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Incidence and biomarkers of pregnancy, spontaneous abortion, and neonatal loss during an environmental stressor: Implications for female reproductive suppression in the cooperatively breeding meerkat

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ABSTRACT

Meerkats are group-living, insectivorous herpestids in which subordinate members provide extensive care for the dominant female's young. In contrast to some cooperative breeders, subordinate female meerkats are physiologically able to reproduce and occasionally do so successfully; their attempts are more frequently 'suppressed' via eviction or infanticide by the dominant female. Spontaneous abortion and neonatal loss occur with some regularity, further negatively impacting reproductive success. Here, we compared the reproductive outcomes and endocrine profiles, including of serum progesterone (P_4), serum estradiol (E_2), and fecal glucocorticoid metabolites (fGCm), of dominant and subordinate dams residing within their clans in the Kalahari Desert of South Africa. Our study spanned years of drought, which reduced insect abundance and represented a substantial environmental stressor. Meerkat pregnancies were identified at mid-term and culminated either in spontaneous abortions or full-term deliveries, after which pups were either lost prior to emergence from the natal den (usually within 2 days of birth) or emerged at 2–3 weeks. Neonatal loss exceeded fetal loss for all females, and contributed to narrowing the status-related disparity in female reproductive output seen during less arid periods. Although E_2 concentrations were significantly lower in subordinate than dominant females, they were sufficient to support gestation. Absolute E_2 concentrations may owe to androgenic precursors that also attain highest concentrations in dominant dams and may mediate aggression underlying female reproductive skew. Pregnancies terminating in fetal loss were marked by significantly lower P_4 concentrations in mid-gestation and modestly lower E_2 concentrations overall. Consistently high fGCm concentrations further increased across trimesters, particularly (but not consistently) in subordinates and in aborted pregnancies. Environmental stressors may modulate reproductive outcomes in meerkats through their influence on sex steroids and their effects on intragroup competition. The social and eco-physiological factors affecting intraspecific variation in reproductive output, even in obligate cooperative breeders, may be most apparent during extreme conditions, reflecting the benefits of long-term studies for assessing the impact of climate change.

1. Introduction

1.1. The biopsychosocial model of fetal loss

Fetal loss negatively impacts mammalian reproductive success; yet, owing to difficulties of study, we know remarkably little about the incidence of and circumstances surrounding spontaneous abortion in mammals, particularly in the wild. One of the major hypotheses advanced to explain adverse pregnancy outcome beyond the selective elimination of genetically unfit embryos [1,2], involves prenatal

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maternal stress (i.e., the biopsychosocial model; reviewed in [3]). Studies of the stress-related etiology of fetal loss fall into four broad categories: (1) The most common are clinical studies of human populations, which are focused on the network of physiological processes [4] and psychosocial predictors [5–7] associated with pregnancy maintenance versus reproductive failure, with goals of prevention or intervention to minimize recurrent miscarriages. (2) Experimental laboratory studies (mostly of rodent, rabbit or nonhuman primate models) [8–11] generally share the goals of human studies. (3) In studies of farm animals (primarily ungulates), researchers investigate the predictors of fetal wastage with the aim of minimizing economic losses [12–14]. (4) Least common are studies of zoo animals [15] or wild populations (mostly of primates), in which researchers examine natural variation in fetal loss with the aim of understanding the evolutionary (and conservation) implications of social, demographic, and ecological factors associated with fetal loss (hares: [16]; ungulates: [17]; primates: [18–22]), many of them using recently developed noninvasive techniques to evaluate endocrine biomarkers [23,24]. Our study falls within this last category, but, uniquely, is focused on a social carnivoran and obligate cooperative breeder, the meerkat (*Suricata suricatta*). We examine reproductive outcomes in the wild, in both dominant and subordinate dams, and use various endocrine biomarkers to assess the role of fetal or neonatal loss in the reproductive suppression of subordinate females.

1.2. The cooperatively breeding meerkat

Meerkats are small-bodied, social mongooses that live in harsh environments in territorial groups or clans of up to 50 individuals [25,26]. They are considered to be singular cooperative breeders, with one dominant female per group breeding most regularly [27–29]. Subordinates are usually offspring or siblings of the dominant pair and (with the exception of lactation) provide the majority of infant care. Subordinate females contribute to suckling the offspring of dominant females [30], and helpers of both sexes guard, carry, provision, and protect juveniles born in their group [25,27], thereby investing significant energetic resources in raising the offspring of others. As in many other singular cooperative breeders [31–34], subordinate meerkats occasionally attempt to breed and sometimes rear young successfully [28].

