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Review

Intergenerational transfers may have decoupled physiological and chronological age in a eusocial insect

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Abstract

Life-history theory generally predicts that there should be no selection for longevity beyond the limit of reproductive capacity. However, the capacity to increase fitness may not end when individuals reach a state of functional sterility. Recent studies show that intergenerational transfers of resources from post-reproductive parents can increase the offspring's fitness, and analytical theory shows that age-trajectories of transfers may shape the course of senescence in social organisms. In eusocial insects, female roles are partitioned so that one phenotype or ''caste'' reproduces while another is responsible for resource transfers: the reproductive ''queens'' are arrested in a continuous reproductive mode, while transfer-activities such as hygienic behaviors, guarding, foraging and further food processing (''nursing'') that increases the nutritional value of provisions are conducted by sterile ''workers''. Worker honey bees normally perform these tasks in a sequence so that nursing inside the protected nest is conducted prior to more risky exterior hive activities such as guarding and foraging. However, foragers may revert to nurse-activity in response to demographic changes, and worker bees can also develop into a stress resistant survival form with a 10-fold increase in lifespan. This elastic division of parental functions is believed to increase colony fitness. Further, it generates a stage-dependent trajectory of senescence that is difficult to address with established theories of aging. In the following, we show how a recent theory that includes resource transfers can be used to elucidate patterns of senescence in eusocial, non-reproducing individuals like the honey bee worker.

Keywords: Intergenerational transfer; Physiological and chronological age; Eusocial insect

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1. Introduction

Social demographers have often dealt with aging and fertility separately from parenting. Yet, a recent contribution to the evolutionary theories of aging that links age-specific patterns of intergenerational transfers to mortality (Lee, 2003), suggests a new approach in this line of research (Rogers, 2003). Lee (2003) focuses on parental investment and transfers of resources between individuals of different ages. The work joins an economic model of exchange between individuals with an evolutionary theory of aging, and has been referred to as the most comprehensive aging theory to date (Rogers, 2003). The formalism can generate strong testable predictions, but an empirical evaluation of the theory requires measurements of transfers that would ideally include numerous care behaviors (e.g., feeding, warming, fanning and guarding) (Lee, 2003). Thus, the divergence between Lee's formalism and established theories that do not incorporate intergenerational resource transfers is challenging to assess.

Established evolutionary theories of aging, i.e., the mutation accumulation framework (Medawar, 1952) and the antagonistic pleiotropy (Williams, 1957) framework, including the disposable soma theory (reviewed by Kirkwood and Rose, 1991), seek to explain why mortality increases with age. The theories all predict that the principal determinant in the evolution of longevity is the level of extrinsic mortality. If this level is high, life expectancy in the wild is short, and there is little selection for high levels of somatic maintenance; if the level of extrinsic mortality is low, selection would postpone deleterious gene effects and direct greater investment into building and maintaining a durable soma (reviewed by Kirkwood and Austad, 2000). None of these theories incorporate resources transferred to offspring (Lee, 2003), and none of them were explicitly designed to address aging patterns in alloparental care givers, which may be of particular interest to aging research (Amdam and Omholt, 2002; Omholt and Amdam, 2004).

Eusocial organisms are characterized by the presence of a sterile worker caste that engages in alloparental care behaviors such as cleaning, nursing, guarding and foraging. Lee's (2003) transfer theory predicts that social species with continuing care for offspring can show complex qualitative life-history patterns such as decline in juvenile mortality with age, and selection for reduced fertility as well as higher mortality. The formalism might not fully account for the evolution of sterile worker castes, but trajectories of senescence in a eusocial species may, nevertheless, serve as an important explanatory test-case for this theory of aging. The honey bee (*Apis mellifera*) is emerging as one key model for research on longevity in eusocial species (Omholt and Amdam, 2004; Rueppell et al., 2004). In the following, therefore, we use patterns of food transfers, senescence and frailty in the honey bee worker caste to exemplify how a theoretical framework that incorporates intergenerational transfers can be meaningfully applied to aging in a eusocial species.

2. Biological background

The honey bee has a long and rich history as an experimental organism. The activities within a bee colony are easy to quantify, and patterns of nursing and food exchange have