable activity to extract energy from the environment and fuel an individual's metabolic machinery (Wilmore and Costill, 2001). The energy yield of food is expressed in calories (cal) or joules (J, with 1 cal= 4.184 J) and is determined by three macronutrients providing energy: carbohydrates, proteins and lipids (Robbins, 1993a; Lambert, 2011; National Research Council, 2003a, 2003b, 2003c).

Carbohydrates are present in food in different forms. First, the most rapidly absorbed and metabolized carbohydrates are soluble sugars, which represent a readily accessible source of energy. Soluble sugars include (i) monosaccharides (single carbohydrate unit) such as glucose, which is the primary carbohydrate providing energy to metabolism, and (ii) disaccharides (two monosaccharides bound together) such as sucrose or lactose, i.e. fruit and milk sugars, respectively. Second, complex sugars, or polysaccharides, are large carbohydrates that include starch and fiber. In contrast to starch which is digestible by mammals, fiber requires fermentation in the gut to release energy, particularly insoluble fiber such as hemicellulose and cellulose, i.e. plant cell wall components. Proteins are the second major macronutrient. Unlike carbohydrates, proteins are not only a source of energy but also a source of amino acids. Proteins represent a critical part of animals' diet since some amino acids cannot be metabolically synthesized and have to be provided through food. Proteins have a fundamental role to play in growth and tissue maintenance. Lastly, lipids (i.e. fat) are a macronutrient providing twice as much energy as carbohydrates and protein. Lipids are stored in adipose tissue which forms a major bodily energy reserve. They act as a back-up resource from which energy can be drawn upon in case of emergency. In addition to their substantial energy contribution, lipids are also critically involved in other aspects of bodily functions such as in steroid hormone production (Gorbach et al., 1989).

Although they do not yield energy, micronutrients have to be ingested aside from macronutrients in order to provide a healthy diet (Robbins, 1993b, 1993c; National Research Council, 2003d, 2003e; Lambert, 2011). These micronutrients include minerals and vitamins which have key roles in biological processes and body maintenance.

Animals have to extract several important nutrients from their environment in order to gain energy, maintain their energy balance and sustain their metabolism. It is therefore vital that feeding behavior respond to specific needs by providing the adequate nutritional and energetic supply. These requirements have ultimately shaped the way animals feed.

2.2.2. Feeding adaptations

Introduced and developed within the last fifty years, the optimal foraging theory aims at predicting animals' foraging behaviors, i.e. how they 'make decisions' on how to obtain food (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971; Pyke et al., 1977). This approach tackles several aspects of foraging behaviors in a patchy environment, such as food patch selection, food patch exploitation (e.g. when leaving a food patch), movements between food patches (e.g. direction, speed, target destination) and diet selection (Pyke et al., 1977). The optimal foraging theory is fundamentally based on the assumption that a behavior maximizing net energy intake, with regards to the time and energy spent foraging, has been selected. Foraging 'decision-making' has therefore been, more or less, optimized in relation to different set of variables (Pyke, 2019). This theory has provided an important and useful framework in understanding animal feeding behavior (Pyke, 2019).

Adaptations in feeding behavior are crucial to maintaining energy balance. Importantly, these feeding adaptations or 'strategies' are not static but rather tuned to both environmental and metabolic conditions. They aim at redirecting energy intake and expenditure toward a fluctuating optimum that largely depends upon external and internal factors. Cues from the environment (e.g. food availability and distribution) and cues from the individual's internal state (e.g. internal "detectors" of negative energy balance or of specific nutrient requirements, as suggested by Rozin (1976)) influence mechanisms associated with the control of food intake (Stubbs and Tolkamp, 2006). This allows individuals to feed according to their environmental constraints and metabolic needs, contributing to maintaining energy balance (Stubbs and Tolkamp, 2006; Rozin, 1976). Feeding strategies can be different between species, between populations and also between individuals according to their age, sex or social rank among other factors (Harrison, 1983; Soumah and Yokota, 1991). Below, I focus on two important drivers of feeding behavior, namely resources in the habitat (in terms of quantity and quality) and female reproductive state. I present how these factors can impact the way individuals feed, more specifically for how long they feed and what they feed on.

Maintaining energy balance as food availability and/or quality decreases is challenging and as stated above, feeding strategies can be very different from one species to another. Therefore, different responses in terms of feeding behavior have been reported in wild species coping with fluctuating resources in their habitat. An important coping mechanism is the modulation of feeding time. For example, a nutritional deficit can be compensated by consuming more food through longer feeding bouts. Access to only low-quality food resources can then typically induce an increase in feeding time (Muruthi et al., 1991; Agetsuma and Nakagawa, 1998). In contrast, feeding time can also decrease as food availability declines since poor habitats lower feeding opportunities (Albani et al., 2020). In such food shortage situations, another possible coping mechanism is to adopt a low selectiveness in food consumption (Goodson et al., 1991). It is, for example, common that seasonality in food availability triggers cyclic modification in diet composition, with certain food being consumed only during one period of the year (Hill, 1997). Additionally, a decline in preferred food (i.e. overselected high-quality food) can induce a nutritional compensation with the consumption of 'fallback' food (i.e. relatively low-quality food which becomes a major dietary component when preferred foods are scarce), such as tubers in hunter gatherers or figs in gibbons (*Hylobates albibarbis*; Marshall and Wrangham, 2007; Lambert and Rothman, 2015; Marlowe and Berbesque, 2009; Marshall et al., 2009). Modulations of feeding time and diet composition are therefore two important feeding adaptations to cope with a reduction of food quantity and quality in the habitat.

Regardless of the environment, reproducing females typically cope with the energetic costs of reproduction by modifying their feeding behavior. Two opposite strategies have been described. With the first strategy, gestating or lactating females feed less and ingest less energy than non-reproducing females in order to rest more. By doing so, they minimize energy expenditure induced by activity and foraging, and therefore conserve energy (Harrison, 1983; Miller et al., 2006). The other strategy consists in increasing energy intake during gestation and lactation (Korine et al., 2004). There are two non-exclusive ways through which females can increase their energy intake. First, females can allocate more time to feeding (Muruthi et al., 1991; Rödel et al., 2016). Second, females can become more efficient when feeding, i.e. enhance energy intake per feeding bout (Muruthi et al., 1991). To do so, reproducing females can feed faster (increase in ingestion rate; McCabe and Fedigan, 2007) or they can feed more selectively, modifying their diet composition toward the most nutritional food (Clutton-Brock et al., 2009; Mellado et al., 2005). The latter is particularly important since reproducing females typically require specific nutrients such as proteins to support gestation and lactation (Kusina et al., 1999). It is for example common for a female to adapt her diet in order to fulfill the protein requirements of reproduction (Herrera and Heymann, 2004; Miller et al., 2006; Silk, 1987). Moreover, in order for reproducing females to maximize net intake, their increase in energy intake can also be combined with additional compensatory mechanisms that lower energy expenditure, such as a decrease in physical activity (as presented in part 2.1; Goldberg et al., 1991; Gamo et al., 2013) or in metabolic rate (Korine et al., 2004). To conclude, an increase in energy intake during female reproduction can result from increasing feeding time, increasing ingestion rate or changing diet composition. These feeding adaptations have a major impact on female fitness since deficits in energy or nutrient intake can have drastic consequences in reproductive performance (Roberts et al., 1985; Kohrs et al., 1980).

Although feeding adjustments are fundamental to enhance reproductive success they can be complicated, if not impossible, to implement since feeding behavior is also shaped by environmental conditions. Therefore many mammals living in a seasonal environment have adapted to synchronize reproductive events with food resource fluctuations (Jönsson, 1997; first identified in birds: Drent and Daan, 1980). Such species have consequently become seasonal in their reproduction and different strategies have been described depending on how species synchronize breeding with peaks in food availability. While some species breed after a peak of resource availability and therefore depend on endogenous cues and fat stores to reproduce (capital breeders; e.g. bighorn ewes (*Ovis Canadensis*): Festa-Bianchet et al., 1998); others living in a predictable environment mate prior to a peak of food availability to synchronize lactation with food abundance (income breeders; e.g. Antarctic fur seals

(*Arctocephalus gazelle*): Oftedal et al., 1987). Some species can also meet halfway on the seasonal breeding spectrum and use mixed strategies in their mating pattern (relaxed-income breeders; Weddell seals (*Leptonychotes weddellii*): Wheatley et al., 2008). Integrating current and/or future external energy supply with reproduction timing has thus become a crucial behavioral adaptation to reproduce successfully in a seasonal habitat.

Species have behaviorally adapted in the face of external and internal energetic challenges by adjusting the way they interact with their environment and how they extract energy and nutrients from it. In addition to behavioral adaptations, species have also adapted physiologically, i.e. with regards to the biology of their body. For example, the composition and activity of the gut microbiota can vary in times of cold or food shortage which appears to be an effective mechanism buffering against a decline in energy balance (Chevalier et al., 2015; Amato et al., 2015; Sommer et al., 2016; Baniel et al., 2021). Hormones are also involved in many stages of the metabolic process ranging from energy intake and storage to energy mobilization and expenditure. For that reason, physiological adaptations regarding hormonal level play an important role when coping with energetic challenges.

3. Physiological adaptations

Through evolutionary time, the physiological adaptability of an organism has contributed to the support of metabolic demands and/or the maintenance of homeostasis (i.e. a steady biological state of dynamic equilibrium which is optimal for survival; McEwen and Wingfield, 2003) in response to internal or external sources of disturbances such as female reproduction (Speakman, 2008) or a changing environment (Young et al., 1989). These physiological processes regulating homeostasis rely predominantly on the endocrine system and on the associated hormonal release. Hormones are indispensable organic chemical messengers involved in life history traits (Finch and Rose, 1995) and some of them function as essential modulators of energy metabolism. Below, I present three hormone classes involved in energy assimilation, energy expenditure and energy store mobilization: insulin, thyroid hormones and glucocorticoids.

3.1. Insulin and urinary C-peptide

Insulin is released from the pancreas in response to an increase in blood glucose levels (resulting, for example, from food ingestion; Henquin et al., 2006; Wolever and Bolognesi, 1996; Hedeskov, 1980). This hormone is crucial for energy uptake as it promotes glucose absorption into cells and glucose storage by tissues such as liver, adipose tissue or skeletal muscles (Dimitriadis et al., 2011). In addition to its immediate release following food intake, insulin is on a longer time scale a regulator of energy stores and a signal of energy balance to the brain (Strack et al., 1995). Specifically, insulin acts in the central nervous system by regulating the expression of neurons involved in energy homeostasis (Loh et al., 2017). For example, insulin action on a neurotransmitter called neuropeptide Y induces a reduction in appetite and an increase in energy expenditure (Loh et al., 2017).

The biosynthesis of insulin consists in the breaking down of proinsulin (Kitabchi, 1977), which releases insulin and C-peptide (a small polypeptide) in equimolar amount (i.e. 1:1; Melani et al., 1970; Rubenstein et al., 1969). C-peptide has no biological function and is further excreted into urine at a constant clearance rate (Kruszynska et al., 1987). The concentration of urinary C-peptide (uCP) is positively correlated with circulating insulin (Wolden-Hanson et al., 1993; Hoogwerf and Goetz, 1983; Melani et al., 1970) and therefore, uCP assessment provides an indirect measure of insulin production.

To date studies validating and using uCP levels as a marker of energy balance have been largely performed on primates (Emery Thompson, 2016a). Many studies have provided evidence that uCP (and therefore insulin) concentrations are positively linked to changes in body mass (Deschner et al., 2008; Ellison and Valeggia, 2003; Girard-Buttoz et al., 2011; Hoogwerf and Goetz, 1983; Kruszynska et al., 1987; Wolden-Hanson et al., 1993) and thus, to changes in energy balance (Bergstrom et al., 2020). Consequently, factors affecting energy balance, such as environmental conditions, influence uCP levels. For example, uCP levels are positively associated with food availability (Dias et al., 2018; Emery Thompson et al., 2009; Emery Thompson and Knott, 2008; Grueter et al., 2014; Harris et al., 2009; Lucchesi et al., 2020; Sherry and Ellison, 2007; Wessling et al., 2018b) and quality (Emery Thompson et al., 2012, 2009; Fürtbauer et al., 2020; Kurihara et al., 2020; Nurmi et al., 2018). Moreover, uCP levels are positively linked to energy intake, particularly from carbohydrates and proteins (Emery Thompson and Knott, 2008; Henquin et al., 2006; Hoogwerf et al., 1986). However, in spite of favorable feeding conditions, uCP levels can decline in reaction to an increase in energy expenditure induced, for example, by infections (Emery Thompson et al., 2009). The energetic expense associated with physical activity or lactation also typically induce low uCP levels (Sacco et al., 2021; Frisch et al., 1984; Blix et al., 1982; Dias et al., 2018; Emery Thompson et al., 2012). uCP concentration therefore rises in reaction to energy intake and declines with energy expenditure. These uCP level fluctuations illustrate the fact that insulin production and the induced amount of energy stored are modulated according to energy balance.

