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Influence of diet and stress on reproductive hormones in Nigerian olive baboons

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ABSTRACT

A female mammal's reproductive function and output are limited by the energy she is able to extract from her environment. Previous studies of the interrelationships between energetic circumstances and reproductive function in a variety of mammal species have produced varied results, which do not all support the common assumption that higher female reproductive hormone levels, specifically progesterone, indicate better ovarian function and greater reproductive potential, and are associated with lower energetic stress. In the present study faecal progesterone and glucocorticoid levels were assessed in two troops of olive baboons (*Papio anubis*) in the same population. They face similar ecological challenges, except that one troop crop-raids, potentially affecting its energetic intake and stress levels. The energy intake of individual females was assessed by combining detailed feeding observations with nutritional analysis of food samples. The crop-raiding troop experienced 50% higher energy intake rates and 50% lower glucocorticoid levels compared to the non-crop-raiding troop alongside substantially lower progesterone levels. This suggests that energetic stress is associated with elevated progesterone levels and may be the cause of the non-crop-raiding troop's lower reproductive output. By comparing groups which differ little, except in terms of food access, and also by directly assessing energy intake, our study addresses some of the design limitations of previous research investigating variation in progesterone levels and energetic stress. It therefore has the potential to contribute to greater understanding of the factors affecting differences in reproductive and stress hormone levels and reproductive function in mammals experiencing different energetic circumstances.

1. Introduction

One of the most fundamental constraints on a female mammal's reproductive success is the amount of energy she is able to extract from her environment, coupled with the ease of this extraction (Bronson, 1989; Wade and Schneider, 1992). Despite this link and the associations between malnutrition and reduced ovarian function that have been demonstrated amongst laboratory and livestock animals since the mid twentieth century (Donaldson et al., 1970; Gombe and Hansel, 1973; Imakawa et al., 1983; Leathem, 1966; Mulinos and Pomerantz, 1940; Roman et al., 2005), the relationship between energetic intake and reproductive function is still far from clear (Schneider, 2004). In addition, the investigation of these effects in naturalistic settings, which is necessary to confirm their functional and adaptive importance, has been limited. One method that has been used is to compare the reproductive success or function of two groups with differential access to energetic resources. Studies have included comparisons of wild vs. captive animals, demonstrating that captive animals, which have easier access to high quality food sources, have enhanced reproductive function compared to their wild conspecifics (Bentley, 1999; Altmann and Altmann, 1977; Garcia et al., 2006) and comparisons of wild animals in different quality habitats, showing enhanced reproductive function associated with habitats containing better quality food sources (Emery Thompson, 2012; Emery Thompson et al., 2007). In humans, comparisons of women living in more and less economically developed countries have found evidence for enhanced reproductive function amongst the former, including earlier age of menarche, shorter inter-birth intervals and higher ovarian hormone levels (Bentley, 1999; Ellison et al., 1993; Ellison, 2003).

Abbreviations: EIA, Enzyme Immuno-Assay; GC, 11b-dihydroxy-CM (glucocorticoid metabolite); GGNP, Gashaka-Gumti National Park; GLMM, Generalised Linear Mixed Model; IZW, Leibniz Institute for Zoo and Wildlife Research; PdG, 5B-Pregnane-3A-20A-Diol (progesterone metabolite).

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Much of this previous research assumes that higher reproductive hormone levels, especially progesterone levels, indicate better ovarian function and hence greater reproductive potential. Progesterone plays a major role in mammalian reproductive function with its effects varying depending on reproductive stage (Norris, 2007). Prior to ovulation, low progesterone levels allow the secretion of gonadotrophin, which stimulate follicular development and ovulation, whereas post-ovulation, high progesterone levels induce uterine secretion and help maintain early pregnancy (Albrecht and Townsley, 1976; Norris, 2007). Consistent with this, positive correlations between luteal progesterone levels and conception probability have been found in various mammalian species (Emery Thompson, 2005; Lenton et al., 1982; Liu et al., 1988; Maslar, 1988; Nadler and Collins, 1991; Stewart et al., 1993; Stouffer, 1988; Wasser, 1996).

A positive association between progesterone levels and energy balance is well documented in human studies, with progesterone levels known to vary with nutritional status, diet and energy expenditure (Bentley et al., 1998; Ellison, 2003, 1990). On the basis of this evidence, Ellison (1990) hypothesised a graded continuum of ovarian dysfunction in response to negative energy balance with lower levels of progesterone secretion during the luteal phase characterising the mildest form of ovarian suppression. Further evidence for this relationship comes from experimental studies demonstrating reduced circulating progesterone levels in livestock and laboratory animals on restricted diets (Donaldson et al., 1970; Gombe and Hansel, 1973; Imakawa et al., 1983; Roman et al., 2005) as well as a few studies of free-ranging non-human mammals that have shown positive associations between energy balance and progesterone levels (Emery Thompson et al., 2007; Foley et al., 2001).

