



Research paper

Estimation of energetic condition in wild baboons using fecal thyroid hormone determination

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ABSTRACT

Understanding how environmental and social factors affect reproduction through variation in energetic condition remains understudied in wild animals, in large part because accurately and repeatedly measuring energetic condition in the wild is a challenge. Thyroid hormones (THs), such as triiodothyronine (T3) and thyroxine (T4), have a key role in mitigating metabolic responses to energy intake and expenditure, and therefore are considered important biomarkers of an animal's energetic condition. Recent method development has shown that T3 and T4 metabolites can be measured in feces, but studies measuring THs in wild populations remain rare. Here we measured fecal T3 metabolites (mT3) in baboons, and tested whether the conditions of collection and storage used for steroid hormones could also be used for mT3; we focused on mT3 as it is the biologically active form of TH and because fecal T4 metabolites (mT4) were below detection levels in our samples. We also tested if mT3 could be determined in freeze-dried samples stored for long periods of time, and if these concentrations reflected expected biological variations across seasons and reproductive states. Our results show that mT3 can be measured with accuracy and precision in baboon feces. The conditions of collection and storage we use for steroid hormones are appropriate for mT3 determination. In addition, mT3 concentrations can be determined in samples stored at -20°C for up to 9 years, and are not predicted by the amount of time in storage. As expected, wild female baboons have lower mT3 concentrations during the dry season. Interestingly, mT3 concentrations are lower in pregnant and lactating females, possibly reflecting an energy sparing mechanism. Retroactive determination of mT3 concentration in stored, freeze-dried feces opens the door to novel studies on the role of energetic condition on fitness in wild animals.

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1. Introduction

The energetic condition of an animal depends not only on the amount of energy it has stored, but also on its energy balance, i.e., on the difference between its energy intake and energy expenditure (Ellison, 2001). An animal will be in positive energy balance and will gain weight when its energy intake surpasses its energy expenditure, and conversely will be in negative energy balance when the opposite applies. An animal's energy balance in natural environments will be influenced by the physical environment and, in social species, also by the social environment. For instance, seasonal variation in rainfall and temperature can lead to pronounced variation in energy balance over the course of the year

because rainfall and temperature affect food availability; seasonal food shortages may affect not only energy intake but also energy expenditure if animals need to travel farther to encounter food (Alberts et al., 2005; Bronson, 1995; Dunbar, 1992; Johnson et al., 2015; van Schaik and Pfannes, 2005). The impact of food shortage on energy balance may be further exacerbated by adverse ambient temperatures due to the additional costs of thermoregulation (Bronson, 1995). In social species, several aspects of the social environment can impact an animal's energy balance. For instance, the social status of an animal within its group can mediate energy balance if high-ranking animals have priority of access to food and experience fewer feeding interruptions than lower-ranking animals, leading to higher foraging efficiency (Deag, 1977; Ellis, 1995; Holekamp et al., 1996; Koenig, 2002; Saito, 1996; Vogel, 2005). The size of an animal's social group will also influence its energy intake. Individuals in larger social groups are usually at an energetic disadvantage compared to individuals in smaller groups, because of more intense intra-group competition, but this

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disadvantage may be alleviated if larger groups can monopolize better patches of food than smaller groups (Markham et al., 2012; Markham and Gesquiere, 2017; Potts et al., 2015; Wrangham et al., 1993).

Available energy is allocated between several competing processes such as self-maintenance, growth and reproduction. In the wild, most animals have a finite amount of energy available, and trade-offs between survival and reproduction will be necessary if the available energy is insufficient to meet the costs of all these processes (Bronson, 1985; Charnov, 1997; Stearns, 1989). Some species have adapted to periods of low food availability by reproducing seasonally when environmental conditions are favorable (Bronson, 1985). Other species are able to reproduce all year long, relying on their energy reserves, and on their capacity to increase metabolic efficiency and decrease energy expenditure in order to cover the high costs of pregnancy and lactation (Alam et al., 2003; Butte and King, 2005; reviewed in Bronson, 1995). Understanding how environmental and social factors regulate an individual's energetic condition in nonseasonal breeders and how, in turn, an individual's energetic condition mediates the trade-off between reproduction and survival is a topic of considerable interest that has remained understudied in wild animal populations. Indeed, in the wild it is challenging to accurately and repeatedly measure an animal's energy status and energy balance. Factors contributing to this challenge include repeatedly trapping the animal to obtain its weight, as well as recording the amount and energetic value of the food it consumed, and the animal's energetic expenditures, including the energy it spent finding and processing food, mating, caring for its offspring, and maintaining its body temperature.

Until now, changes in glucocorticoid (GCs) levels have often been used as a measure of energetic condition in studying wild animals. GCs are a family of steroid hormones secreted by the adrenal glands in periods of energy deficiency; they are responsible for an increase in feeding behavior and up-regulation of glucose metabolism to provide the energy necessary to restore homeostasis (Landys et al., 2006; Sapolsky et al., 2000; Wingfield et al., 1998). However, GC secretion is also stimulated by psychological stressors, making it challenging to interpret the source of elevated GC concentrations (Sapolsky, 1994). Therefore, obtaining a more direct and fine-grained measure of energetic condition is essential to shed more light on the role of an animal's energetic condition in the regulation of reproduction by environmental and social factors.

