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Immunocompetence of breeding females is sensitive to cortisol levels but not to communal rearing in the degu (*Octodon degus*)

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HIGHLIGHTS

- No evidence that communal rearing enhances female reproductive success and survival
- No evidence that communal rearing enhances offspring immunocompetence or survival
- Females with high fecal glucocorticoids (FGC) increased lymphocytes and monocytes
- Females with low FGC experienced increases in N:L ratios, neutrophils, and total IgG
- Immunocompetence of females is sensitive to FGC but not to communal rearing

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ABSTRACT

One hypothesis largely examined in social insects is that cooperation in the context of breeding benefits individuals through decreasing the burden of immunocompetence and provide passive immunity through social contact. Similarly, communal rearing in social mammals may benefit adult female members of social groups by reducing the cost of immunocompetence, and through the transfer of immunological compounds during allonursing. Yet, these benefits may come at a cost to breeders in terms of a need to increase investment in individual immunocompetence. We examined how these potential immunocompetence costs and benefits relate to reproductive success and survival in a natural population of the communally rearing rodent, *Octodon degus*. We related immunocompetence (based on ratios of white blood cell counts, total and specific immunoglobulins of G isotype titers) and fecal glucocorticoid metabolite (FGC) levels of adults immunized with hemocyanin from the mollusk *Concholepas concholepas* to measures of sociality (group size) and communal rearing (number of breeding females). Offspring immunocompetence was quantified based on circulating levels of the same immune parameters. Neither female nor offspring immunocompetence was influenced by communal rearing or sociality. These findings did not support that communal rearing and sociality enhance the ability of females to respond to immunological challenges during lactation, or contribute to enhance offspring condition (based on immunocompetence) or early survival (i.e., to 3 months of age). Instead, levels of humoral and cellular components of immunocompetence were associated with variation in glucorcorticoid levels of females. We hypothesize that this covariation is driven by physiological (life-history) adjustments needed to sustain breeding.

1. Introduction

Group-living or sociality involves spatial and temporal proximity among individuals that results from the mutual attraction rather than from attraction to the same resource or physical condition [55,72]. Relevant attributes of sociality include group size, group stability, and the extent to which group members display cooperative or competitive interactions [16,72,100]. Thus, sociality is thought to increase with group size, but also with the extent to which group members cooperate to attain food, avoid predators, or rear their offspring, among other aspects [27]. Functionally, sociality is thought to evolve when fitness benefits, namely decreased predation risk, enhanced access to resources, or decreased thermoregulatory costs [19,28,55], outweigh inherent costs

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to group-living, including increased transmission of parasites, pathogens, and competition over resources [2,55]. While fitness benefits of sociality derived from ecological variation have been well identified, proximate mechanisms remain less understood [55].

Determination of proximate underpinnings to these fitness effects remain critical to develop more integrated research programs that facilitate new insights into the physiological causes and consequences of social variation [8]. In particular, it is important that we understand the impact of immunocompetence – the physiological ability of individuals to develop an immune response following exposure to an antigen – on the reproductive success of social species. Biomedical studies on lab or domesticated rodents generally support that social conditions (e.g., individually versus group housing) influence immunocompetence [4]. For instance, it is well known that individuals experiencing low ranking status when housed in groups generally suppress immunocompetence, a time-dependent effect mediated by the stress response [4,83]. In contrast, the influence of other aspects of group-living on immunity such as cooperative behavior remains less understood.

Compared with laboratory species, few studies in natural populations of social species have examined how immunocompetence varies within and across social groups and how this influences reproductive success and survival [4,37]. This lack of information limits our ability to establish the extent to which immunocompetence is a driver of the evolution of sociality or the consequence of challenges operating within groups [48,91]. Achieving this goal has been complicated by the fact that a connection between sociality and immunocompetence is not straightforward [10,41,103]. On the one hand, horizontal pathogen transmission within groups is thought to increase in social species as a result of relatively more frequent physical contact, shared use of space, crowding, and the build-up of waste products [15,18,48]. This hypothesis is generally supported by the observation that, across studies and species, prevalence of contact-borne pathogens and parasites increases with the size of host social groups [15,77], and that greater investment in immunocompetence is associated with individuals in larger (or more cooperative) social groups, presumably to counteract these costs [63,64,68,88,92]. An alternative view is that individuals in social groups reduce their risk of horizontal pathogen transmission through decreasing contact with members of other social groups (i.e., a condition referred to as "social clustering"; [103]). This hypothesis is supported indirectly by within [11] and among [45,98] species comparisons documenting negative or no association between prevalence of pathogens and parasites and the size of host social groups. More direct support comes from across species comparisons reporting lower investment in immunocompetence in more social hosts [85,103]. Taken together, both theoretical and empirical evidence support a complex association between pathogen transmission and sociality, modulated by the parasites' main mode of transmission (e.g., contact-borne vs. mobile vector-borne), or by the extent of social clustering [10,103].