Relative to other cooperatively breeding mammals like mole rats [35,36], callitrichid primates [37], and canids [38–40], meerkats suffer significant predation pressure [41] and are exceptional in the extent of their cooperative activities [42]. Their pronounced need for babysitters [43,44] and sentinels [45] may increase the evolutionary pressures for phenotypic divergence between breeders and helpers [46,47] – phenotypic divergence that is likely to be underwritten, in part, by endocrine mechanisms. Whereas the ultimate evolutionary drivers of cooperative systems have been studied extensively, much less attention has been accorded the proximate physiological mechanisms underpinning extreme ‘reproductive skew’ or the unequal distribution of reproductive output (see also [48,49]).

1.3. Fetal loss as a mechanism of reproductive suppression

Across cooperatively breeding species, various mechanisms account for the stress-related, reproductive suppression of subordinate females, whereby higher glucocorticoid concentrations, arising as a consequence of the stress of subordination, interfere with reproductive function (for a review, see [48]). These mechanisms of reproductive suppression include five major categories: delayed puberty, inhibition of ovulation, implantation failure, spontaneous abortion, and infant mortality [50]. The neuroendocrine impairment of reproductive function evident in certain species [51–53] is not as readily apparent in female meerkats because, despite status-related differences in basal concentrations of estrogen [54–56] and luteinizing hormone [57], all adult female meerkats are physiologically able to reproduce [57]. Nevertheless, subordinates produce roughly one third the number of litters as that produced by dominant females [27]. Perhaps instead of physiological suppression, significant reproductive skew in meerkats owes primarily to behavioral tactics by the dominant female, including the eviction of pregnant subordinates, which often precipitates fetal loss, and the killing or group abandonment of their pups [57,58].

1.4. The biopsychosocial model in meerkats

The role of social stress in contributing to reproductive skew among female meerkats remains equivocal. Examining status-related differences in glucocorticoids (GCs), Carlson and colleagues [54] found that dominant animals were more likely than subordinates to have measurable plasma GCs. Although Barrette and colleagues [59] found no status-related differences in fecal GCs, they reasoned that dominant females would endure the greatest cumulative stress because GCs increase with pregnancy and dominant females reproduce most frequently. A prolific dominant female can conceive again just nine days after parturition and can bear up to four litters per year [59,60]. Although Young and colleagues [56] also found no status-related differences in fecal GCs within female clan members, they [60] found that subordinate females evicted from the clan suffered significantly greater, stress-related fetal loss than did their subordinate counterparts residing within the clan.

Related to these findings, Clutton-Brock and colleagues [61] reported abortion rates within the clan to be significantly greater in subordinate than in dominant females. Although subordinates residing within the clan are no more likely to abort their litters if the dominant female is pregnant than if she is not pregnant [62], they express greater plasma GC concentrations while the dominant female is pregnant than they do at other times [63]. Lacking from studies of social stress in meerkats, however, is a concurrent examination of reproductive hormones and a comparison of the endocrine correlates of abortion between classes of animals residing within the clan.

1.5. Aim of the present study

Previous researchers have identified various maternal factors predicting fetal loss, including species, age, rank, reproductive history, parity, weight, nutritional state, histocompatibility, litter size, and even fetal uterine position [64–68]. Our first aim was to examine maternal factors (particularly female social dominance, while controlling for weight) relative to fetal and neonatal loss, and to test if steroid hormone concentrations during and immediately after gestation might be associated with reproductive outcome in each of the social classes. We thus examined various endocrine biomarkers in dominant and subordinate females during term pregnancies and during spontaneous abortions, as well as during their respective post-pregnancy periods.

Across species, significant environmental factors, including temperature, rainfall or season, and population density or group size, also have been associated with fetal loss [18,61,68]. In the course of monitoring pregnancies in this wild population of meerkats, a drought that spanned several years represented an environmental stressor that may have influenced pregnancy outcomes in one or both of the social classes. Notably, insects constitute the meerkat's primary prey class, and their diversity and abundance fluctuate with temperature and rainfall [69]. Because foraging effort is greatest in pregnant and lactating females [69], these animals could be particularly vulnerable to low prey availability, particularly in larger groups. Thus, our second, integrated aim was to examine pregnancy outcomes and maternal reproductive and stress physiology during a time of substantial environmental stress (namely, a period of lower rainfall relative to earlier study periods). We asked if resident, subordinate dams might be even more prone than dominant dams to abort or if the drought leveled the reproductive ‘playing field.’ Evidence of the latter could be relevant to understanding