Age-related reproductive performance in the parental burying beetle, *Nicrophorus orbicollis*

Stephen T. Trumbo
Department of Ecology and Evolutionary Biology, University of Connecticut, Waterbury, CT 06702, USA

Age-related improvements in reproductive performance have been explained by the selection, constraint, and restraint hypotheses (increased performance related to greater effort and a declining residual reproductive value). Using a laboratory population of the burying beetle, *Nicrophorus orbicollis*, 6 measures of performance were assessed. Consideration of the selection and constraint hypotheses was minimized by reducing mortality to near zero and comparing reproductive outcomes of equal-sized females with equivalent mating and breeding experience. Young and old females were provided a resource for breeding (mouse carcass) and were confronted by a potentially infanticidal intruder (young or old) after offspring were present in the nest. Younger females were more likely to experience a brood failure and were slower to oviposit eggs. Younger intruding females also were less likely to usurp a carcass from a resident female. Age, however, did not affect any measure of reproductive performance once a female had a brood. There were no differences between young and old females in the number and mass of offspring in original or replacement broods, or in the probability of successfully defending offspring against an intruder. In a follow-up experiment with smaller carcasses, there was, again, no significant difference in the ability of young and old females to defend their brood. In *N. orbicollis*, the reproductive restraint observed in younger females appears to inhibit the initiation but not the continuance of reproduction. The usefulness of the residual reproductive, targeted reproductive effort and the maturational limits hypotheses to explain age-related variation in reproductive performance are discussed. *Key words:* aging, burying beetle, contest behavior, indirect effects, maternal effects, *Nicrophorus*, parental care, reproductive effort, senescence. *[Behav Ecol 20:951–956 (2009)]*

Prior to senescence, older individuals often demonstrate superior and more consistent reproductive performance than younger individuals (Garel et al. 2009). There are 3 primary explanations (Curio 1983; Forslund and Pårt 1995). The selection hypothesis proposes that a younger cohort has been exposed to less mortality and, consequently, fewer less-fit individuals have been removed (Laaksonen et al. 2002). The constraint hypothesis proposes that young individuals with less breeding or parenting skills suffer lower reproductive output (Cameron et al. 2000), or that less foraging experience causes younger individuals to initiate reproduction in poorer body condition (Robertson and Rendell 2001). The restraint hypothesis proposes that young individuals provide less reproductive effort because the value of the current brood relative to expected future offspring (residual reproductive value, RRV) is less (Trivers 1972; Tallamy 1982; Clutton-Brock 1984). The restraint hypothesis is difficult to test in isolation because age usually correlates with exposure to mortality and with breeding and foraging experience in the field. Further complication is introduced because of the varied nature of parental investment (Field et al. 2007). The possibility that different components of investment do not respond in concert to aging or other changes in RRV (Pearson et al. 2005; Ardia and Clotfelter 2006; Lock et al. 2007) make it necessary to study multiple elements of reproduction to uncover general patterns in age-related variation in performance.

Although laboratory study of short-lived insects with parental care are ideal models, few such studies have been undertaken. Using the burying beetle, *Nicrophorus orbicollis*, it is possible to reduce mortality to near zero, to provide young and old indi-viduals with equivalent mating and breeding experience, and to use individuals with similar body mass, thereby minimizing consideration of the selection and constraint hypotheses. It is also possible to measure multiple components of reproductive and parental performance (rate of brood failure, time to hatching of young, defense of young, size and number of offspring, and fights to usurp a breeding resource).

Nicrophorus spp. compete for small vertebrate carcasses, rare but high-value resources (Wilson 1971) that they must win from microbes, scavengers, and other burying beetles. They have rapid hormonal, ovarian, and resource preparation responses that aid in this competition (Scott and Traniello 1987; Trumbo et al. 1995). Eggs are oviposited in as little as 12 h, whereas carcass preparation is still ongoing (burial, removal of hair or feathers, and rounding into a ball) (Pukowski 1933). Prepared carcasses are vulnerable to usurpation by other burying beetles during most of the nesting cycle (Trumbo 1990b). The female oviposits in the soil and larvae crawl to the carcass to feed from the resource and to be fed by the parent(s) (Pukowski 1933; Eggert et al. 1998). Maternal effects can be substantial, particularly on mass of offspring (Rauter and Moore 2002; Steiger et al. 2007).