Several social mechanisms (referred collectively to as "social immunity") have been suggested to reduce the burden of individual immunocompetence, including antimicrobial secretions, socially transmitted immune compounds, hygienic behavior, or mutual grooming [17,18,59,69,71]. This possibility has been supported by single species studies in bumble bees (*Bombus terrestris*) and termites (*Zootermopsis angusticollis*), two eusocial insects where social contact enhances survival and ability to resist infection [54,91]. The social immunity hypothesis also is supported by a comparative study where more social species of thrips exhibit higher antimicrobial strength [92]. For other social insects however, some components of individual immunocompetence have been shown to decrease while others decrease with group size [81]. Evidence from social vertebrates is meager on this point. Similar to eusocial insects, some mole-rats are singularly breeding rodents in which most group members delay breeding to help raise the offspring of breeders [61]. Immunocompetence based on spleen mass has been shown to be similar in breeding and non-breeding Natal mole-rats (*Cryptomys hottentotus natalensis*), suggesting that help from non-breeders allows breeders to invest in their own immunocompetence [60]. Natal mole-rats from larger colonies decrease their metabolic costs and parasite abundance, implying energy savings from social living can be diverted into parasite defense [61]. Most intriguingly, immunocompetence based on the phytohemagglutinin-P test has been shown to increase with the number of nonbreeders (helpers) in singularly breeding magpies, suggesting a social effect on immunity [93]. Taken together, available studies on insects support social effects in terms of enhanced immunocompetence, yet different components of individual immunocompetence may be affected differently. Results from the few studies conducted on singularly breeding mammals and birds are consistent with immunocompetence benefits derived from social living, yet evidence remains largely indirect.

In contrast to singular breeders, most group members of plural breeders produce offspring [86]. In species that rear offspring in communal litters, females may nurse non-filial offspring, a form of parental care referred to as allonursing [42,79]. Allonursing may provide different benefits, including an enhancement of repertoire and total amount of immunoglobulin and immune cells available to offspring in colostrum and milk [3,80]. As a result, offspring raised in groups with more females may benefit through enhanced passive immunity and from increased early survival. However, producing better quality offspring in terms of ability to defend from pathogens may come at a cost to breeding females. Females may be required to invest more heavily in individual immunocompetence to provide offspring with immunoglobulins and immune cells, and possibly to defend them from enhanced pathogen transmission from allonursing [80]. Additionally, maternally transmitted immunoglobulins may indirectly enhance or inhibit the offspring's humoral immunocompetence [41]. Thus, it is far from clear how sociality and communal rearing may be beneficial to adult group members and their offspring in communally rearing mammals.

1.1. Model species and hypothesis predictions

Based on previous theory and empirical evidence we examined three hypotheses that are pertinent to degus (*Octodon degus*) as a study model. Degus are diurnal, herbivorous, and social rodents where multiple adult male and female group members share underground nests [31,43]. All female members of groups rear their litters communally [31], engaging in several forms of communal care, including huddling, retrieving and nursing non-descendent offspring [30,32,33,50]. In contrast, male degus huddle over and groom the pups, yet these direct forms of care have no fitness consequences to the offspring [33]. These observations suggest that communal rearing may benefit adult female degus directly through decreasing the burden of individual immunocompetence. Under these conditions, females may divert these savings into other maintenance or reproductive functions. Conversely, females exhibiting greater immunocompetence may be less able to attain such savings, and thus, less capable to divert them into fitness enhancing processes. On the other hand, two observations seem preliminary consistent with the non-mutually alternative hypothesis in which communal rearing and total group size benefit adult female degus indirectly through their offspring by means of enhancing offspring immunocompetence and survival. First, females transfer immunoglobulins to their own offspring during pregnancy and lactation [6]. Second, multiple female and males communally nest during lactation [34,43], implying that offspring are exposed to pathogens and parasites from contact with all adults, including males and females. Finally, we considered hypothesis 3 in which the relatively low inter-year survival of degus resulted in an "all or none" strategy and where any social effects on communal rearing would be weak or absent. We examined eight predictions relevant to validate these hypotheses (Table 1).