



## Juvenile hormone, metabolic rate, body mass and longevity costs in parenting burying beetles



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Levels of juvenile hormone (JH) are elevated during parental care in burying beetles (*Nicrophorus*) at a time when ovarian activity is suppressed, suggesting that JH plays an alternative role to its better known gonadotropic function. Because parental activity in burying beetles is time-intensive, it might be expected to be energetically stressful and to impart longevity costs. We predicted that the active (feeding) stage of care would be associated with elevated JH and greater energy expenditure (higher metabolic rate, lower body mass), and that this stress would result in shorter life span. Parents experimentally manipulated into providing more care for young had increased levels of JH. For females, there was a significant longevity cost associated with parental care but not with mating or egg production. During carcass preparation, females and males that would later regurgitate to larvae showed an initial increase in body mass followed by a significant decrease in mass during the intense period of parental provisioning of young (during and just after the JH peak). Males that provided little care (on small carcasses with a female partner) showed no such anticipatory weight gain. An indirect measure of metabolic rate (VCO<sub>2</sub>) was nearly twice as high in caregiving females compared to nonbreeding females. These results suggest that the energy demands and/or high JH levels during care extract a significant cost on longevity. We propose that JH has evolved to play a novel role in parental care in burying beetles associated with extreme energy demands during feeding of offspring.

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The costs of reproduction structure many fundamental life history parameters such as the timing of breeding, clutch size, inter-clutch intervals, parental care and life span (Calow, 1979; Snell & King, 1977; Trivers, 1972). Reproductive costs for females may result from mating, egg production and caregiving, but the importance of these components are quite variable across species and even within species. Mating costs, for example, can be substantial in some species (Kuijper, Stewart, & Rice, 2006), minimal in others (Reguera, Pomiankowski, Fowler, & Chapman, 2004), and apparently absent in still others (Kotiaho & Simmons, 2003; Reinhardt, Naylor, & Siva-Jothy, 2009). Within a species, the costs of a particular component of reproduction, such as provisioning young, can vary substantially with the availability of food resources for parents (Fletcher et al., 2012). Costs of parental care might be expected to vary with energetic stress. Effective parental care across a wide variety of taxa may require elevated metabolic rates that approach physiological limits, likely explaining weight gain

prior to the most active period of care (McNab, 2002; Moreno, 1989; Reardon & Chapman, 2010; Sadowska, Gębczyński, & Konarzewski, 2013). Among birds, a high value and investment in the current brood may lead to a weaker response to stress and less investment in self-maintenance (Bokony et al., 2009), which might be reflected as a loss in body mass and decrease in life span.

Correlates of reproductive stress such as hormone levels, rates of behaviour, metabolic activity, immune function and changes in body mass can provide insight (Harshman & Zera, 2007), first, into which components of reproduction are the most costly, and secondly, into how natural selection affects reproductive decisions. Among insects, juvenile hormone (JH) regulates allocation of resources to reproductive activities and to self-maintenance, including immunity (González-Tokman, González-Santoyo, Munguía-Steyer, & Córdoba-Aguilar, 2013). Because JH can be upregulated by stimulation of insulin-like receptors (Mutti et al., 2011) and JH increases susceptibility to oxidative stress (Salmon, Marx, & Harshman, 2001), it is not unexpected that JH can be an important mediator of reproductive costs (Tu, Flatt, & Tatar, 2006).

In burying beetles (*Nicrophorus* spp.), much is known about changes in behaviour and immune function during reproduction. There is incomplete information, however, on changes in body

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mass and the role of JH, and nothing known about metabolic rates. The association of JH and metabolic state has received the most study in diapausing insects (Denlinger & Tanaka, 1989; Singtripop, Saeangsakda, Tatun, Kaneko, & Sakurai, 2007) where JH is related to mitochondrial function that may be independent of transcription and translation (Farkaš & Šut'áková, 2001; Stepien, Renaud, Savre, & Durand, 1988). JH can be associated with general metabolic activity, as, for example, cycles of O<sub>2</sub> consumption in larval flesh flies (Denlinger & Tanaka, 1989). There has been little study of the JH–metabolism association in breeding insects, although Sullivan et al. (2003), working with adult worker honeybees found that removal of the source of JH lowered metabolic rates. The JH–energy association may help us understand how JH relates to reproductive costs and why JH has such diverse behavioural and life history effects in adults. Insight might then be gained into why, non-intuitively, JH can have opposite associations with reproductive behaviour in different systems. For example, JH (1) increases social dominance in *Polistes* wasps (Tibbetts & Huang, 2010) but decreases it in a queenless ant (Brent, Peeters, Dietmann, Crewe, & Vargo, 2006), (2) decreases survival in young males of the damselfly *Hetaerina americana* but increases it in old males in the same population (González-Tokman et al., 2013) and (3) is found at low levels during caregiving in a viviparous cockroach and in earwigs (Rankin, McQuiston, & Jackson, 1999; Tobe et al., 1985) but is found at high levels in parenting burying beetles (Trumbo, 1997). Some of the variation in JH effects on the same category of behaviour across species might be explained by species differences in metabolic/energy demands for those behaviours.

