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Feeding upon and preserving a carcass: the function of prehatch parental care in a burying beetle

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Parental care must respond to variation in environmental challenges and some of these challenges result from the altered niche during the evolution of care. One important variable is the quality of the resources for young. Burying beetles prepare small, vertebrate carcasses in varying states of decay as food for their young by removing hair, rounding and applying antimicrobial secretions. The present study examined carcass preparation (prehatch care), an elaborate behaviour whose benefits have been surprisingly difficult to demonstrate. Benefits were assessed by comparing brood success when a parent completed care using a fully prepared carcass or when using a substitute, same-age carcass that had not been prepared by a parent. The outcome was very different depending on whether the substitute carcass was intact (no holes) or had simulated feeding holes that a parent would normally make during the prehatch period. When *Nicrophorus orbicollis* utilized a prepared carcass, the brood mass was no greater than when using an intact, nonprepared carcass. When the substituted nonprepared carcass had simulated feeding holes, however, a prepared carcass resulted in a greater brood mass and heavier larvae on both fresh and aged carcasses. The importance of attending to holes opened in the carcass was clear from the rapid repair of experimentally introduced holes. While offspring fared worse when developing on an aged carcass, the parent's future reproduction and longevity were not compromised, suggesting that parents protect their future reproduction in a challenging environment. It is hypothesized that a primary benefit of resource handling in burying beetles is to minimize microbial activity at holes the parent must make in the carcass, a need that was amplified as carrion beetles evolved to breed on small, preempted carcasses without fly larvae as a nutritional resource.

Parental care is a complex trait expressed in varying environments (Smiseth, Kölliker, & Royle, 2012) and can be sensitively adjusted to the needs of offspring (Mas, Haynes, & Kölliker, 2009; Moczek, 1998). To understand the function of a specific component of care, it is important to be able to demonstrate its benefit and to relate that benefit to the solution of a potential challenge. Some challenges may be selective agents at the origin of care (prime movers, Wilson, 1975) while others take on new importance only after the emergence of care. Dung beetle parents, for example, are sensitive and responsive to desiccation of the larval food, a problem that is amplified by the necessity for parents to divide the resource into small brood balls (Schwab, Riggs, Newton, Moczek, & McPeek, 2016; Sowig, 1996). Important parental traits, then, may be solutions to problems created as the niche evolves. An important challenge for many animals is the microbial community they encounter in the environment (Barribeau, Parker, & Gerardo, 2014; Barthel et al., 2014) and these challenges are often heightened by family life within the confines of a nest (Boos, Meunier, Pichon, & Kölliker, 2014; Tranter, Graystock, Shaw, Lopes, & Hughes, 2014). Controlling the microbial community can be especially important when nutritional resources are provisioned for offspring within the nest (Rozen, Engelmoer, & Smiseth, 2008; Strohm & Linsenmair, 2001).

Variation in the microbial environment can also affect decisions about the allocation of effort towards current versus future offspring (Reavey, Warnock, Vogel, & Cotter, 2014; Uller, Isaksson, & Olsson, 2006). When a parent is faced with a challenging environment during care, the parent can either bear the cost itself (Jones & Reynolds, 1999) or protect its own survival by providing less effective care (Tolonen & Korpimäki, 1996). The parental response provides insight into an important component of life history, a parent's expectation of future breeding (iteroparity potential). When resources are difficult to obtain during care, for example, parents of long-lived species might be expected to transfer costs to the current brood to protect future fecundity (Mauck & Grubb, 1995; Navarro & González-Solís, 2007). Parents nearing terminal investment, however, are expected to absorb costs while attempting to maintain normal provisioning of current young (Elliott et al., 2014).

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Estimating the benefits of a particular component of care can be difficult, especially for a component near the beginning of a complex sequence of care. When early stages of care are disrupted, the parent may abandon breeding or the young may fail to survive. In birds, for example, building a nest introduces an important stimulus for further parental care; removal or disruption of the nest may prevent normal breeding (Collias & Collias, 1984; Lehrman, 1958), making it difficult to estimate the benefits of nest building. This experimental difficulty can be overcome in some systems, in which a less modified nest or resource can be substituted for the typical version, allowing the breeding cycle to be completed (e.g. Capodeanu-Nagler et al., 2016). The altered performance of offspring and parent can then be used to estimate the benefits of the modification occurring at an early stage of the parental cycle.