Although females have the potential to breed several times (Scott 1998; Nagano and Suzuki 2007), there are a number of lines of evidence that suggest that opportunities for procuring a carcass are very limited. Females engage in reproductive behavior with a low rate of production of offspring such as brood parasitism by smaller, satellite females (Müller, Eggert, and Dressel 1990), utilization of an older, deteriorating carcass that has been partially consumed by a prior burying beetle brood (Müller 1987; Trumbo 2006), and utilization of a very small carcass that supports less than one-tenth the number of young that can be optimally reared (Müller Eggert, and Furlkroger 1990; Trumbo 1990a). Reproductive success of *N. orbicollis* declines between the first and second reproductive attempts even with the benefit of experience (Scott and Traniello 1990), which suggests that a single reproductive

cycle increases the rate of senescence, consistent with a life history of limited reproductive opportunities (Williams 1966). Scott and Gladstein (1993) have modeled the duration of male parental care and concluded that a male on a carcass with young behaves as if there were no further reproductive opportunities. In addition, overwintering mortality is significant, either for larvae or for adult nonbreeders (Smith 2002; Schnell et al. 2008). Females in the field that complete a reproductive cycle likely have poor prospects of breeding in a second year. Anecdotally, this is supported by the rarity of females in the beginning of the breeding season exhibiting characteristics of prior reproduction such as a worn exoskeleton, injuries from combat, or high infestation of phoretic symbionts. These findings suggest that being the primary breeder on an ideal-sized resource in good condition is rare and that even successful females complete only a few reproductive attempts, at best, whereas smaller females may never be a primary breeder (Tallamy and Brown 1999; Müller et al. 2007).

In the present work, the reproductive performance of primiparous young and old *N. orbicollis* females with equivalent body mass, and equivalent mating and breeding experience was compared. It was possible to minimize consideration of the selection and constraint hypotheses by controlling the environment in the laboratory. A follow-up experiment using smaller carcasses (reducing the value of the current brood) was undertaken to increase the probability of finding a predicted effect of the restraint hypothesis (greater defense of offspring by older females). These tests of the restraint hypothesis found that younger females demonstrate lower reproductive performance when initiating reproduction (higher rate of brood failure, more time to hatching of offspring, lower probability of usurping a resource) but no difference in performance for continuing an ongoing reproductive attempt (number and size of offspring, defending against a usurper).

MATERIALS AND METHODS

Rearing beetles

A laboratory population of *N. orbicollis* was derived from wild-caught beetles from Bethany, CT, and kept at 20 °C, 15:9 h light:dark. A surplus of adult females was reared to supply a sufficient number of beetles of the proper size for experimental work. At emergence, adults were placed in mixed-sex groups in containers ($11 \times 18 \times 33$ cm) for 10 days before being isolated in smaller containers (9-cm diameter, 5-cm depth). Young females were kept in these individual containers for 12–16 days and were 22–26 days old at the start of the experiment. Old females were kept in individual containers for 42–48 days and were 52–58 days old at the start of the experiment. For a 24-h period, both 10 and 3 days prior to the start of a trial, each female had a male introduced into her container. Young and old females, therefore, had equivalent opportunities for social and mating interactions: 10 days initially in mixed-sex groups and 2 24-h exposures to a single male. Because all food was provided in the same manner (small pieces of chicken liver, <1 g), older females were not able to gain an advantage in foraging experience. All females were starved for 48 h prior to the start of a trial to more equalize body mass. Subsets of young and old females ($N = 26$ each), not used in experimental trials, were weighed to compare body mass under the rearing protocol. The body mass to pronotal width ratio did not differ for young and old females under the rearing conditions employed ($t = 0.20$, df $= 50$, $P = 0.84$). Mortality rates were low and were similar for young and old females. Of all beetles isolated 10 days after emergence, only 3 of 244 young and 4 of 216 old females died prior to the age at which these groups were used in experiments (Fisher's Exact test, $P = 0.71$).

Experimental trials

From the larger population of females reared in the conditions described above, young and old individuals were selected to establish 4 treatments: young resident/young intruder, young resident/old intruder, old resident/young intruder, and old resident/old intruder ($N = 36$ each). To get an adequate sample of successful intrusions, the resident female was paired against an intruder whose pronotum was 5–9% wider (see Trumbo and Valletta 2007). The resident female was placed in a translucent breeding container ($11 \times 18 \times 33$ cm), two-thirds filled with soil, with a mouse carcass (24–28 g) that was covered with a paper towel (15:9 h light:dark). Previous work had demonstrated that a female without a male partner in a breeding container that permitted light to enter would usually, but not always, produce a brood. Beginning 4 days after the female was established with the carcass, the carcass was checked for the appearance of larvae. Trials without larvae by the end of day 6 were scored as brood failures and terminated. If larvae were observed on the carcass, the intruder was introduced away from the carcass and covered with soil. These trials were checked 2 days after introducing the intruder. If larvae were still present (larvae defended successfully), the intruder was removed and the resident was allowed to continue to care for her young (original broods). If no larvae were alive 2 days after introducing the intruder (complete infanticide, see Trumbo and Valletta 2007), the resident female was removed and the intruding female was allowed to attempt to produce a brood (replacement broods). On the day larvae dispersed from the nest, they were counted and weighed.

Defense of the brood—small carcasses

To examine the effect of age of the resident on defense of the brood on a less valuable resource, young and old females were reared as above. Two treatments were established: young resident/old intruder, old resident/old intruder ($N = 36$ each). Females were established on 10–12 g carcasses. Subsequent procedures were as described above.