3.2. Thyroid hormones

The thyroid gland is part of the neuroendocrine system and specifically belongs to the HPT axis (hypothalamic-pituitary-thyroid axis). The stimulation of this gland induces the release of thyroid hormones into the bloodstream. These hormones are involved in mammalian growth and development (Behringer et al., 2014; Gobush et al., 2014; Keogh et al., 2013; Parra et al., 1980; Yousef and Luick, 1971). Additionally, thyroid hormones have a fundamental role to play in energy metabolism since they act as regulators of metabolic rate (Kim, 2008; Hulbert, 2000). Triiodothyronine (T3) is considered the biologically most active form of thyroid hormones and its production induces an increase in metabolic activity and thus in the associated energy expenditure (Kim, 2008; Rosenbaum et al., 2000). The regulation of this hormone is a crucial physiological adaptation in the face of energetic challenges (Chatzitomaris et al., 2017).

First, when coping with a decrease in energy intake, T3 typically decreases which lowers the metabolic rate and saves energy (Eales, 1988; Flier et al., 2000). This decline in T3 in relation to low energy intake has been shown in food-restriction experiments (Deschner et al., 2020; Fontana et al., 2006; Brecchia et al., 2006; Blake et al., 1991; Blum et al., 1980; Harlow and Seal, 1981; Merimee and Fineberg, 1976; Schaebs et al., 2016), and further supported in studies assessing energy intake in wild species (Jesmer et al., 2017). Second, a rise in T3 production has been reported in situations inducing an increase in metabolic demands such as physical activity (Hackney et al., 2012), mating (Cristóbal-Azkarate et al., 2016) or pregnancy (Chatzitomaris et al., 2017; Dias et al., 2017; Glinoer, 1997). Lastly, as mentioned earlier, the metabolic expense of energy is dissipated as heat. By modulating metabolic rate and energy expenditure, thyroid hormones are therefore involved in heat generation, i.e. thermogenesis (Bianco et al., 2005; Dauncey, 1990; Laurberg et al., 2005; Silva, 2006). The link between thyroid activity and ambient temperature was introduced more than a century ago (Mills, 1918). Since then experimental and field studies have provided evidence that heat exposure typically triggers a decline in thyroid hormones (El-Nouty et al., 1978; Sejian et al., 2014), whereas cold exposure induces the opposite effect, i.e. a rise in thyroid activity (Bauman and Turner, 1967; Kaethner and Good, 1975) and in T3 concentration (El-Nouty et al., 1978; Gale, 1975; Oki and Atkinson, 2004). In conclusion, T3 functions as an endocrine control of 'fuel consumption' by modulating the metabolic rate and expense of energy in relation to nutritional status and metabolic demands.

3.3. Glucocorticoids

The adaptive response to homeostasis-threatening situations induces the release of the metabolic hormone class of glucocorticoids (e.g. cortisol or corticosterone) and is commonly referred to as the stress response (first introduced as the "general adaptation syndrome": Selye, 1946; Charmandari et al., 2005; McDougall-Shackleton et al., 2019). Glucocorticoids are secreted in the adrenal glands along the HPA axis (hypothalamic-pituitary-adrenal axis) and they are the primary mediators of allostasis, i.e. processes maintaining stability (homeostasis) through changes (Romero et al., 2009; McEwen and Wingfield, 2003). These hormones act as inhibitors of body functions that are not immediately essential for survival (e.g. digestion, growth or reproduction; Sapolsky et al., 2000; Charmandari et al., 2005) and in doing so, glucocorticoids redirect energy allocation. They also increase energy availability by impeding glucose absorption and promoting energy mobilization from energy stores (through gluconeogenesis and lipolysis; Exton et al., 1972). Overall, glucocorticoids trigger an increase in readily available energy (i.e. blood glucose level) in the face of a psychological stressor (Creel et al., 2013) or, more importantly here, an energetic challenge.

An increase in glucocorticoids has been reported in animals facing a decrease in environmental resources both in terms of quantity (Champoux et al., 1993; McLarnon et al., 2015; Conn et al., 1995; Malcolm et al., 2014) and quality (Chapman et al., 2015; Foerster et al., 2012; Pokharel et al., 2019). Therefore a decline in nutritional status, induced by low energy intake, commonly leads to a rise in glucocorticoids to mobilize energy stores in times of shortage (Laver et al., 2020; Lodge et al., 2013; Jeanniard du Dot et al., 2009). In addition, increasing energy availability through a rise in glucocorticoids has been observed in times of heightened energy expenditure. For example, physical activity (Girard and Garland, 2002;

Hackney et al., 2012; Markham et al., 2015), female reproductive states (Dunn et al., 2013; Emery Thompson et al., 2010; Dantzer et al., 2010; Goymann et al., 2001; Laver et al., 2020), cold ambient temperatures (de Bruijn and Romero, 2018) or infections (Behie and Pavelka, 2013) can induce high glucocorticoid concentrations. Overall, the endocrine control of energy allocation and availability through glucocorticoid production is a physiological adaptation in response to fluctuating energetic needs and energy balance.

Insulin, thyroid hormones and glucocorticoids are hormones involved in energy metabolism and the modulation in their production is adaptive to various energetic challenges. They have a large influence on survival as their dysfunction or absence can lead to death (Katsarou et al., 2017; Triandafillou et al., 1982; Darlington et al., 1990). Importantly, besides uCP, T3 and glucocorticoids can be measured non-invasively through urine as their urinary concentrations correlate with circulating levels (Burke and Eastman, 1974; Crockett et al., 1993). This hormonal assessment from a non-invasively collected matrix such as urine has revolutionized studies on energetics (i.e. studies investigating mechanisms involved in different components of energy metabolism such as energy acquisition, energy storage or energy utilization). The urinary concentrations of uCP, T3 and glucocorticoids provide a gateway to the evaluation of energy balance and physiological adaptations in response to energetic challenges. Specifically, while uCP allows an evaluation of overall energy balance, T3 and glucocorticoids bring a complementary energetic picture with regards to metabolic rate (energy expenditure) and energy mobilization, respectively. Therefore, assessing and integrating these hormones is a powerful approach when studying energetics and this will be detailed in the next section.

4. This thesis

4.1. Thesis aim

Behavioral and physiological adaptations contribute to the support of metabolic needs and alleviate the costs energetic challenges can have on fitness. These adaptations are various and might act in concert in supporting energy demands, body maintenance and survival in challenging times (Nie et al., 2015). However, to date few studies have provided an integrative approach by considering, for example, how energetic challenges can *simultaneously* impact (i) several hormones involved in energy metabolism or (ii) both behavior and hormones. Such investigations are needed to shed light on complementary adaptations that have emerged concomitantly and to assess on a fine-scale energetic conditions induced by different challenges among mammals. This integrative approach will allow a better evaluation of the magnitude of the energetic costs of various challenges which will lend valuable insight into the way such energetic constraints might have driven life history traits in different species. The main aim of this dissertation is to investigate physiological and behavioral responses to various energetic challenges in order to provide an integrative picture of the set of adaptations acting in concert when coping with a challenging situation.

Specifically, the first aim of this thesis is to combine several energetic markers to assess the physiological reaction to different energetic challenges. While most studies have provided insights on how energetic challenges affect one specific biomarker of energy balance (e.g. Dias et al., 2018; Fürtbauer et al., 2020; Laver et al., 2020), very few have taken the path of combining several markers. Simultaneously assessing several energetic markers offers a promising approach to look from different windows at the core sustaining an individual's life, i.e. its energy metabolism. This way, we can tease apart several determinants of an individual's energy condition (e.g. energy assimilation, energy expenditure, energy mobilization) and investigate their respective, and complementary, shifts in reaction to energetic challenges (Emery Thompson, 2016b). For example, assessing glucocorticoids alongside another energetic marker such as thyroid hormones would parse the respective contribution to energy mobilization and energy expenditure and therefore help in determining the energetic condition of an individual. Specifically, an increase in glucocorticoids (i.e. rise in energy mobilization) would be indicative of an energy deficit when combined with a decrease in thyroid hormones (i.e. reduced metabolic rate and energy expenditure), while it would illustrate heightened energy demands while combined with a rise in thyroid hormones.

To date only a handful of studies have jointly assessed glucocorticoids with thyroid hormones. These studies aimed at understanding foraging strategies (Jesmer et al., 2017), disentangling psychological stressor from energetic challenge (Ayres et al., 2012; Joly et al., 2015; Pritchard et al., 2020; Vynne et al., 2014) or investigating the effects of various energetic challenges on individuals' energetic condition (Dias et al., 2017). Some provided evidence that food availability or energy intake did not influence thyroid hormone or glucocorticoid levels (Pritchard et al., 2020) while others found an increase only in thyroid hormones (Dias et al., 2017) or in both hormones (Jesmer et al., 2017). The discrepancy of the few results available illustrates the need for further investigation in understanding how thyroid hormones and glucocorticoids are affected by energetic challenges in different species. This dissertation aims at contributing to this growing body of research by jointly assessing thyroid hormones and glucocorticoids and examining how they react to various energetic challenges.

The second aim of this thesis is to combine a physiological marker with behavior to assess the energetic impact of a major challenge faced by female mammals. Reproduction has provided a stimulating field of research for studies on energetics. Numerous studies have examined the energetic costs of female reproduction through a behavioral (e.g. Clutton-Brock et al., 2009; Korine et al., 2004; Muruthi et al., 1991) or physiological (e.g. Gesquiere et al., 2018; Gholib et al., 2018; Grueter et al., 2014) approach. Although these studies have largely contributed to enlightening the behavioral or hormonal shifts associated with the substantial costs of female reproduction, their results typically lead to new questions or extrapolation. For example, when no differences in uCP levels are found between females at different reproductive states, does it mean that reproduction is not costly enough to trigger changes in female energy balance? Probably not. It rather suggests that reproducing females have likely adopted behavioral shifts to buffer these costs and maintain similar uCP levels to non-reproducing females (Fürtbauer et al., 2020; Grueter et al., 2014). Such cases illustrate the importance of combining a behavioral approach with hormonal assessment in order to further investigate how energetic costs can potentially be offset or buffered by behavioral shifts (Girard-Buttoz et al., 2014). Therefore, this dissertation also aims at providing an additional study to the limited corpus of research investigating the energetic costs of female reproduction from both a physiological and a behavioral perspective.

In conclusion, with this dissertation, the effects of several energetic challenges are investigated through a multifaceted prism: either by combining two energetic markers or by combining behavior with an energetic marker. Species living in a seasonal habitat are a model of choice for such studies on energetics as they typically experience various challenges in relation to fluctuations in environmental conditions.

4.2. Study species

The population of Assamese macaques (*Macaca assamensis*) at Phu Khieo Wildlife Sanctuary in Thailand provides a good model for studying the behavioral and physiological impact of energetic challenges. First, they live in a habitat exhibiting two distinct seasons: a cold dry season (from November to February; Figure 1) and a hot rainy season (from March to October), in which minimum ambient temperature reaches 5 ºC and 23 ºC, respectively (Richter et al., 2016). The habitat is also characterized by repeated patterns of fluctuating resource availability and this in spite of a large variability between years (Heesen et al., 2013; and see Figure 1 to visualize fluctuations in fruit availability during one year). Fruit availability appears to be a determinant of energy intake and activity patterns in this population (Heesen et al., 2013; Richter et al., 2016). Therefore, changes in ambient temperatures, in energy intake and in physical activity might represent three potential energetic challenges that females have adapted to cope with and they might individually trigger shifts in energy metabolism.

Second, as in all mammalian species, another major energetic challenge experienced by females is reproduction. Peak of lactation is synchronized with a peak of fruit availability (Heesen et al., 2013). Fruit availability also modulates conception rates (Heesen et al., 2013). As females seem to rely both on exogenous and endogenous cues to conceive, the population has been described as relaxed-income breeders (Heesen et al., 2013). Additionally, females bear visible costs when reproducing since lactating females exhibit poor physical condition (Heesen et al., 2013), suggesting a decline in their energetic condition. At the onset of the mating season, which spans from October to February (Figure 1; Fürtbauer et al., 2010), a female's energetic condition will determine whether or not she will conceive in the respective mating season. Females who gave birth late in the previous year will typically skip a year and exhibit a two-year interbirth interval (Fürtbauer et al., 2010). This indicates that females need some time to recover from their previous reproductive investment before being able to conceive again. The energetic costs of reproduction are clearly illustrated in this population and motivates further investigation on that regard, in terms of physiological and behavioral shifts potentially occurring during the reproductive cycle.

