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Digest: Deprivation of parental care reveals the value of sibling cooperation in burying beetles

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What conditions favor cooperation in sibling interactions? In burying beetles of the genus *Nicrophorus*, Prang et al. found that dependence on parental care cannot solely explain the degree of offspring cooperation. While only larvae of independent species cooperated when receiving pre-hatching care, both independent and dependent species cooperated in the absence of pre-hatching care. This finding suggests that offspring cooperation has persisted from an early ancestor of the genus *Nicrophorus* to the present species, highlighting the evolution from facultative to obligatory social behavior.

The evolution of sociality requires social interactions between family members. While parental care has been hypothesized as a major driver for maintaining a social life, the role of sibling interactions remains relatively understudied. Recent work suggests that cooperative behaviors among siblings, compared to competitive interactions, can profoundly advance our understanding of animal sociality, especially in ancestral family systems (Kramer and Meunier 2019). A key question to address is whether the degree of sibling cooperation depends on the degree of parental care dependence. It is predicted that more independent juveniles are more likely to cooperate and benefit from each other, whereas juveniles that depend more on parents for growth and survival should compete for parental care. Burying beetles of the genus *Nicrophorus* presents a promising model system because different species vary in the extent of dependency on parental care from facultative to obligatory (Capodeanu-Nägler et al. 2016), when their juveniles develop inside prepared carcass nest (pre-hatching care) and receive post-hatching care from parents.

In this study, Prang et al. (2021) propose to test if the degree of sibling cooperation depends on the degree of offspring dependence on parental care using three burying beetle species differing in dependence on parental care, with *N. orbicollis* being the most dependent, *N. vespilloides* intermediately dependent, and *N. pustulatus* the least dependent. Prang et al. thus predict that *N. orbicollis* juveniles should be selected to compete for parental care, whereas *N. pustulatus* should show signs of cooperation, and *N. vespilloides* should show an intermediate level of cooperative interactions.

To test this idea, the authors experimentally manipulated the occurrence and extent of sibling cooperation by controlling for initial juvenile number in the presence or absence of pre-hatching parental care, e.g., fur removal, burial, and antimicrobial defense of carcasses. They then measured the growth and survival of juveniles when they had no access to post-hatching care, which has previously been found to induce cooperative interactions between siblings (Schrader et al. 2015). It is predicted that the juveniles of

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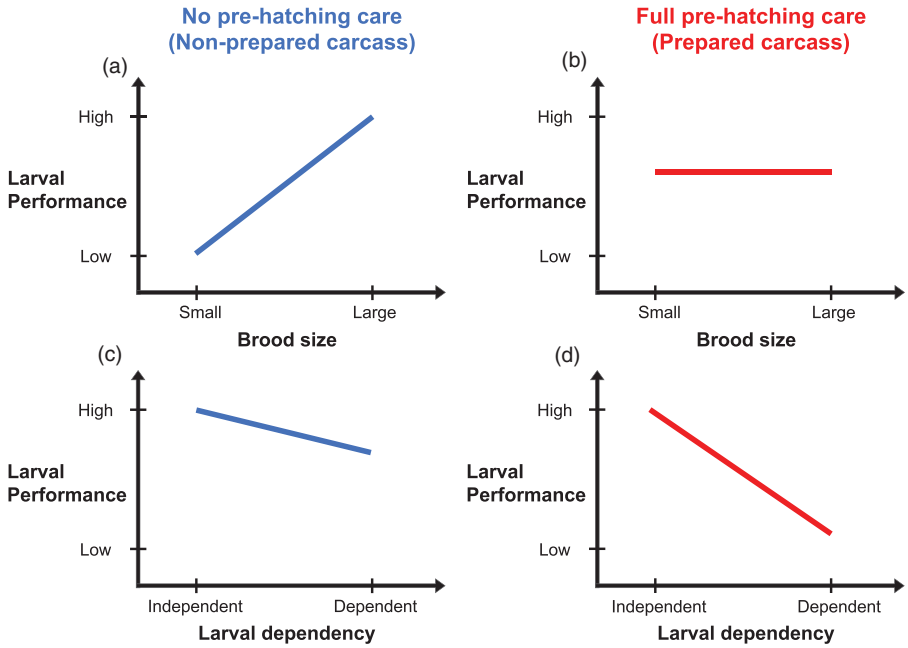

Figure 1. Simplified generalized graphical representation of the patterns described by Prang et al. (2021) that illustrates that (A) brood size improves larval performance on non-prepared but not on (B) prepared carcasses. Larvae of dependent species showed (C) higher growth and survival rates on non-prepared carcasses, but not on (D) carcasses with pre-hatching care, whereas larvae of independent species showed high survival rates throughout.

N. pustulatus should survive better than *N. vespilloides*, followed by *N. orbicollis*, and that brood size positively influences larval performance, especially for more independent species, and that these cooperative benefits should be more pronounced in harsh environments in the absence of pre-hatching care.

The authors found evidence of sibling cooperation, such that larval survival rate and growth increased with increasing brood size, which was found only on non-prepared carcasses (Fig. 1). Nevertheless, contrary to the authors' expectation, this trend did not differ among the three species, suggesting all species benefit from sibling cooperation in harsh environments. On parentally prepared carcasses (i.e., benign environments), only the most independent species, *N. pustulatus*, still benefited from sibling cooperation because increasing brood size positively predicted an increase in larval growth.

While manipulations of the presence of parental care and initial brood size were experimentally controlled to unveil the role of sibling cooperation, carcass size is intrinsically a vital element to be considered and may not always be unlimited in natural conditions (Sun et al. 2022). This is because *Nicrophorus* beetles tend to choose differently sized carcasses depending on their own body size and adjust their clutch size accordingly. The largest species, *N. orbicollis*, might facilitate sibling cooperation by laying more eggs and choosing larger carcasses, whereas juveniles of smaller species, whether independent of parental care or not, usually must compete because they tend to be reared on limited carcass resources. We suggest future studies evaluate the role of resource availability and parental care in shaping evolutionary transitions from competition to cooperation in social life.

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