Recent advances in non-invasive assessment of thyroid hormones (THs) in feces create a novel opportunity to achieve the goal of a more accurate measure of energetic condition. Two major THs are secreted by the thyroid gland: triiodothyronine (T3) and its prohormone, thyroxine (T4). T4 is the major form in the blood, but T3 is the biologically active form. T3 and T4 are largely transported bound to proteins, such as thyroglobulin, and less than one percent is found in a free form in the blood (Robbins, 1992). THs have key roles in growth and development, in the regulation of the basal metabolic rate (BMR), and in the metabolism of proteins, lipids and carbohydrates. When food is limited, and energy demands exceed energy intake, T4 conversion into T3 is substantially reduced, so that free and total T3 concentrations decrease (Eales, 1988; see review by Chatzitomaritis et al., 2017). This down-regulation of T3 allows animals to conserve their energy reserves and thereby increase the chance that they can meet energy demands. By contrast, when food is not limited, and energy intake exceeds energy expenditure, total T3 concentrations are up-regulated in response to increased energy demands—i.e., during molting (Gobush et al., 2014), somatic growth (Behringer et al., 2014), testicular development (Wagner et al., 2008), mating (Cristobal-Azkarate et al., 2016), pregnancy (Chatzitomaritis et al., 2017; Glinoe, 1997), and exposure to low temperatures (Cristobal-Azkarate et al., 2016).

Traditionally, TH concentrations have been determined in blood or urine (Behringer et al., 2014; Genin and Perret, 2000; Ortiz et al., 2010; Wingfield et al., 2003), but collecting blood or urine in wild animals is not always feasible. Because THs are excreted in the bile of birds and mammals (DiStefano, 1988; DiStefano and Sapin, 1987; Taurog et al., 1951), their concentrations can be determined in feces, providing a valuable non-invasive tool to measure an animal's energetic condition. Recent studies have validated and applied fecal determination of T3 metabolites in several species including killer whales (*Orcinus orca*), monk seals (*Monachus schauinslandi*), caribou (*Rangifer tarandus*), and northern spotted owls (*Strix occidentalis caurina*) (Ayres et al., 2012; Gobush et al., 2014; Hayward et al., 2011; Joly et al., 2015). Four studies have measured T3 metabolites in primate feces: two have been conducted in wild populations and two in captivity (wild barbary macaques, *Macaca sylvanus*, Cristobal-Azkarate et al., 2016; wild howler monkeys, *Alouatta palliata*, Dias et al., 2017; captive howler monkeys, *Alouatta palliata*, Wasser et al., 2010; captive yellow breasted capuchins, *Sapajus xanthosternos*, Schaebs et al., 2016).

Here we validate the measurement of T3 metabolites in the feces of wild savannah baboons (hereafter “baboons”). Baboons are large semi-terrestrial monkeys that are wide spread across sub-Saharan Africa (Henzi and Barrett, 2003; Jolly, 1993). They are eclectic omnivores with a diverse diet that encompasses grass, fruits, flowers, shrub leaves, tree gum, and insects (Alberts et al., 2005; Altmann, 1998; Altmann, 2009; Norton et al., 1987). Baboons are considered nonseasonal breeders, as they breed throughout the year, but nevertheless exhibit slight seasonality in their reproduction that is a function of food availability and their energetic reserve (Alberts et al., 2005; Altmann, 1980; Bentley-Condit and Smith, 1997; Bercovitch and Harding, 1993; Janson and Verdolin, 2005; Melnick and Pearl, 1987). Pregnancy and lactation are highly energetically demanding states in human and non-human primates (Altmann, 1980; Prentice et al., 1996; Thompson, 2013). During pregnancy, extra energy is needed to cover the costs of the development and maintenance of the fetus and associated tissues (i.e. placenta, enlargement of blood volume, enlargement of the uterus), as well as the costs associated with the increase in BMR (Butte and King, 2005; Cikriki et al., 1999). During lactation, extra energy is needed for milk production as well as infant carrying (Altmann, 1980; Barrett et al., 2006; Butte and King, 2005). A corollary to these costs of reproduction in humans and other nonseasonal primates is that females transition from amenorrhea to cycling, and from cycling to pregnancy, only when they have a surplus of energy (Ellison, 2003; Rosetta et al., 2011; Thompson et al., 2012; Valeggia and Ellison, 2004; 2009).

Baboons, like humans and other nonseasonally breeding primates, show evidence that their reproduction is energy limited. Female baboons are more likely to start cycling (onset of puberty) or to resume cycling following post-partum amenorrhea, in periods of food abundance, after they have regained a positive energy balance (Alberts et al., 2005; Gesquiere et al., in press). The probability of conception may also vary with rainfall and body condition (Beehner et al., 2006b; Bercovitch, 1987; but see Gesquiere et al., in press). Social factors such as dominance rank and group size also affect a baboon's access to food, their energy balance, and consequently their fitness. For example, high-ranking female baboons mature earlier, have shorter inter-birth intervals (IBIs) between successive live births, and show higher offspring survival than low-ranking females (Altmann and Alberts, 2003), advantages that seem to result from their priority of access to food resources and their higher foraging efficiency (Barton, 1993; Post et al., 1980). By contrast, female baboons in large groups spend more time foraging (likely a consequence of within-group competition for food resources), mature later, and have longer IBIs than those in smaller groups (Altmann and Alberts, 2003; Bulger and Hamilton, 1987; Wasser and Starling, 1988). These data all point to energetic condi-

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