Third, female Assamese macaques exhibit a stable dominance hierarchy characterized by conflict avoidance and feeding tolerance between females with strong social bonds (Heesen et al., 2014). This may explain why, in spite of the contest feeding competition induced by the distribution and quality of food items in their habitat (Heesen et al., 2013; Schülke et al., 2011), dominance rank is not a determinant of energy intake, reproductive success and glucocorticoid levels in this population (Heesen et al., 2013; Fürtbauer et al., 2014). This is advantageous when studying energetics as social rank can therefore be discarded from any potential drivers of female energetic condition. Moreover, in addition to fruits, Assamese macaques rely on many other food items to fulfill their nutritional requirements (Heesen et al., 2013; Schülke et al., 2011). Such diversity in the diet is common among primate species (Milton, 1984; Lambert and Rothman, 2015) and is a stimulating feature for studies investigating potential shift in dietary composition in relation to energetic challenges. Lastly, energetic markers can be assessed non-invasively in this population as studies have previously validated the assessment of uCP, T3 and cortisol from urine samples in macaques species (Girard-Buttoz et al., 2011; Sadoughi et al., 2021; Bahr et al., 2000).

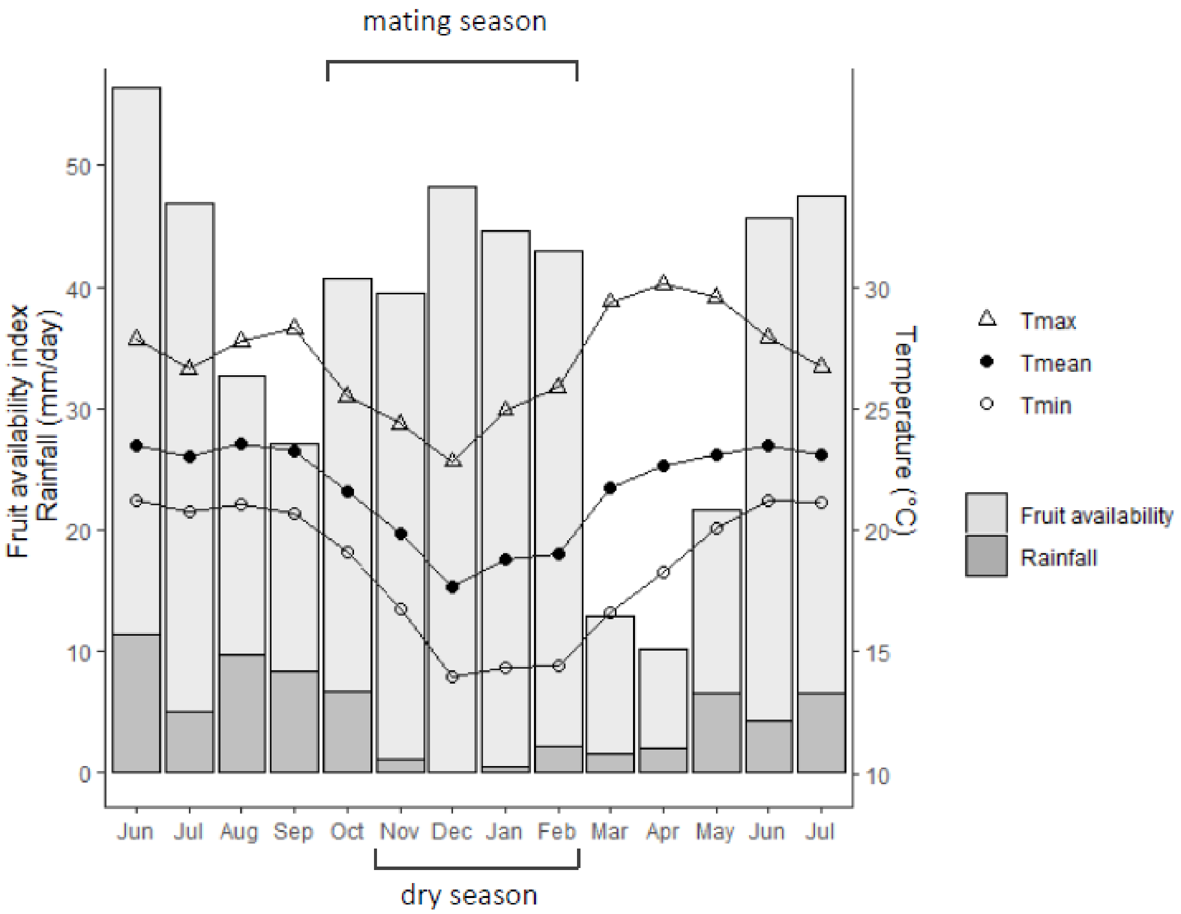

Figure 1. Variation in monthly average of fruit availability, rainfall, mean ambient temperature (Tmean), maximum ambient temperature (Tmax) and minimum ambient temperature (Tmin) through one year (from June 2017 to July 2018).

In conclusion, female reproduction, seasonal fluctuations in energy intake, physical activity and ambient temperature are potential energetic challenges that female Assamese macaques have adapted to. These challenges may trigger shifts in behavior, especially in feeding behavior, and potentially induce modulations in uCP, T3 and cortisol production. The concomitant investigation of behavioral and physiological responses to energetic challenges would therefore be particularly relevant and informative, especially for species living in a seasonal habitat, such as Assamese macaque.

4.3. Thesis content

To investigate energetics in wild female Assamese macaques, I focused on four potential energetic challenges experienced by this seasonal species: (i) a low energy intake assessed via behavioral and nutritional data, (ii) an increase in physical activity estimated from daily travel distances, (iii) thermogenesis when facing cold ambient temperatures and (iv) reproduction (gestation and lactation). I studied how these challenges may impact female activity budget, feeding behavior and/or energy metabolism. To do so, I assessed uCP, T3 and cortisol levels from urine samples. With the aim of providing an integrative picture of the behavioral and physiological consequences of various energetic challenges, I conducted my investigation through two main chapters (Figure 2).

In the second chapter of this thesis, I combined the assessment of two energetic markers, T3 and cortisol, and investigated how the four energetic challenges may individually drive the production of these hormones. This first study aims at disentangling the physiological adaptations involved in metabolic rate and energy mobilization in response to different challenges.

In the third chapter, I focused on one challenge, i.e. reproduction, and I investigated the energetic costs of gestation and lactation through the behavioral and physiological shifts they may induce. Specifically, in addition to measuring uCP levels, I assessed females' activity budget and dissected several components of their feeding behavior in order to compare all these different metrics across females in different reproductive states. This second study will help in understanding different and complementary coping mechanisms in females facing the substantial energetic demands of reproduction.

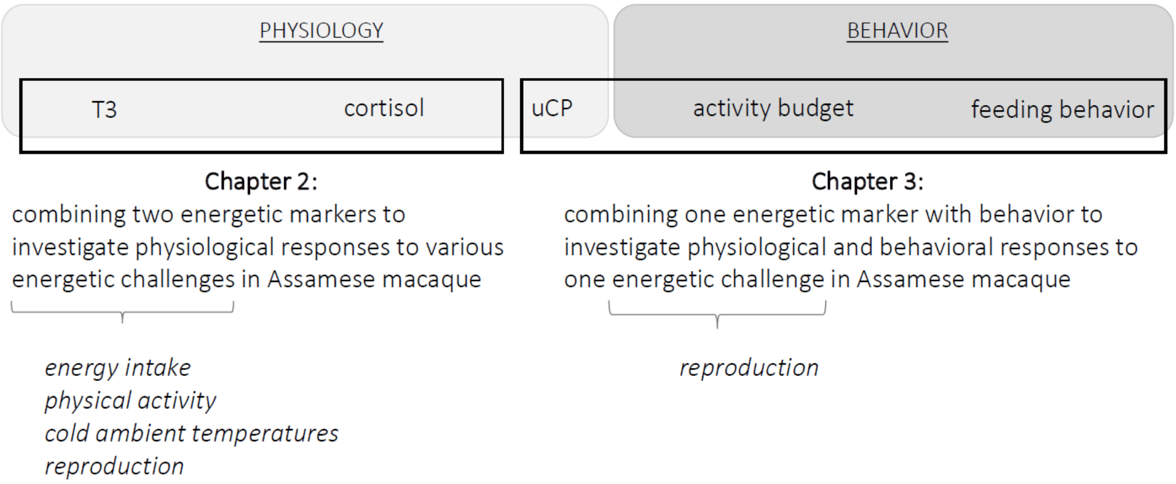

Figure 2. Visualization of the content of chapters 2 and 3 of this thesis.

CHAPTER 2

Triiodothyronine and cortisol levels in the face of energetic challenges from reproduction, thermoregulation and food intake in female macaques

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Abstract

Energy availability drives an individual's fitness and can be affected by diverse energetic challenges. The assessment of hormones involved in metabolic activity and energy mobilization provides a gateway to the study of physiological adaptations in response to changes in energy availability. Here, we investigated immunoreactive urinary total triiodothyronine (uTT3, thyroid hormone secreted through the hypothalamus-pituitary-thyroid axis and regulating the basal metabolic rate) alongside glucocorticoids (i.e. urinary cortisol, uCort, secreted through the hypothalamus-pituitary-adrenal axis and mediating energy mobilization) in wild female Assamese macaques (*Macaca assamensis*). Combining more than 2,900 h of behavioral data from 42 adult females with physiological data from 382 urine samples, we evaluated both uTT3 and uCort in relation to potential energetic challenges encountered by a female, namely fluctuations in energy intake, travel distance, reproductive state and minimum ambient temperature. As predicted, levels of both hormones changed in response to variation in energy intake with a tendency toward a positive effect on uTT3 and a significant negative effect on uCort levels. Unexpectedly, neither hormone was influenced by variation in travel distance. Reproductive state affected both hormones with higher levels of uTT3 and uCort in the second half of gestation. Finally, a decrease of minimum temperature triggered an increase in uCort but unexpectedly not in uTT3. Collectively, our results highlight the respective contribution of two endocrine axes when facing energetic challenges and the underlying metabolic strategies to cope with them. Overall, assessing thyroid hormones together with glucocorticoids provides an integrative picture in the evaluation of an individual's energy status.

Key words

Thyroid hormones; Glucocorticoids; Energy intake; Energy expenditure; Travel distance; Reproduction; Ambient temperature; Primate; Energy mobilization; Metabolic activity

CHAPTER 3

The effect of reproductive state on activity budget, feeding behavior, and urinary C-peptide levels in wild female Assamese macaques

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Behavioral Ecology and Sociobiology (accepted)

Abstract

The source of maternal energy supporting reproduction (i.e. stored or incoming) is an important factor determining different breeding strategies (capital, income or mixed) in female mammals. Key periods of energy storage and allocation might induce behavioral and physiological shifts in females, and investigating their distribution throughout reproduction helps in determining vulnerable phases shaping female reproductive success. Here, we examined the effects of reproductive state on activity budget, feeding behavior, and urinary C-peptide (uCP) levels, a physiological marker of energy balance, in 43 wild female Assamese macaques (*Macaca assamensis*). Over a 13-month study period, we collected 96,266 instantaneous records of activity and 905 urine samples. We found that early lactating females and non-gestating – non-lactating females follow an energy-saving strategy consisting of resting more at the expense of feeding and consuming mostly fruits which contributed to enhancing their energy intake and feeding efficiency. We found an opposite pattern in gestating and late lactating females who feed more at the expense of resting and consume mostly seeds, providing a fiber-rich diet. Storing food into cheek pouches increased throughout gestation while it decreased all along lactation. Lastly, we found the highest uCP levels during late gestation. Our results reflect different feeding adaptations in response to the energetic costs of reproduction and suggest a critical role of fat accumulation before conception and metabolizing fat during gestation and lactation. Overall, our study provides an integrative picture of the energetics of reproduction in a seasonal species and contributes to our understanding of the diversity of behavioral and physiological adaptations shaping female reproductive success.