Burying beetles face microbial challenges because they use a discovered carcass to provision their young within a nest. Their elaborate carcass preparation behaviour is hypothesized to cope with this challenge (Arce, Johnston, Smiseth, & Rozen, 2012; Rozen et al., 2008). Carcass preparation in the present study is used synonymously with prehatch parental care, as manipulation of the resource is the primary activity during this period that is thought to benefit young. A single female will bury a carcass, strip it of hair or feathers, round it into a ball and apply anal and oral secretions to the exposed surface over several days (Pukowski, 1933). The anal secretions of both parents and larvae have demonstrated antimicrobial activity (Arce, Smiseth, & Rozen, 2013; Arce et al., 2012; Duarte et al., 2016; Hall et al., 2011) and such activity is elevated when the need is greater during breeding (Cotter & Kilner, 2010; Steiger, Gershman, Pettinger, Eggert, & Sakaluk, 2011). Despite intense experimental work on this beetle–microbe system, which includes identification of immunity-related genes related to a microbial challenge and metagenomic study of the microbial community and its transmission to the next generation (Jacobs et al., 2016; Palmer et al., 2016; Vogel, Badapanda, & Vilcinskas, 2011; Wang & Rozen, 2017), the value of carcass preparation is uncertain. In three species of *Nicrophorus*, prehatch care did not affect the number or size of offspring, as only posthatch care was found to be important (Capodeanu-Nagler et al., 2016). Prehatch care in *Nicrophorus vespilloides* Herbst (other than opening the carcass for larvae to access food) did not affect the mass of the brood on either fresh (Eggert, Reinking, & Müller, 1998; Rozen et al., 2008) or aged (7-day) carcasses (Rozen et al., 2008, mass of the brood was not directly reported but can be estimated by combining their Figure 2a and Figure 2b). With aged carcasses, offspring that did not receive prehatch care were more numerous but smaller in size, leading to the conclusion that the value of resource handling is only manifest with older carcasses (Rozen et al., 2008).

Other experimental approaches also suggest that the benefits of carcass preparation for young are limited. A poorly constructed brood ball by *N. vespilloides* parents did not affect offspring success (De Gasperin, Duarte, Troscianko, & Kilner, 2016). Using *Nicrophorus orbicollis* Say, Trumbo, Sikes, and Philbrick (2016) found that applying antibacterial washes to intact carcasses as they age did not improve production of beetle broods (an 'intact' carcass is used here to indicate a carcass without holes through the skin). Without a clear understanding of how carcass preparation improves beetle fitness, it will be difficult to focus the expanding work on burying beetle–microbe interactions.

None of the experimental approaches to date have accounted for parents' repair of their own feeding holes during carcass preparation, a behaviour ignored despite Pukowski's (1933) emphasis that it is done immediately after each feeding bout. Forensic scientists have found that traumatic injury to a corpse (breaks through the skin) dramatically increase the rate of decay (Mann, Bass, & Meadows, 1990) and these breaks are an important determinant of the rapidity of insect succession (Connell & Slatyer, 1977). Putnam (1978), opened holes in small mouse carcasses with a dissecting needle and deduced that holes substantially increase microbial activity. A burying beetle female must intentionally 'injure' the carcass to obtain nutrients for breeding and parental care because, unlike other carrion beetles (nonparental silphids), she typically exploits a carcass without blowfly larvae on which to feed. During the prehatch period, a female increases her own body mass approximately 10% while producing a clutch that is typically 10–20% of her body mass (Trumbo & Xhihani, 2015), indicative of the extensive feeding that must occur. In the present study, I investigated the possibilities that the challenge posed by microbial deterioration is magnified because of parental feeding holes and that carcass preparation and repair mitigates those costs. I hypothesized that a critical component of prehatch parental care is to minimize microbial activity at holes that the parents themselves must open in the carcass.

Using *N. orbicollis*, I first tested whether substituting a nonprepared, intact (no holes) carcass for a prepared carcass would affect the mass of the brood, similar to previous methodology that found that prehatch care does little to increase the conversion of resource mass to offspring mass. I then examined whether introducing holes to a carcass as it ages would decrease its value for beetle brood. Finally, I estimated the value of carcass preparation by simulating how the brood would fare if an adult female found a fresh or aged carcass, then buried it and opened two feeding holes but otherwise performed no carcass preparation behaviour, as an alternative to substituting an intact carcass, as described above. I also assessed the effect on the parent's future reproductive performance and longevity to determine whether parents or offspring bear the cost of using an aged carcass for breeding and to determine who bears the cost of using a resource that has not been prepared. These costs are important for integrating behaviour with life history. A finding that parents bear the majority of costs, indicating a low perceived value for their future reproduction, would be evidence that burying beetles are functionally semelparous, as suggested by Tallamy and Brown (1999).

METHODS

General Methods

All the beetles used in experiments were laboratory-reared *N. orbicollis* derived from a wild population from Bethany, Connecticut, U.S.A. (41°27′36 N, 72°57′37″W). The colony is restarted each summer. Beetles were isolated shortly after emergence in small containers (7 cm diameter, 3.5 cm height) and fed on slivers of chicken liver three times per week and kept at 20 °C on a 15:9 h light:dark cycle. Females were mated to two males of the same family (but a different family than the female) on consecutive nights 4–8 days before the start of a trial. Females from 13 families were used in experiment 1 and 18 families for experiment 2. Females in experiment 4 were selected randomly with respect to family as females had to be matched by both age of carcass and for timing of the arrival of larval rather than by family. Breeding occurred in containers (35 × 11 × 18 cm) three-fifths filled with commercial topsoil and kept in the dark. Females were presented a mouse carcass (RodentPro Inc., Inglefield, IN, U.S.A.) that was previously frozen. Containers were checked starting 10 days after presentation of the carcass to determine when larvae had dispersed from the nest. After dispersal, larvae were counted and weighed (±0.01 g) to assess number of larvae, mean mass of larvae and total mass of the brood. In experiments 1 and 4, a nonprepared carcass that was substituted for a prepared carcass was initially set aside and buried in soil from the field for the same duration as the prehatch period. The care and handling of beetles followed the ethical guidelines as established by