Parental care among insects takes many forms, varying from passive guarding during a nonfeeding state to active provisioning and nest upkeep (Trumbo, 2012). The finding that JH is elevated during parental care of the burying beetle *Nicrophorus orbicollis* Say, when the ovaries are suppressed, was initially unexpected. In other parental insects, JH titres or JH synthesis is likely low during caregiving or brooding, and application of JH analogues can terminate care (Tallamy, Monaco, & Pesek, 2002; Trumbo, 2002 and references therein). Trumbo and Robinson (2008) suggested that a key difference is that parental care is very active in burying beetles. The female parent works close to maximal capacity except with the very smallest broods (Fetherston, Scott, & Traniello, 1990; Rauter & Moore, 2004), where paired *N. orbicollis* females spend more than 80% of their time processing carrion, regurgitating to young, maintaining the carcass and controlling the microbial environment in the nest. While some species can offset reproductive costs with less investment in immunity (Rolf & Siva-Jothy, 2003; Zuk & Stoehr, 2002), caregiving in burying beetles occurs at a time of elevated individual and social immunity in adults, probably because of the microbe-rich resource being utilized and the need to offset the lower level of immunity in young larvae (Cotter, Littlefair, Grantham, & Kilner, 2013; Cotter, Topham, Price, & Kilner, 2010; Steiger, Gershman, Pettinger, Eggert, & Sakaluk, 2011, 2012; Urbański, Czarniewska, Baraniak, & Rosiński, 2014). Some species can also reduce the costs of reproduction by withholding care, but this offset is limited in our study species because the first two instars of *N. orbicollis* will not develop without regurgitations (Trumbo, 1992). The combination of elevated behavioural activity, immune investment and JH levels during regurgitation to young suggests that caregiving might be expected to impose significant costs.

In the present study, we predicted that (1) mating, egg production and parental care would result in longevity costs, with the greatest cost associated with care; (2) the regurgitation stage of care would also be associated with a loss in body mass and with elevated JH levels; and (3) the regurgitation stage of parental care in *N. orbicollis* would be a time of elevated resting metabolic

rate, comparable to the high levels of energy expenditure and stress in caregiving mammals and birds (McNab, 2002). We investigated the relationships between activity, JH, metabolism and costs of reproduction in *N. orbicollis* in four ways. (1) We partitioned the longevity costs of reproduction into mating, egg production/carcass preparation and posthatching care by terminating reproductive bouts at different stages, and assessing the effects on life span. (2) We developed the most complete profile in a subsocial invertebrate of changes in body mass prior, during and after breeding in males and females on small and large carcasses, to reflect the energetics of breeding. (3) We compared metabolic rates of breeding age *N. orbicollis* females that were providing active care versus females that were not breeding. (4) We assessed JH levels of beetles manipulated into providing more care, first in single males (*N. orbicollis*) forced to provide all care versus paired males, which provide less care, and second in males and females providing care on large versus small carcasses. This last comparison utilized *Nicrophorus pustulatus* Herschel because this species will produce the largest broods of any *Nicrophorus* (Trumbo, 1992), a capacity related to its ability to exploit a large amount of resource in nests of snake eggs (Blouin-Demers & Weatherhead, 2000; Smith, Trumbo, Sikes, Scott, & Smith, 2007). The results demonstrate strong correlations between regurgitating to young, JH level, metabolic rate and body mass, and provide evidence that posthatching care of young is the most costly component of reproduction. Our results also suggest that elevated JH in burying beetles has been co-opted for a novel role in parental care.

#### Study Animals

A single female burying beetle or a male–female pair will bury a small vertebrate carcass, strip it of hair or feathers and apply secretions to control the microbial environment (Rozen, Engelmoer, & Smiseth, 2008) during carcass preparation (the first 3–4 days after discovery of the resource). Oviposition begins less than 24 h after discovery and is usually complete by day 3. Both males and females are reported to increase their body mass on the carcass (day 1, *Nicrophorus vespilloides*: Steiger, Gershman, et al., 2012; day 3, *N. orbicollis*: Panaitof, Scott, & Borst, 2004; by the time larvae hatch, day 3 or 4, *N. vespilloides*: Jenkins, Morris, & Blackman, 2000). JH in *N. orbicollis* spikes in both males and females immediately after a carcass is discovered (Trumbo, Borst, & Robinson, 1995), although this may not be related to subsequent ovarian development and deposition of vitellogenin (Panaitof & Scott, 2006; Scott & Panaitof, 2004). JH levels then decline but will later reach a higher peak during the most active period of parental care, that is, during the first 48 h that larvae are on the carcass (days 4–6) when most of the processing and regurgitation of carrion occur (Panaitof et al., 2004; Scott, Trumbo, Neese, Bailey, & Roe, 2001; Trumbo, 1997). During the late nesting period, larvae feed almost exclusively from the carcass and the parent(s) becomes less active but will defend against intruders. Male care is much more variable than female care in both duration and intensity. Males feed larvae less than females and they leave the nest sooner, especially on a smaller carcass (Fetherston et al., 1990; Trumbo, 1991). Males increase their activity and duration of care substantially if the female is removed, but female behaviour in the reverse manipulation changes little, probably because females may be working close to their maximum potential, except on the very smallest carcasses (*N. orbicollis*: Fetherston, Scott, & Traniello, 1994; Rauter & Moore, 2004; *N. vespilloides*: Smiseth & Moore, 2004; Smiseth, Dawson, Varley, & Moore, 2005; *Nicrophorus quadripunctatus*: Suzuki & Nagano, 2009). Reproduction has clear longevity and fecundity costs in *N. orbicollis* (Creighton, Heflin, & Belk, 2009) but mixed effects in

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