Key words

Reproduction; Activity budget; Diet composition; Energy intake; Feeding efficiency; Urinary C-peptide

CHAPTER 4

General discussion

The overall aim of this thesis was to contribute to the understanding of the physiological and behavioral responses to energetic challenges in mammalian females. I investigated how energy-demanding situations affected female hormone levels, activity budget and feeding behavior. This integrative approach allowed the evaluation of different sets of complementary adaptations that emerged in the face of various challenging situations. Female Assamese macaques (*Macaca assamensis*) provided a good model for the purpose of my research as they have to cope with different potential energetic challenges, naturally occurring in their seasonal habitat in Thailand (e.g. fluctuations in fruit availability and ambient temperature). I collected behavioral and nutritional data together with urine samples. From the latter, I assessed three different physiological markers of energy metabolism: glucocorticoid (cortisol) metabolite levels, and, for the first time in this species, urinary C-peptide of insulin (uCP) and thyroid hormone (triiodothyronine, or T3) metabolite levels. In the first study (Chapter 2), I combined markers of energy mobilization (cortisol) and metabolic rate (T3) to jointly investigate their modulation in response to potential energy-costly situations. The results showed that depending on the undergoing energetic challenge, the induced rise in cortisol will be combined with either an increase or a decrease in T3 levels. In the second study (Chapter 3), I focused on one specific energetic challenge, namely reproduction, and examined its effect both on female behavior (activity budget and feeding behavior) and energy balance (uCP levels). The results revealed both behavioral and physiological adaptations throughout the reproductive cycle. An overview of the results from chapters 2 and 3 are depicted below (Figure 1).

In this general discussion, I first combine the results of chapters 2 and 3 in order to provide an overview of the energetic picture in female Assamese macaques. Second, I integrate the results of the present thesis into the growing body of research on energetics. I specifically review the state of the art regarding the three energetic markers in primates. Third, I suggest future research directions for forthcoming studies on energetics and highlight the importance of addressing research questions on energetics through a multifaceted approach. I stress the value of integrative approaches consisting in measuring several physiological markers and adding behavior into the energetic picture. Fourth, I present research implications with regards to wildlife conservation.

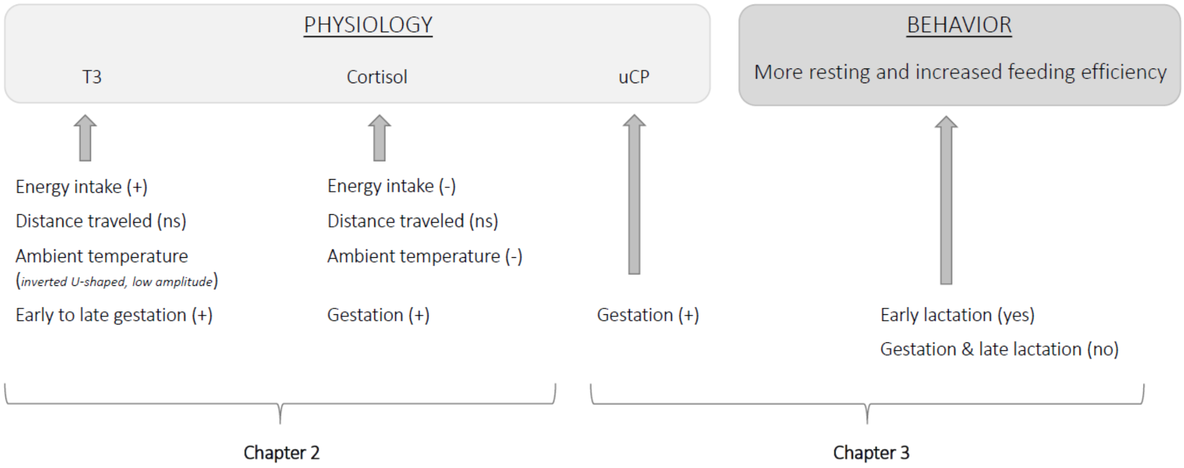

Figure 1. Overview of the results. Direction of effects of various challenges is indicated in parentheses.

(+): induces a significant increase (trend in the case of the effect of energy intake on T3 levels)

(-): induces a significant decrease

(ns): non-significant effect

1. Energetics in female Assamese macaques

1.1. Energy intake

In times of low energy intake, female Assamese macaques mobilize their fat stores, as illustrated by the increase in glucocorticoid (cortisol) level (Chapter 2). They simultaneously tend to lower their metabolic rate as suggested by a decline in T3 levels, in order to conserve energy (Chapter 2). Interestingly, when controlling for female reproduction and travel distance, variation in fruit availability does not influence female uCP levels and thus energy balance (Chapter 3). Two options could explain these comparable levels of uCP as fruit availability changes. First, it might be that the physiological responses involving energy mobilization from fat stores and reduction in energy expenditure by slowing down metabolic rate are good coping mechanisms when fruit availability is low, i.e. when energy intake decreases (Heesen et al., 2013). Second, it may be that the high levels of glucocorticoids as energy intake decreases trigger insulin resistance (Zhou et al., 2016; Geer et al., 2014). This potential modulation in insulin sensitivity would therefore impede the interpretation of uCP levels and the inference of energy balance as energy intake fluctuates. While I could not disentangle these two possibilities, I could still highlight that energy intake gets low enough to trigger a physiological response in female Assamese macaques. Whether or not this affects their energy balance remains unclear.

1.2. Female reproduction

Female Assamese macaques exhibit an increase in energy demands over the course of gestation as illustrated by an increase in both glucocorticoids and T3 (Chapter 2). In late gestation, females mobilize their fat stores and have a faster metabolism. Females therefore spend energy by drawing upon their energy reserves and by supporting an increased metabolic activity. In addition, late gestating females become more resistant to insulin, as illustrated by their high uCP levels (Chapter 3). Insulin resistance might participate in fulfilling the energetic demands of gestation. This symptom, comparable with a mild form of gestational diabetes, keeps energy intake away from maternal uptake. Readily available energy can instead be spared for the fetus needs while the mother relies on lipid oxidation (Butte, 2000). This metabolic shift toward lipid oxidation is also supported by the increase of glucocorticoids during gestation (Chapter 2). Interestingly, gestating females do not follow a behavioral energy saving strategy as they do not spend more time resting and do not enhance their feeding efficiency (Chapter 3). Taken together, the results from chapters 2 and 3 highlight that physiological, and not behavioral, responses mainly contribute to the energetic support of gestation.

With the present dissertation, I also highlight another energetic pattern during lactation in Assamese macaques. Lactating females do not exhibit any physiological signs of undergoing energetic deficit. Their T3, glucocorticoid and uCP levels are indeed similar to non-gestating – non-lactating females' (Chapters 2 and 3). Early lactating females follow a behavioral energy-saving strategy consisting in spending more time resting at the expense of feeding and being more efficient when feeding. This behavioral coping mechanism seems sufficient enough not to require additional physiological support. In contrast to gestating females, early lactating females rely particularly on behavioral, and not physiological, responses to offset the costs of lactation.

With this dissertation, I provide evidence that female Assamese macaques do not exhibit low energy balance during reproduction. Their relaxed-income breeding system, with female fat reserves modulating the ability to conceive (Heesen et al., 2013), together with physiological and behavioral shifts during gestation and lactation (Chapters 2 and 3) might efficiently overcome the energetic costs of reproduction.

1.3. Ambient temperature and travel distances

Cold ambient temperature faced by female Assamese macaques does not seem to be challenging enough to trigger thermogenesis through an increase in T3 (Chapter 2). However, a decline in ambient temperature does induce an increase in glucocorticoid levels (Chapter 2). The fact that the study population does not face a long-lasting and extreme cold might explain why a glucocorticoid release is enough to overcome the energetic costs of thermoregulation.

Lastly, from chapters 2 and 3 it appears that T3, glucocorticoid and uCP levels are not affected by travel distances (and either by traveling time in the case of T3 and glucocorticoids; Chapter 2). This absence of physiological responses suggest that female Assamese macaques do not have to overcome high energy expenditure induced by walking travel distances.

1.4. Future investigations

From this dissertation it appears that among the energetic challenges investigated, fluctuations in energy intake and reproduction are the costliest ones as they respectively induce the activation of two endocrine axes and a combination of physiological and behavioral responses. This dissertation provides an important step toward the evaluation of the energetic challenges faced by the study population and a better understanding of the physiological and behavioral coping mechanisms involved. Two gaps of knowledge remain to be filled in future studies. First, it would be very informative to know more on potential behavioral shifts in response to other challenges than reproduction. A female may decrease her behavioral energy expenditure by allocating less time into foraging and/or resting more when energy intake is limited. Behavioral thermoregulation (e.g. huddling), especially during cold nights, may also help to overcome low ambient temperatures. These behavioral adaptations might mitigate the energetic costs of low energy intake and thermoregulation. Second, as physiological data accumulates, I encourage future studies to test the potential physiological and behavioral effect of interacting energetic challenges. For example, females at different stages of the reproductive cycle may exhibit different magnitudes in their physiological responses to a similar challenge (Foerster et al., 2012; Dias et al., 2017). The absence of a strong synchrony in reproduction patterns in Assamese macaques would allow such investigations as females do not experience the same environmental conditions at the same time within their respective cycle. Investigating the potential effect of interacting energetic challenges would require a large data set encompassing several years with physiological data for the same female giving birth at different time within the mating season across years.

This thesis adds to the growing body of literature on energetic markers and provide some directions for future investigations in Assamese macaques. Next, I will integrate my findings into the broader picture of energetics in wild populations. I will specifically focus on primates as they have been the study model of most studies on energetics. The following interpretation and synthesis should hold on a broader mammalian taxonomic level.

2. Overview of energetic marker use in primates

Table 1 summarizes the results of different studies on energetics (including this thesis) assessing non-invasively uCP, T3 or glucocorticoid levels in primates. From this table, it appears that physiological responses to energetic challenges in primates do not always coincide and that several gaps and uncertainties remain to be addressed in the future. I will provide a brief review for each marker below.

2.1. uCP

2.1.1. uCP and energy balance, energy intake, food intake

The relevance of uCP as a physiological marker of energy balance in non-human primates emerged from feeding experiments in bonobos and macaque species, showing a positive association between uCP levels and food access or food dietary content (see Table 1; studies # 4; 18; 19).

Table 1. Overview of results on uCP, T3 and glucocorticoids in wild primates

					Predictors of variation in energetic marker levels									
#	Species	Location	Sex	Energetic marker	Energy intake	Food availability	Diet quality	Feeding time	Reproduction	Ambient temperature	Physical activity	Other	Notes	References
1	*Homo sapiens sapiens*	Minnesota, USA	F+M	uCP	(+)									Hoogwerf et al., 1986
2	*Homo sapiens sapiens*	Toba community, Argentina	F (lactating)	uCP					Lactation stage (+)					Ellison and Valeggia, 2003
3	*Homo sapiens sapiens*	France	F	uCP	(-)						Energy expenditure (-)	Energy balance (+)		Bergouignan et al., 2012
4	*Pan paniscus* (captive)	Frankfurt Zoo, Germany	F+M	uCP			(+)						Feeding experiment	Deschner et al., 2008
5	*Pan paniscus*	LuiKotale, DR Congo	F	uCP			(+)	(ns)	Late gestation › Non-gestating		Travel distance (ns)			Nurmi et al., 2018
6	*Pan paniscus*	LuiKotale, DR Congo	M	uCP					Copulation (ns); Mate competition (ns)					Surbeck et al., 2015
7	*Pan paniscus*	Kokolopori Bonobo Reserve, DR Congo	F+M	uCP		(+)								Lucchesi et al., 2020
8	*Pan troglodytes verus*	Fongoli, Senegal	F+M	uCP		Total food availability (+)							No correlation uCP & uGCs	Wessling et al., 2018a
8'	*Pan troglodytes verus*	Taï East & Taï South, Ivory Coast				Ripe fruit availability (+)							No correlation uCP & uGCs	Wessling et al., 2018a
9	*Pan troglodytes verus*	Taï North, Ivory Coast	F+M	uCP	(ns)	(+)					Energy expenditure (ns)			Valé et al., 2020
10	*Pan troglodytes schweinfurthii*	Kibale, Uganda	F	uCP					Lactation stage (+)					Emery Thompson et al., 2012
11	*Pan troglodytes schweinfurthii*	Kibale, Uganda	M	uCP		(+)	(+)					Infection (-)		Emery Thompson et al., 2009
12	*Pan troglodytes* (captive)	Yerkes Regional Primate Center, USA	F+M	uCP		Captive › Wild								Sherry & Ellison, 2007
12'	*Pan troglodytes schweinfurthii*	Kibale, Uganda	M	uCP		(+)								Sherry & Ellison, 2007
12''	*Pongo pygmaeus*	Gunung Palung, Indonesia	F+M	uCP		(+)							Serum C-Peptide (+)	Sherry & Ellison, 2007
13	*Pongo pygmaeus*	Gunung Palung, Indonesia	F+M	uCP	(+)	(+)								Emery Thompson & Knott, 2008
14	*Gorilla beringei beringei*	Volcanoes, Rwanda,	F	uCP		(+)			(ns)					Grueter et al., 2014
15	*Papio ursinus*	Da Gama Park, South Africa	F+M	uCP		(+)	*Spring ‹ Summer & Winter*		Gestation › Lactation & Cycling				Energy-rich seeds in summer; human food in winter	Fürtbauer et al., 2020
16	*Papio anubis*	Gashaka-Gumti, Nigeria	F	uCP	(ns)				(ns)		(-)			Lodge, 2012
17	***Macaca assamensis***	**Phu Khieo, Thailand**	**F**	**uCP**		**(ns)**			**Late gestation › Lactation, NGNL**		**Travel distance (ns)**			**This dissertation, Chapter 3**
18	*Macaca mulatta* (captive)	WRPRC, USA	F+M	uCP		(+)							Feeding experiment	Wolden-Hanson et al., 1993
19	*Macaca mulatta & Macaca fascicularis* (captive)	DPZ, Germany	F+M	uCP		(+)							Feeding experiment	Girard-Buttoz et al., 2011
20	*Macaca mulatta*	Cayo Santiago, Puerto Rico	M	uCP				(ns)	Copulation (-)		Traveling time (-); Restlessness (-)	Resting time (ns)		Higham et al., 2011b
21	*Macaca fascicularis*	Gunung Leuser, Indonesia	M	uCP		(ns)		(ns)	Mate-guarding (ns)		Height climbed (-) trend			Girard-Buttoz et al. 2014
22	*Macaca fuscata yakui*	Yakushima Island, Japan	F	uCP		(+)								Kurihara et al., 2020
23	*Alouatta palliata*	La Flor de Catemaco, Mexico	F	uCP		(+ in cycling)			(ns)					Cano-Huertes et al., 2017
24	*Alouatta palliata*	Los Tuxtlas, Mexico	F (lactating)	uCP		(+)		(ns)	Early ‹ Late lactation		Activity index (ns)		Activity index incl. feeding	Dias et al., 2018
25	*Cercocebus sanjei*	Udzungwa Mountains, Tanzania	F	uCP					Early gestation › Preconception & Early lactation					McCabe & Emery Thompson, 2013
26	*Colobus guereza*	Kibale, Uganda	F (lactating)	uCP		(+)								Harris et al., 2009
27	*Cebus imitator*	Sector Santa Rosa, Costa Rica	F	uCP	*Feeding competition (-)*				(ns)			Energy balance (+)	Low energy intake when intense feeding competition	Bergstrom et al., 2020
28	*Sapajus appella* (captive)	University of Chicago, USA	F	uCP							Physical exercise (-)		Stronger uCP decrease as exercising at faster speeds	Sacco et al., 2021