Despite support for the notion that the relationships between energetic status, progesterone and reproductive function are positive, some studies show the opposite relationship. In deer, undernourished females exhibited elevated progesterone levels, relative to well fed females, during both the pre-breeding period (red deer: *Cervus elaphus*) (Cook et al., 2001) and during pregnancy (white-tailed deer: *Odocoileus virginianus*) (Bahnak et al., 1979; Plotka et al., 1983; Verme, 1965), apparently due to the production of adrenal progesterone as a result of stress (Cook et al., 2001; Plotka et al., 1983). Stress induced adrenal progesterone production can act to inhibit reproduction in cycling females, by inhibiting LH production, ovulation and fertilization processes, whilst high progesterone levels during pregnancy can prevent spontaneous abortion, which can be triggered by high levels of glucocorticoids (Norris, 2007). Results from African elephants also support this, with progesterone and glucocorticoid levels co-varying (Foley et al., 2001). In contrast, several laboratory studies of non-human primates have demonstrated declines in progesterone levels as a result of stress (Albrecht and Townsley, 1976; Hayashi and Moberg, 1990; Williams et al., 2007; Xiao et al., 2002, 1999).

The varied results of these studies indicate that the relationships between stress, progesterone and reproductive function are complex and far from clear. In addition, most of the studies that seem to demonstrate differences in progesterone levels, or other measures of reproductive function, between groups of people or animals, alongside differences in energy intake or balance, have not made any direct energetic measurements. Instead they have used proxies for energy balance or intake such as differences in habitat quality or food availability or, in the case of humans, assumed differences in diet and work load between women living in more and less economically developed countries. Another possible issue is that these comparisons are often between groups that differ in more than one respect, for example comparing women living in different countries with different climates, life-styles and recent evolutionary histories.

In the current study we address some of these issues by comparing the progesterone levels, glucocorticoid levels and energy intakes of two groups of olive baboons (*Papio anubis*) within one population in the Gashaka-Gumti National Park (GGNP) in Eastern Nigeria. The two troops live within 10 km of each other and experience very similar weather patterns, habitat composition and floral and faunal communities (Warren et al., 2011). The major difference between the two troops is that one supplements its diet of wild-foods with crops raided from agricultural fields and stores within its home range, whereas the other troop is entirely wild feeding (Warren et al., 2011). Crop-raiding and other forms of food-enhancement have been found to have positive effects on the body condition and reproductive success of non-human primates (e.g., Altmann and Alberts, 2005; Mori et al., 1997), which is thought to be due to the energetic benefits provided by having access to energy rich food sources (Strum, 1991). Crop-raiding may also have an impact on physiological stress levels, either increasing stress due to human-wildlife conflict (Ahlering et al., 2011; Higham, 2006), or decreasing stress due to increased food availability, in the same way that increases in the availability of wild foods decrease physiological stress levels in non-human primates (e.g., Emery Thompson et al., 2010).

The current study aims to estimate the energetic intake of the two baboon troops at GGNP, and to measure their progesterone and glucocorticoid levels, in order to assess whether any energetic differences are associated with differences in reproductive function and stress levels. Previous research on the GGNP baboons has found evidence for activity budget and reproductive effects of food-enhancement. The crop-raiding troop spends less time feeding and travelling and more time resting and socialising than the wild-feeding troop, and also exhibits significantly shorter inter-birth intervals and substantially lower infant mortality (Warren et al., 2011). Comparison of energetics and reproduction between the two troops provides an excellent opportunity to investigate potential associations and interactions between variation in energetic stress, reproductive hormone levels and output, more directly and with fewer confounding variables than in previous naturalistic studies.

2. Materials and methods

2.1. Study site and subjects

This study took place in GGNP, Nigeria, on the 16 adult female members of two troops of olive baboons, habituated and monitored since 2000 (Ross et al., 2011; Sommer and Ross, 2011; Warren et al., 2011). Kwano troop, which is entirely wild-feeding and occupies a relatively undisturbed area within the National Park, comprised 30-38 individuals, including 11 adult females during the study period. Gamgam troop ranges just outside the border of the National Park, and comprised 20-22 individuals, including five adult females. The members of Gamgam troop regularly supplement their diets of wild foods with crop foods raided from agricultural fields and stores (Warren et al., 2011). Since habituation Gamgam troop has experienced a 43% increase in group size (modal group sizes: 2000–2002 = 14; 2009 = 20) compared to a 32% increase by Kwano troop (modal group sizes: 2000–2002 = 28; 2009 = 37) (Higham, 2006). Previous authors have suggested that Gamgam's initially small group size may have been due to a recent fissioning event promoted by their crop-raiding behaviour (Warren, 2008).

Data collection took place from March to December 2009, not including July, and consisted of 14 dry season, (mid-April to mid-October) and 18 wet season (mid-October to mid-April) weeks. Alternate weeks were spent with each troop and each day