Table 1. continued

#	Species	Location	Sex	Energetic marker	Predictors of variation in energetic marker levels								Notes	References
					Energy intake	Food availability	Diet quality	Feeding time	Reproduction	Ambient temperature	Physical activity	Other		
29	*Pan paniscus* (captive)	Frankfurt Zoo, Germany	F+M	uT3	(+)		(+)						Feeding experiment; Positive correlation uCP & uT3	Deschner et al., 2020
30	*Papio cynocephalus*	Amboseli, Kenya	F	fT3		*Dry season < Wet season*			Cycling > Gestating & Lactating				Low food availability during dry season	Gesquiere et al., 2018
31	*Macaca mulatta & Macaca fascicularis* (captive)	DPZ, Germany	F+M	uT3		(+)							Feeding experiment; Positive correlation uCP & uT3	Sadoughi et al., 2021
32	***Macaca assamensis***	**Phu Khieo, Thailand**	**F**	**uT3**	**(+) trend**				**Late gestation > Early gestation**	**Tmin (inverted U-shape)**	**Travel distance (ns); Travel time (ns)**			**This dissertation, Chapter 2**
33	*Macaca sylvanus*	Atlas Mountains, Morocco	M	fT3		*Foraging time (-)*			Mating activity (+)	Tmin (-)			Foraging time: inversed measure of food availability	Cristóbal-Azkarate et al., 2016
34	*Macaca fuscata* (semi-captive)	KUPRI, Japan	F+M	fT3						Tmin (ns); Tmax (-); Winter > Summer			Provisioned animals	Thompson et al., 2017
34'	*Alouatta palliata*	Hacienda La Pacifica, Costa Rica	F+M	uT3						Tmin (-); Tmax (+); Wet (cool) season > Dry season				Thompson et al., 2017
35	*Alouatta palliata*	Los Tuxtlas, Mexico	F+M	fT3			Fruit intake (+); Young leaf intake (-)		Gestation > Lactating & Cycling	Tmin (ns); Tmax (ns)	Activity index (+); Travel rate (ns)		Activity index incl. feeding; Negative correlation fT3 & fGCs in males	Dias et al., 2017
36	*Sapajus xanthosternos* (captive)	Frankfurt Zoo, Germany	M	fT3	(+)		(+)						Feeding experiment	Schaebs et al., 2016
37	*Pan troglodytes verus*	Fongoli, Senegal	F+M	uGCs						(ns)			No correlation uCP & uGCs	Wessling et al., 2018a
37'	*Pan troglodytes verus*	Taï East & Taï South, Ivory Coast	F+M	uGCs						(+)			No correlation uCP & uGCs	Wessling et al., 2018a
38	*Pan troglodytes schweinfurthii*	Kibale, Uganda	M	uGCs		(-)								Muller & Wrangham, 2004
39	*Pan troglodytes schweinfurthii*	Kibale, Uganda	F	uGCs			(- in lactating)		Cycling non-estrous < Cycling estrous, Lactating & Gestating					Emery Thomspon et al., 2010
40	*Papio anubis*	Gashaka-Gumti, Nigeria	F	fGCs	*Crop-raiding < Non-crop-raiding*				Gestation stage (+)	(ns)		Progesterone (+)	High energy intake in crop-raiding troup	Lodge et al., 2012, 2013
41	*Papio anubis*	Kwano, Nigeria	F	fGCs		Vine fruit availability (-); Tree fruit availability (ns)			(ns)	Tmax (+); Tmin (+)				McLarnon et al., 2015
41'	*Papio anubis*	Gamgam, Nigeria	F	fGCs		Vine fruit availability (ns); Tree fruit availability (ns)			(ns)	Tmax (ns); Tmin (ns)			Crop-raiding troup	McLarnon et al., 2015
42	*Papio cynocephalus*	Amboseli-Longido, Kenya-Tanzania	F	fGCs						Tmax (ns)	Travel distance (+)			Markham et al., 2015
43	*Papio cynocephalus*	Amboseli, Kenya	F (gestating)	fGCs					Gestation stage (ns)			Infection (+)		Beenher et al., 2006
44	*Papio cynocephalus*	Amboseli, Kenya	F	fGCs		*Dry season > Wet season*		Entire year (ns); Dry season (+)	Gestation > Early lactating and Cycling	Tmax (+)			Low food availability during dry season	Gesquiere et al., 2008
45	*Papio cynocephalus*	Amboseli, Kenya	M	fGCs		*Dry season > Wet season*				Tmax (ns)			Low food availability during dry season	Gesquiere et al., 2011

Table 1. continued

#	Species	Location	Sex	Energetic marker	Predictors of variation in energetic marker levels: Energy intake	Food availability	Diet quality	Feeding time	Reproduction	Ambient temperature	Physical activity	Other	Notes	References
46	*Papio hamadryas ursinus*	Moremi Game Reserve, Botswana	M	fGCs					Consortship (+)	(ns)				Bergman et al., 2005
47	*Papio hamadryas ursinus*	De Hoop, South Africa	F	fGCs					Cycling ‹ Gestating & Lactating	*Daylight duration* (-)			Short daylight duration: low temperatures	Weingrill et al., 2004
48	*Theropithecus gelada*	Simien Mountains, Ethiopia	M (leaders)	fGCs		*Dry season - Wet season*				Tmin (-); Tmax (-)		Altitude (+)	Low food availability during dry season	Beenher & McCann, 2008
49	*Theropithecus gelada*	Simien Mountains, Ethiopia	F (gestating)	fGCs	*Rainfall (ns)*				Gestation stage (+)	Tmin (ns)			Rainfall predicted food availability	Carrerra et al., 2020
50	*Mandrillus sphinx* (semi-captive)	CIRMF, Gabon	F	fGCs					Gestating › Lactating & Cycling				Provisionned colony	Setchell et al., 2008
51	*Macaca mulatta & Macaca fascicularis (captive)*	DPZ, Germany	F+M	uGCs		(-)							Feeding experiment	Sadoughi et al., 2021
52	***Macaca assamensis***	**Phu Khieo, Thailand**	**F**	**uGCs**	**(-)**				**Late gestation › Early gestation, Lactation & NGNL**	**Tmin (-)**	**Travel distance (ns); Travel time (ns)**			**This dissertation, Chapter 2**
53	*Macaca assamensis*	Phu Khieo, Thailand	M	fGCs					Mate-guarding (ns); Mating › Non-mating season					Schülke et al., 2014; Ostner et al., 2008
54	*Macaca assamensis*	Phu Khieo, Thailand	F (gestating)	fGCs		Prenatal fruit availability (-)								Berghänel et al., 2016
55	*Macaca assamensis*	Phu Khieo, Thailand	F	fGCs					Acyclic ‹ Gestating & Lactating; Consortship (ns)					Fürtbauer et al., 2014
56	*Macaca nigra*	Tangkoko-Batuangus, North Sulawesi	F	fGCs					Gestation › Lactating & Cycling					Gholib et al., 2018
57	*Macaca fascicularis*	Gunung Leuser, Indonesia	M	fGCs					# Cycling females (+); Pre-mating season (+)	Tmean (ns); Tmin (ns); Tmax (ns); deltaT (ns)				Girard-Buttoz et al., 2009
58	*Macaca sylvalus*	Atlas Mountains, Morocco	M	fGCs						Tmin (-)			Social buffering effect	Young et al., 2014
59	*Alouatta palliata*	Los Tuxtlas, Mexico	F+M	fGCs		(ns)					Travel distance (ns); Time budgets (ns)			Gómez-Espinosa et al., 2014
60	*Alouatta palliata*	Los Tuxtlas, Mexico	F+M	fGCs			(-)		Cycling ‹ Gestating & Lactating		Travel time (+)		Negative correlation fruit consumption & travel time	Dunn et al., 2013
61	*Alouatta palliata*	La Flor de Catemaco, Mexico	F+M	fGCs			(ns)		Lactating › Gestating & Cycling	Tmin (ns); Tmax (ns)	Activity levels (+); Travel rate (ns)		Negative correlation fT3 & fGCs in males	Dias et al., 2017
62	*Alouatta palliata*	Leona Vicario, Mexico	F+M	fGCs	Energy intake (ns); Protein intake (-)	Fruit availability (+); Young leaf availability (ns)			(ns)					Martinez-Mota et al., 2016
63	*Alouatta pigra*	Monkey River, Southern Belize	F+M	fGCs			(-)							Behie & Pavelka, 2013
64	*Alouatta pigra*	Monkey River, Southern Belize	F+M	fGCs		(-)				Tmax (ns)				Behie et al., 2010
65	*Alouatta pigra*	Campeche, Mexico	F+M	fGCs					(ns)					Rangel-Negrín 14
66	*Cercopithecus mitis*	Kakamega Forest, Kenya	F	fGCs		Fruit availability (ns); Young leaf availability (-); Non-preferred food availability (+)	(-)	Feeding time (+); Feeding time fallback food (+); Feeding time preferred food (-)	Other ‹ Late gestation & Early lactation		Traveling time (ns); Travel distance (ns)	Fiber content in feces (+)		Foerster et al., 2012

Table 1. continued

					Predictors of variation in energetic marker levels									
#	Species	Location	Sex	Energetic marker	Energy intake	Food availability	Diet quality	Feeding time	Reproduction	Ambient temperature	Physical activity	Other	Notes	References
67	*Cercopithecus mitis albogularis*	Gede Ruins, Kenya	F+M	fGCs		Preferred food item availability (-); Food provisionning (-); Fruit availability (ns)		Feeding time (ns); Feeding non-preferred fruit (+)	(ns)			Feeding effort (+)		Foerster & Monfort, 2010
68	*Procolobus rufomitratus*	Kibale, Uganda	F+M	fGCs			(-)					Infection (+)		Chapman et al., 2015, 2007, 2006
69	*Cebus capucinus*	Sector Santa Rosa, Costa Rica	F	fGCs					Gestation › Lactating & Other	*Dry season › Wet season*			High temperatures in dry season	Carnegie et al., 2011
70	*Ateles geoffroyi yucatanensis*	Quintana Roo State, Mexico	F+M	fGCs		*Dry season › Wet season*							Low food availability during the dry season	Rangel-Negrín 2009
71	*Lemur catta*	Beza Mahafaly, Madagascar	F	fGCs					Late gestation › Early lactation			Feeding effort (+) *(Dry season › Wet season)*		Cavigelli, 1999
72	*Lemur catta*	Berenty Reserve, Madagascar	F	fGCs		*Harsh season › 'Normal' seasons*							Food scarcity during the harsh season	Pride, 2005
73	*Propithecus verreauxi*	Kirindy Forest, Madagascar	F+M	fGCs			(-) trend		Late gestation › Early gestation, Lactation & Other	deltaT (+)				Rudolph et al., 2020
74	*Microcebus murinus*	Kirindy Forest, Madagascar	F+M	fGCs		*Dry season › Rainy season*						Water availability (-)	Low food availability during the dry season	Hämäläinen et al., 2015

Table shows uCP, T3 and glucocorticoid (GC) results from wild and captive primates (females and males). Hormones were mesured from urine (u) or fecal (f) samples. Direction of the effects is indicated in parentheses.
(+): significant positive effect; (-): significant negative effect; (ns): non significant effect
Italics indicate when indirect measures have been used. Bold indicates the results of the present dissertation
Tmax= maximum ambient temperature; Tmin= minimum ambient temperature; deltaT= Tmax–Tmin; NGNL= non-gestating – non-lactating

Since then, the use of uCP to assess energy balance in wild primates has become a stimulating field of research. Recently, a positive association found between uCP levels and energy balance assessed from nutritional and behavioral data in capuchin monkeys has provided evidence of the usefulness of uCP assessment in the wild (# 27).

Regarding energy intake, several studies have investigated its effect on uCP levels in wild species. To date, only one has assessed energy intake and found a positive relationship with uCP levels in wild orangutans (# 13). The other studies used indirect measures of energy intake and nutritional condition: diet quality, feeding time and food availability. uCP seems to be positively predicted by diet quality in bonobos, chimpanzees and chacma baboons (# 5; 11; 15) and to be independent from feeding time as suggested by consistent findings from studies on macaques and howler monkeys (# 5; 20; 21; 24). Lastly, fourteen of the twenty-eight uCP studies investigated the link between uCP levels and food availability in wild populations and mixed results were found. Twelve reported a positive relationship while two studies conducted on female Assamese macaques (this dissertation; # 17) and on males long-tailed macaques (# 21) found an absence of patterns. With the current limited body of research, I would suggest that for females, the discrepancy of results between uCP levels and food availability could be explained by breeding strategies.

An absence of a relationship between uCP and food availability was found in female Assamese macaques who are relaxed-income breeders. These females therefore not only rely on their accumulated fat stores to reproduce but also on exogenous clues (e.g. daylight duration). The positive association between uCP and food availability was found in female apes, chacma baboons, howler monkeys and colobus, i.e. primate species that are typical capital or non-seasonal breeders (Brockman and van Schaik, 2005; Knott, 2001; Polo and Colmenares, 2016; Emery Thompson and Wrangham, 2008; Di Bitetti and Janson, 2000; Teichroeb and Sicotte, 2008). In these species, females reproduce as soon as their energetic condition allow them to do so and they are therefore particularly dependent upon food abundance to invest in reproduction. The preponderant role of endogenous cues in driving reproduction in capital and non-seasonal breeders might explain why energy balance and thus uCP levels are tightly linked to food availability in these species. The fact that an absence of relationship between uCP and food availability was found in a relaxed-income breeder, while a positive relationship was found in capital and non-seasonal breeders might be the consequence of the stronger influence of food abundance fluctuation on the endocrine response in the latter (Brockman and van

Schaik, 2005). This has to remain speculative as studies are very scarce. More investigations on female relaxed-income breeders such as muriquis, marmosets or rhesus macaques (Brockman and van Schaik, 2005) would be valuable to move the question forward.

2.1.2. uCP and female reproduction

Among the eight studies investigating the effect of different stages of the female reproductive cycle on uCP, four studies found comparable uCP levels throughout the reproductive cycle in gorillas, olive baboons (*Papio anubis*), howler and capuchin monkeys (# 14; 16; 23; 27). The four others found a different pattern, with female bonobos, chacma baboons, Assamese macaques (this dissertation) and Sanje mangabeys (*Cercocebus sanjei*) exhibiting high uCP levels during gestation (# 5; 15; 17; 25). The reason why some females exhibit high uCP levels during gestation while others do not is unclear. Although this increase of uCP during gestation in female primates seem not to be consistent, two factors might explain this rise in uCP levels. First, in capital breeders, high uCP levels during gestation can be due to the accumulation of fat stores that may not only occur prior conception but also during gestation, as suggested by Brockman and van Schaik (2005). So a change in uCP levels might be related to changes in feeding behavior and fat accumulation prior and during gestation in capital breeding females. Second, high levels of uCP in gestating females can be induced by insulin resistance. A potential way to tease apart these two sources driving an increase in uCP would be to differentiate early and late gestation as insulin resistance typically arises in the later stages of gestation (Spellacy and Goetz, 1963; Cousins et al., 1980). High levels of uCP in late gestation likely illustrates insulin resistance (as found in Assamese macaques; # 17) whereas high uCP in early stages might be related with capital breeding (as found in Sanje mangabeys; # 25). A case where gestating females exhibit high uCP levels in chacma baboons with no differences between early and late stages also illustrates the possibility of a mixed strategy, with fat accumulation during gestation and a progressive insulin resistance (# 15).

Lactation is the most costly stage of reproduction in female mammals (Gittleman and Thompson, 1988). In spite of this, all studies comparing uCP levels between lactating and cycling primates reported no difference between these two states (# 14; 15; 16; 17; 23; 25; 27). Behavioral coping mechanisms have been suggested to offset the energetic costs of lactation. Only two of these studies (including this dissertation) investigated the effects of reproduction both on female uCP levels and behavior and were therefore able to evaluate (and confirm; as found in this dissertation) behavioral mechanisms offsetting the costs of reproduction on energy balance in wild primates (# 17; 23).

2.1.3. uCP and physical activity

Only nine of the twenty-eight uCP studies examined the effect of energy expenditure through physical activities on uCP levels in primates. A decrease in uCP with physical expense was reported in two controlled experimental studies (# 3; 28). Two field studies conducted on males found a similar pattern, with uCP levels decreasing as traveling time or height climbed increased (# 20; 21). In contrary, two other field studies showed that female uCP level was not affected by travel distances (# 5; 17), suggesting that walking distances may not be energetically challenging enough to induce a decrease in energy balance. A potential difference between the effect of physical activities on male and female uCP levels within the same population would need further investigation. It may be that males expend more energy than females during a physical activity as they typically have larger body size and the energy expenditure of traveling is a function of body mass (Valé et al., 2020). Males may therefore be more likely to exhibit a decrease in their uCP levels in response to a physical expense.

2.1.4. Potential caveats with uCP

One field study reported no pattern between uCP levels and thoroughly assessed energy intake and expenditure (# 9). I would propose two potential explanations. First, this absence of relationship could simply highlight the fact that energy intake and expenditure are both very complicated to assess reliably in wild species. Assessing uCP levels would therefore be a useful tool to alleviate this issue and be able to assess energy balance in wild species (as suggested in # 9). Second, uCP is maybe more complicated to interpret than we think as energy intake and expenditure are not the only drivers of uCP levels. As seen earlier, insulin sensitivity is not static and influences uCP levels. Changes in insulin sensitivity does not occur solely during gestation as physical activity might also enhance insulin sensitivity (Bergouignan et al., 2012). For example, energy intake in subjects who have to exercise induces relatively less insulin production than subject who do not exercise, stressing the enhanced insulin sensitivity in exercising subjects (Bergouignan et al., 2012). This flexibility in insulin sensitivity can therefore lead to unexpected correlations between energy intake and uCP levels (# 3). In addition, some studies have suggested that uCP might be more sensitive to energy expenditure than intake (Emery Thompson et al., 2009; Higham et al., 2011b).

2.1.5. Next steps with uCP

Studies on uCP has provided evidence that this energetic marker can capture signals of energy intake and energy expenditure. Most importantly, uCP responds to energy intake and expenditure in opposite directions and therefore provides a direct assessment of energy balance. However, we need more studies in order to understand to what extent uCP is associated with energy intake and how diet composition and/or physical expense can potentially add noise to the relationship. The next important question to tackle with regards to uCP is whether fluctuations in physical expense could affect insulin sensitivity and thus, the extent to which uCP responds to energy intake. I encourage future studies to investigate a potential effect of an interaction between energy intake and expenditure on uCP levels in wild primates.

2.2. T3

2.2.1. T3 and energy intake, food intake

My thesis (Chapter 2) is the first study investigating the relationship between energy intake and T3 in a wild primate (# 32). Other investigations were conducted through feeding experiments in captive primates (# 29; 31; 36). In line with their results, I found that T3 tended to rise as energy intake increased. T3 level appears to capture energy intake in wild primates and this would deserve additional support from future studies conducted in other wild primates.

It also appears that a reduction in T3 levels is initiated in response to one food item (probably the most nutritive one) becoming scarce as suggested by a study in mantled howlers assessing T3 from fecal samples (# 35). However, as found in humans, it may also be that diet composition, specifically carbohydrate (e.g. fibers) and protein content, modifies the gut microbiota and transit time which may affect metabolite composition in feces (David et al., 2014; Tanes et al., 2021; Milton and Demment, 1988; Wrick et al., 1983). As fruits are typically rich in carbohydrates and young leaves in proteins, it is possible that the difference in T3 response to nutrient content reported by Dias et al. (2017; #35) is due to the gut microbiota activity. These potential influence of dietary composition has to be borne in mind when assessing T3 from fecal samples.

2.2.2. T3 and female reproduction

Studies examining the effect of reproduction on female T3 levels are very scarce and show a lack of consistency in their results. Female Assamese macaques and howler monkeys exhibit an increase in T3 levels during gestation (# 32; 35) while baboons exhibit an opposite pattern with low T3 levels during gestation and lactation (# 30). It may be that the degree of seasonal fluctuations of food availability is a driver of these metabolic differences. Contrary to Assamese macaques and howler monkeys, baboons live in a very pervasive habitat with major differences between dry and rainy seasons in terms of food availability. Not exhibiting a general increase in circulating T3 during reproduction may be a metabolic strategy sparing energy when living a habitat with important environmental constraints (Gesquiere et al., 2018). This is an emerging field of research that deserves further investigation in order to better understand different metabolic strategies in response to reproduction in female primates and how this can be related to ecological pressures.

2.2.3. T3 and ambient temperature

To date only four studies (including this dissertation), investigated the effect of ambient temperature on T3 in wild primate species. Tropical species such as Assamese macaques and howler monkeys do not experience extreme variations in temperature and this might explain why they do not exhibit an increase of T3 as ambient temperature decreases (# 32; 35; but see 34). Species living at higher latitudes such as Japanese and Barbary macaques experience much stronger amplitudes of thermal fluctuation across seasons. This might therefore explain why these macaque species exhibit an increase of T3 as ambient temperature decreases (# 33; 34).

2.2.4. T3 and physical activity

Lastly, this dissertation provides the second investigation regarding the link between physical activity and T3 levels in a wild primate. As found in howler monkeys, T3 levels in Assamese macaques are not affected by variation in traveling time (or travel distance; # 32; 35).

2.2.5. Next steps with T3

Contrary to uCP, T3 levels increase in response to both energy intake and expenditure and therefore do not provide an assessment of energy balance. Instead, the non-invasive assessment of T3 lends itself as a very promising tool in order to better understand metabolic strategies in energetically challenging times. A more widespread use of this energetic marker in the future will help in determining shifts in metabolic rate in response to thermoregulatory needs in species experiencing different magnitude of cold or heat stress in their natural habitats. I also encourage future studies to assess T3 in order to evaluate potential changes in energy expenditure with regards to physical expense.

2.3. Glucocorticoids

2.3.1. Glucocorticoids and energy intake, food intake

Only a handful of studies (including this dissertation) investigated glucocorticoid output in relation to caloric intake in a wild primate species (# 40; 52; 62). Interestingly and contrary to expectations, one study found that fecal glucocorticoid level was not negatively associated with energy intake but with protein intake (# 62). In addition, an increase in diet quality (high fruit consumption) appears to induce a decrease in glucocorticoid concentrations (# 39, 60; 63; 66; 68; 73). Feeding on less preferred food items induces an increase in glucocorticoids (# 66; 67). Besides highlighting a potential impact of a poor nutritional condition, the increase in fecal glucocorticoid levels in times of low protein intake and low-quality diet could also highlight a possible effect of nutrient content in gut microbiota and in fecal glucocorticoid metabolite output (David et al., 2014; Dantzer et al., 2016). As for fecal T3, more investigations are needed to disentangle the effect of energy intake from nutrient intake on fecal glucocorticoid metabolites. Future studies could for example control for specific nutrient intake when investigating the effect of total energy intake on energetic markers assessed in fecal samples.

The effect of food availability on glucocorticoids has been extensively investigated. In most species an increase in food availability induces a decline in glucocorticoid levels (# 38; 41; 64; 67). Some studies provided evidence that it is the availability of specific food item that predict glucocorticoid output (# 41; 66; 67). When preferred food items become available, intergroup encounters and resource defense can also induce a rise in glucocorticoids through social stress and lead to a positive relationship between food availability and glucocorticoid levels (# 62).

2.3.2. Glucocorticoids and female reproduction

To date, different patterns regarding glucocorticoid levels during reproductive cycle have been stressed. Although few inconsistencies within species can be acknowledged, evidence of an increase in glucocorticoids in gestating and/or lactating females have been provided in a wide variety of primate species (# 44; 47; 50; 52; 55; 56; 60; 61; 66; 69; 71; 73). During gestation, an increase of glucocorticoid concentrations can be induced by several factors. Besides a potential effect of heightened maternal needs during gestation, the increase of glucocorticoid concentrations can also be explained by an increase in cortisol binding proteins (cortisol-binding-globulin; Demey-Ponsart et al., 1982; Nenke et al., 2017) and/or a stimulation of the maternal HPA-axis by the placental production of corticotropin-releasing hormone (McLean and Smith, 1999; Mastorakos and Ilias, 2003).

2.3.3. Glucocorticoids and ambient temperature

There is a lot of discrepancy regarding the effect of ambient temperature on glucocorticoid levels in wild primates. Some species, including female Assamese macaques, exhibit an increase in glucocorticoids as minimum ambient temperature decreases which illustrates a physiological reaction to ambient cold (# 48; 52; 58). Evidence of a heat stress has also been highlighted in some primate species (especially in savannah habitats), as illustrated by a positive correlation between ambient temperature and glucocorticoid levels (# 37; 41; 44).

Potential differences in physiological response between males and females within a population would need further investigation (# 44; 45).

2.3.4. Glucocorticoids and physical activity

Lastly regarding the relationship between physical expense and glucocorticoid release in wild primates, only few studies have tackled this question and different patterns have been found. Traveling seems energetically expensive enough to trigger an increase in glucocorticoid levels in some populations (# 42; 60). However, in other primate populations, traveling does not induce a glucocorticoid response (# 52; 59; 66).

2.3.5. Next steps with glucocorticoids

Assessing glucocorticoids lends itself useful to evaluate which challenges require energy mobilization in a wild population. Contrary to uCP and T3, glucocorticoids are nonspecific as they respond to psychological stressors in addition to energetic challenges which can add noise to a signal. In spite of this, the relevance of assessing glucocorticoid metabolite levels in future studies on energetics is apparent in order to understand some inconsistencies in the results found so far. This marker of energy mobilization should particularly receive more attention with regards to thermoregulation and physical expense in wild primates.

2.4 Conclusion

Data start to accumulate in the burgeoning field of research that is the study of energetics through non-invasive markers of energy metabolism. This lends valuable insight into the evaluation of challenges and physiological coping mechanisms in different classes of wild primates living under different environmental pressures. Table 1 highlights the overall need for more data on uCP, T3 and glucocorticoid levels in wild primates. The use of non-invasive markers of energy have been particularly investigated in apes as they represent half of uCP studies and a quarter of T3 studies. On the contrary, other primate species are under-represented in Table 1. I therefore encourage future studies to focus on strepsirrhine and platyrrhine families (apart from howlers). In addition, I strongly recommend future studies to address research questions on energetics through integrative approaches since they promote the interpretation of results on energetic markers. I will present these recommendations below.

3. Future research directions and recommendations for studies on energetics

In this dissertation I used powerful approaches consisting in the combination of several energetic markers, the combination of energetic markers and behavior, and the assessment of several potential energetic challenges. Such holistic and integrative approaches are scarcely used in studies on energetics. For example, only few studies in Table 1 have concomitantly assessed several energetic markers (this dissertation; Dias et al., 2017; Wessling et al., 2018). Integrative approaches represent a next important step in studies on energetics as they have proven useful in many situations.

3.1. An integrative physiological approach: importance of combining several physiological markers

The endocrine system is complex given the myriad of factors driving hormonal production and cross-talks between endocrine axes (Widmaier, 1992). It is therefore particularly challenging to investigate an individual's physiological state as a whole. Measuring several hormones at once alleviates this issue and provides a major advance in studies on physiology in wild species.

Studies pairing cortisol with another hormone levels such as estrogen, progesterone or testosterone have allowed a better understanding of the association between different endocrine pathways and reproductive function (Foley et al., 2001), health (Muehlenbein and Watts, 2010), bonding behaviors (Rincon et al., 2020) or maternal behavior (Bardi et al., 2003). For example, studies initially provided evidence that maternal behavior can be driven by low postpartum cortisol levels (Bahr et al., 1998) and high estrogen levels (Maestripieri and Zehr, 1998). Later, a more integrative study combining the measurement of these two hormones showed that one single hormone is not enough to predict maternal behavior as it is the cortisol/estrogen ratio that explain whether a mother will be more or less responsive to her newborn's needs (Bardi et al., 2003).

Regarding energetics, pairing glucocorticoid and thyroid hormone levels proves relevant for different purposes. First, based only on glucocorticoid levels, it is impossible to parse out the relative contribution of nutritional and psychological factors to glucocorticoid modulations. As thyroid hormones are affected by nutritional, yet not psychological stressors in mammals (Behringer et al., 2018), combining thyroid and glucocorticoid measurement helps in disentangling psychological stressors (induced for example by human disturbance or predation) from a nutritional deficit (Ayres et al., 2012; Dias et al., 2017; Joly et al., 2015; Pritchard et al., 2020; Vynne et al., 2014). For instance, Ayres et al. (2012) showed that a population of killer whales (*Orcinus orca*) was more affected by a nutritional deficit than by a psychological stressor as modulations of both glucocorticoid and thyroid hormone levels were induced by prey availability.

Second, assessing glucocorticoids together with thyroid hormones helps in revealing foraging strategies in wild species (Jesmer et al., 2017). In moose (*Alces alces*), Jesmer et al. (2017) found that glucocorticoids can be unexpectedly positively correlated with energy intake, in a similar way as thyroid hormone. The authors suggested that this atypical hormone-energy relationship in large bodied mammals might illustrate their state-dependent foraging strategy, i.e. they increase energy intake as their energy reserves decrease. As energy reserves slowly change in relation to energy intake in large mammals, high levels of glucocorticoids (low energy reserves) can be found together with high thyroid hormone level (high energy intake; Jesmer et al., 2017).

Lastly, modulations in energy mobilization and energy expenditure in response to various challenges can be disentangled by jointly assessing glucocorticoids and thyroid hormones (Chapter 2; Dias et al., 2017) which allows a fine-scale estimation of individual energetic status. This joint assessment helps in evaluating whether challenges induce energy deficit, illustrated by high glucocorticoid levels and low thyroid hormone levels (e.g. low energy intake: Chapter 2); or substantial energetic demands, illustrated by high levels of both glucocorticoids and thyroid hormones (e.g. late pregnancy: Chapter 2; activity rate: Dias et al., 2017; molting: Gobush et al., 2014). Therefore, the simultaneous assessment of glucocorticoids and thyroid hormones have enhanced our ability to determine a specific source of stress, foraging strategies and energetic status in wild species.

Pairing these two hormones would also enable to address unanswered questions or uncertainties raised by previous research. I will provide three examples of such contexts in which the joint assessment of thyroid hormones and glucocorticoids would promote the interpretation of previous findings. First, many studies reported an increase in glucocorticoid levels during gestation (# 40; 44; 50; 56; 69; 71; 73). It would be informative to know whether this increase in glucocorticoids is only due to the physiological shifts induced by gestation, such as the placental influence on the maternal HPA-axis (McLean and Smith, 1999) or whether it is confounded with a rise in maternal energetic demands, that would be captured by a concomitant increase in thyroid hormones (as found in Assamese macaque: Chapter 2). Second, some studies reported a rise of glucocorticoids during low food availability (# 38; 64; Dantzer et al., 2016), in unprotected habitats (Rangel-Negrín et al., 2014) or in low-ranking gestating females (Carrera et al., 2020). These authors could not determine whether this release in glucocorticoids was induced by psychological stressors or nutritional shortage. This uncertainty can be addressed by assessing thyroid hormones in addition to glucocorticoids. Third, some energetic challenges are non-independent (e.g. food availability and travel distances) leading to difficulties when investigating the source of an increase in glucocorticoids (Dunn et al., 2013). Assessing thyroid hormones in addition to glucocorticoids would help in determining whether a rise in glucocorticoids is due to heightened energy demands (illustrated by a parallel increase in T3) or to an energy deficit (illustrated by a parallel decline in T3). With these few examples in mind, it becomes apparent that assessing these two energetic markers at once is relevant in many situations and would contribute to filling some gaps of knowledge that previous studies could not entirely tackle by assessing a single marker.

Therefore, I would strongly encourage future studies on energetics to assess whenever possible more than one non-invasive energetic marker and to consider measuring glucocorticoids and thyroid hormones as this approach provides one of the most integrative pictures of the physiological and energetic state in wild animals. To my knowledge, only one non-invasive study assessed the concurrent levels of glucocorticoids and thyroid hormones with a third hormone, progesterone (Vynne et al., 2014). The authors found that although maned wolves (*Chrysocyon brachyurus*) experienced some psychological stress (rise in glucocorticoid levels) when chasing rodents in agricultural fields, this negative influence of anthropogenic disturbance was likely outweighed by nutritional (high thyroid hormone levels) and fitness (high levels of progesterone) benefits associated with cropland access. This is a promising approach for future studies aiming at investigating the link between energetic status and reproductive function in wild species. Other studies on energetics used blood samples to measure glucocorticoids and thyroid hormones together with other hormones involved in energy metabolism (e.g. leptin, aldosterone, insulin like growth factor 1: Keogh et al., 2013; Jeanniard du Dot et al., 2009; St. Aubin et al., 1996). These studies provide stimulating ideas for potential physiological markers that would be worth validating in non-invasively collected matrices as they may be used in addition to glucocorticoids and thyroid hormones in field-friendly studies on energetics.

3.2. An integrative physiological and behavioral approach: relevance of combining a physiological marker with behavior

An additional way toward a more comprehensive investigation of the energetic costs of a challenge is to pair physiological markers with behavior. Examining the effects of a challenging situation through the behavioral window contributes to the assessment of energetic costs from the potential behavioral shifts used to offset them. Looking at the same time through the physiological window helps in determining whether the behavioral shifts are enough to cope with the challenge or whether a physiological reaction is also needed. This ‘double-window’ observation is a useful integrative approach to quantify the magnitude of the costs induced by an energetic challenge. The relevance of this approach is particularly apparent when investigating adaptations in response to substantial energy demands.

I want to bring attention to the fact that an absence of physiological responses to a challenge does not always mean an absence of costs. Looking only from a physiological side could lead to a substantial underestimation of the costs induced by a challenge. A complementary behavioral approach allows disentangling whether there are no costs or whether these costs are somehow offset. A behavioral coping mechanism is an integral part of the set of adaptations to a challenging situation and should be considered and assessed whenever possible as it might mitigate the hormonal response. In addition, in a similar way behavior can influence hormone levels in a challenging situation, the hormonal response can also induce behavioral shifts. For example, evidence shows that glucocorticoid levels can affect foraging behaviors (Chmura et al., 2016; Zhang et al., 2020; la Fleur, 2006; Tataranni et al., 1996). A physiological and a behavioral response to a challenge can be interlinked, with one influencing the intensity of the other. Assessing at once both the hormonal and behavioral responses to a challenge is therefore crucial as they can act in concert as coping mechanisms and modulate one another. Although to date such an integrative approach has been scarcely used, few studies provide evidence of the importance of watching physiological consequences under the light of behavioral ones and vice versa. These studies shed more light on the energetic costs of infections (# 11), food scarcity (# 26), mate guarding (# 21) or female reproduction (this dissertation; # 17; 23).

This dissertation shows that the assessment of behavioral responses to reproduction enhances the interpretation of physiological responses. It allows a better evaluation of the costs of reproduction and the coping mechanisms involved. Female Assamese macaques exhibit an increase in energy demands over the course of gestation (Chapter 2) and some of the energetic requirements of gestation are fulfilled through a physiological adaptation involving insulin resistance and fat store use rather than compensatory behavioral shifts (Chapter 3). A different pattern is expressed during lactation, as energy-saving behavioral adaptations during early stages (Chapter 3) contribute to offsetting the energetic costs of lactation as illustrated by similar levels of uCP, T3 and cortisol levels in lactating and non-gestating – non-lactating females (Chapters 2 and 3). Therefore, simultaneously assessing behavioral and physiological responses to reproduction allowed the determination of the coping mechanisms involved at different stages of the reproductive cycle (physiological adaptation during gestation and behavioral adaptation during lactation). Comparing the results found in Assamese macaques with the ones coming from the handful of studies investigating the behavioral and physiological effects of female reproduction helps in evaluating the costs of reproduction. Specifically, reproducing females can maintain similar uCP levels to other females by exhibiting substantial (Assamese macaques: this dissertation), very weak (olive baboons: # 16) or no shifts (mantled howlers: # 23) in activity budget. The energetic costs of reproduction therefore require different intensities in behavioral shifts in order to be offset.

I would like to raise awareness on the fact that potential behavioral shifts to offset the energetic costs induced by a challenge do not always coincide with the emergence of this energetic challenge. This adds complexity in linking a challenge to the set of coping mechanisms that have emerged in response to it as these mechanisms are not necessarily expressed all together. A behavioral shift can be exhibited prior to a challenge. Seasonality in energetic challenges can be associated with predictability in the occurrence of future challenges. Species can typically 'get ready' for an incoming mating season or dry season by storing energy that will soon be required. In such cases, compensatory behavioral shifts can be expressed in anticipation of a challenge-to-be. In this dissertation, investigating behavior in non-gestating – non-lactating females, i.e. before a future energetic investment in reproduction, tackles this potential 'anticipation' of future costs. The results showed, as found in other female mammals, that behavioral shifts consisting in storing and saving energy prior reproduction is an integrative part of the breeding strategy in female Assamese macaques (Chapter 3; Miller et al., 2006). Similarly, male rhesus macaques (*Macaca mulatta*) build-up and conserve energy during the birth season to be energetically prepared for the next demanding mating season (Higham et al., 2011b). A behavioral shift prior to a challenge has therefore to be considered as it might adapt fat reserves at the onset of a challenging situation. These fat stores will contribute to the ability of animals to offset incoming energetic costs. They also influence animals' physiological state (Girard-Buttoz et al., 2011). A behavioral 'anticipation' is therefore important to bear in mind when assessing the energetic costs of a challenge and determining the associated coping mechanisms.

With this dissertation, I highlight the importance of combining several non-invasive physiological markers and combining physiological markers with behavior. I encourage future studies on energetics to use such holistic approaches in order to provide a more comprehensive investigation of the different mechanisms expressed in wild species to cope with energetic challenges. This would help in alleviating the complexity of teasing apart several adaptations acting in concert and in determining their relative importance in the face of different energetic challenges. Besides the complexity associated with the evaluation of behavioral and physiological adaptations to different energetic challenges, I would like to acknowledge the fact that the assessment of these energetic challenges is also complex. Below I present some usual pitfalls that must be considered when assessing energetic challenges.

3.3. The challenge of assessing challenges

Controlled experimental studies can easily impose a specific energetic challenge on animals and therefore clearly assess its behavioral and physiological consequences (e.g. feeding restriction experiments: Deschner et al., 2020; Girard-Buttoz et al., 2011; Laver et al., 2020; Sadoughi et al., 2021). It is of course a very different story in the wild. Investigating the isolated effects of one specific energetic challenge in wild species is particularly difficult, as it requires the assessment of all other potential factors to control for their respective effects. While some potential energetic challenges can be effortlessly assessed (e.g. ambient temperature), others require more time and labor in their evaluation.

Energy intake is one of the most challenging factors to quantify. For that reason, a large majority of studies on energetics uses indirect measurements of energy intake. However, caution should be taken when doing so, especially when no relationship between energy intake and potential proxies has been established previously in a population. Feeding time can be an inaccurate indirect assessment of energy intake insofar as there remains uncertainty regarding what individuals feed on, how nutritional it is and how fast they eat it, i.e. parameters driving energy intake (Conklin-Brittain et al., 2006; Kurihara et al., 2020; Schülke et al., 2006). The inadequacy of feeding time to assess nutritional condition is particularly evident by the absence of relationship with uCP (# 5; 20; 21; 24) and the inconsistencies in glucocorticoid results (# 44; 66; 67). Feeding time could have an opposite effect on glucocorticoids depending on season (# 44) and on what food item is being consumed (# 66; 67). These different effects of feeding time on glucocorticoids highlight the importance of considering what the individuals is feeding on rather than crude feeding time.

Similarly, food availability can be a misleading proxy of energy intake as individuals might compensate for an absence of preferred food items by modifying their diet composition and consuming fallback food items for example (Lambert and Rothman, 2015; Wessling et al., 2018a). In some species food availability is not a determinant of energy intake (Martínez-Mota et al., 2016). Moreover, food availability can be a proxy for other factors such as feeding competition (Martínez-Mota et al., 2016; Pride, 2005), foraging time (Majolo et al., 2013) or daily path length (Harris et al., 2009). In such cases, a physiological response to variation of food availability might illustrate a psychological stress or energy expenditure in addition to energy intake.

Quantifying energy intake per se is therefore crucial as it decreases uncertainty due to any potential confounding effects associated with an indirect measure. Although a direct assessment of energy intake is labor intensive and requires rich feeding and nutritional data, it is necessary in studies on energetics in populations for which no established proxy is available. To date, in addition to this dissertation, few studies have managed to measure energy intake in wild populations (Heesen et al., 2013; Emery Thompson and Knott, 2008; Knott, 1998; Koch et al., 2017; Kurihara et al., 2020; Lodge, 2012; Martínez-Mota et al., 2016; Valé et al., 2020).

Investigating the effects of various and thoroughly assessed energetic challenges on concomitant adaptations in a wild population is fundamental when addressing research questions on energetics. Holistic and ecologically relevant approaches help in determining the energetic pressures faced by a population in its natural habitat and what behavioral and physiological coping mechanisms are associated with these challenges. This would have relevant research implications, particularly with regards to wildlife conservation.

4. Research implication on climate change effects and wildlife conservation

Studies on energetics allow us to determine what challenges are energetically costly and how these costs can be behaviorally and physiologically offset in wild species. An energetic challenge is particularly costly when it induces a response that almost reaches the limit of the physiological capacity of a population (e.g. dive duration when foraging is limited by oxygen stores in marine mammals; Williams et al., 2011). The aggravation of an already-costly challenge could have severe consequences on the vulnerability of the population and its ability to keep inhabiting its home range. Assessing behavioral and physiological responses to energetic challenges provides a useful toolbox for conservation purposes especially with regards to climate change and human disturbance (Reed et al., 2011). The effects of climate change in a population lead to the emergence of new energetic challenges and aggravations of already existing ones. In addition to its direct heat consequence, climate change has other indirect consequences such as aridity, home range restriction or bottlenecks in energy supply (Gibert, 2019; Moritz et al., 2008). These consequences limit population dynamics and induce distribution shifts and disease risks (Previtali et al., 2009; White, 2008; Rosalino et al., 2019; Humphries et al., 2004; Gallana et al., 2013).

Studies on energetics have a predictive power regarding how populations would respond in the face of new and changing environmental challenges and how their life history traits will be altered by climate change (Bozinovic and Pörtner, 2015; Chevin et al., 2010; Fuller et al., 2016; Isaac, 2009; Pacifici et al., 2018; Wingfield et al., 1997). Glucocorticoids have been used as the main tool in predicting future challenges (Wikelski and Cooke, 2006). This hormone can however be complicated to interpret when assessed alone in conservation studies (Busch and Hayward, 2009). For that reason, integrating physiological markers and specifically the combination of glucocorticoids with thyroid hormone is a tool used in studies on energetics aiming at monitoring energetic challenges in wild populations and guiding conservation decisions (Ayres et al., 2012; Gobush et al., 2014; Jesmer et al., 2017; Joly et al., 2015; Vynne et al., 2014). In addition, predicting species vulnerability in the face of climate change and accordingly planning relevant conservation actions would markedly benefit from integrative studies on energetics combining physiology and behavior (Cooke et al., 2015; Hetem et al., 2014; Németh et al., 2013). Anticipating which and how species would likely suffer first from climate change and enhanced energetic challenges is a crucial and needed step toward an improved wildlife population management (Tédonzong et al., 2020; LeDee et al., 2021).

I therefore encourage researchers to address questions on energetics through integrative approaches such as the ones presented in this dissertation. This would not only provide a better assessment of individual energetic condition but also yield valuable materiel to protect vulnerable populations as they are facing climate change and human disturbance. The relevance of integrative studies on energetics lay emphasis on the importance of building bridges between scientific fields. Collaborations between endocrinologists, ethologists, evolutionary biologists and conservation biologists (among others) would promote integrative studies on energetics.

SUMMARY

Energy is a key requirement of life. It is involved in life history traits such as body maintenance, growth and reproduction. Energy is a limiting resource and therefore has to be strategically allocated. When facing an energetic challenge (e.g. low food availability), an individual energy balance, i.e. the difference between energy intake and expenditure, is likely to decrease, leading to shifts in energy-allocation strategies. Such challenging situations can bear drastic fitness consequences and two important adaptations have emerged in order to offset these energetic costs. First, individuals can modify their behavior to maximize energy intake and/or decrease energy expenditure. By adapting their feeding behavior and activity budget, individuals can therefore compensate the costs induced by energetic challenges. Second, physiological adaptations also participate in overcoming such costs. Major hormones such as insulin, thyroid hormones and glucocorticoids are involved in energy metabolism since they regulate energy assimilation, energy expenditure (through metabolic rate) and energy store mobilization. Their concentrations are typically modulated in times of energy deficit or heightened energy demands. A considerable advantage of these hormones is that they can be assessed non-invasively from urine samples.

Behavioral and physiological shifts contribute to offsetting energetic costs. However, to date few studies have used an integrative approach investigating how such adaptations can act in concert when facing an energetic challenge. Such investigations are needed to determine complementary adaptations that have emerged concomitantly and to assess on a fine-scale energetic conditions induced by different challenges among mammals. In addition, this integrative approach will allow a better evaluation of the magnitude of the energetic costs of various challenges which will lend valuable insight into the way such energetic constraints might have driven life history traits in different species.

In this thesis, I aim at investigating the behavioral and physiological responses to potential energetic challenges faced by female Assamese macaques (*Macaca assamensis*) in their seasonal natural habitat. I specifically examined the effects of cold ambient temperature, physical activity, low energy intake and female reproduction on female behavior and hormone levels. I collected behavioral and nutritional data and assessed urinary C-peptide (uCP, a

marker of insulin production), triiodothyronine (T3, a thyroid hormone) and cortisol (one of the main glucocorticoids in vertebrates) levels.

The results showed that the four energetic challenges triggered a specific combination of physiological and behavioral responses. First, low ambient temperatures induced a rise in cortisol but no rise in T3. This likely illustrates the fact that ambient temperatures did not decrease low enough or for long enough to trigger thermogenesis through an increase in T3 levels. A rise in cortisol alone might therefore be enough for female to cope with cold temperatures. Second, travel distance was not associated with a cortisol or a T3 response, suggesting that walking distances are not very energetically demanding in females. Third, a rise in cortisol was paired with a decline in T3 when energy intake is low. Energy intake can therefore be limited enough for females to mobilize their fat stores and reduce their metabolic rate in order to support their energetic needs and save energy, respectively. Fourth, a rise in cortisol was combined with a rise in T3 during late gestation, illustrating elevated energy requirements at this stage of the reproductive cycle. In addition, uCP levels were also high in late gestation which is likely induced by insulin resistance and maternal metabolic shifts in order to spare readily available energy to the fetus needs. The interpretation of similar levels of cortisol, T3 and uCP between lactating and non-gestating – non-lactating females were promoted by the integration of behavioral responses. Contrary to the other reproducing females, early lactating females follow a behavioral energy-conserving strategy (they rest more and feed efficiently), which might offset the energetic costs of lactation.

This dissertation contributes to the growing body of literature in the use of non-invasive markers of energy. Integrating my findings with the other reported ones, I also highlight some uncertainty and inconsistencies and suggest some directions for future investigations. Lastly, my dissertation provides a powerful integrative approach when investigating energetic costs. I shed light on the importance of tackling research questions on energetics through a multifaceted prism by considering both physiological and behavioral responses, since one promotes the interpretation of the other.

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DECLARATION

I hereby declare that I have written this thesis entitled 'Energetics in wild female Assamese macaques (*Macaca assamensis*): a behavioral and physiological approach' independently and with no other aids or sources than quoted.

Göttingen, 23rd of March 2021

Sonia Touitou