Statistical analysis

Frequency of brood failure was examined using a χ^2 analysis with Yates' correction. Data on the day that larvae arrived on the carcass were analyzed using a Mann–Whitney U test because of the noncontinuous nature of the dependent variable (day 4, 5, or 6). Defense of the brood in the initial experiment was examined using a $2 \times 2 \times 2$ log-linear analysis of frequency data (success or complete infanticide, young or old resident, young or old intruder). Interactive effects were included in the analysis whether or not they were significant as suggested by Cox and Snell (1989). A χ^2 analysis was used to examine the relationship between successful brood defense and age of resident for data from small carcasses (as a conservative measure, Yates' correction was not employed because this follow-up experiment was designed to confirm a hypothesis of no difference based on results from the first experiment). The number of larvae and mean mass of larvae in a brood were analyzed using a 2-way analysis of variance (young or old intruder, original or replacement brood). Nonsignificant interactions were not included in the models reported. All analyses were 2-tailed and performed using SAS (2007).

RESULTS

Initiating reproduction

Young resident females were more likely to experience a brood failure (no larvae by the end of Day 6, 16 of 72) than old resident females (6 of 72, $\chi^2 = 4.35$, $P = 0.04$, Yates correction). Of residents that initiated a brood successfully, the day that larvae arrived on the carcass was later for young than for old females (Figure 1). This indicates that young residents took longer to begin oviposition compared with old residents.

Defense of the brood

Successful defense of the brood against a larger intruder was examined for effects of age of the resident and age of the intruder. The age of the resident had no effect on successful defense ($G^2 = 0.00$, df = 2, $P = 0.99$, $2 \times 2 \times 2$ log-linear analysis, Figure 2). Older intruders, however, were 28.1% more likely than younger intruders to usurp a carcass from a resident ($G^2 = 9.90$, df = 2, $P = 0.007$). There was no significant age of resident $\times$ age of intruder interaction ($G^2 = 0.04$, df = 2, $P = 0.98$).

Overall, older intruders were far more successful (36 of 62) in usurping a carcass than younger intruders (18 of 60). An alternative explanation for the greater success of older intruders is that some younger intruders may not have been sexually mature, and therefore would not attempt to usurp. If the number of brood failures by resident young ($N = 16$) and old ($N = 6$) females is used as an estimate of the number of intruders unwilling to contest, then a reanalysis can be performed, estimating that 36 of 56 motivated old intruders would have been successful at usurping, and 18 of 44 young intruders would have been successful. The difference is still significant ($\chi^2 = 4.52$, $P = 0.03$, Yates correction). This is a highly conservative reassessment because not all brood failures are related to beetles unwilling to contest, and because young intruders were introduced 4–6 days after the start of the experiment (26–32 days old at introduction).
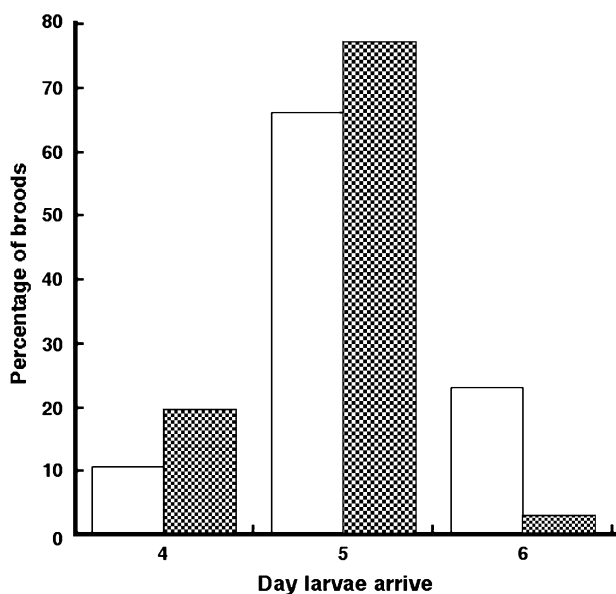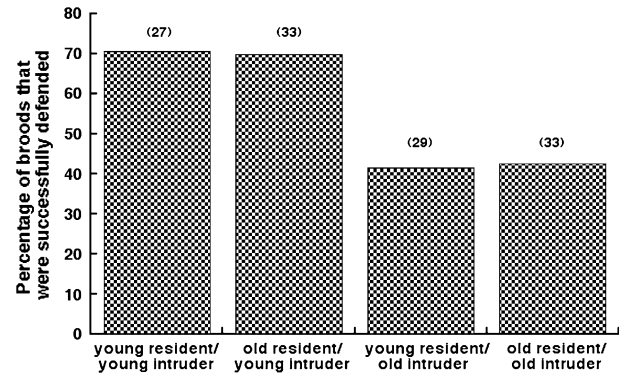

Figure 2
The percentage of trials in which the resident female successfully defended her brood against a potentially infanticidal intruding female. Sample sizes are shown above the bars.

Number and size of offspring

The number of offspring produced was significantly related to whether the offspring were reared in an original or replacement brood ($F_{1,119} = 10.09$, $P = 0.02$) but not to whether the female parent was young or old ($F_{1,119} = 0.74$, $P = 0.39$, Figure 3a). Similarly, the mean mass of offspring was related to whether offspring were from original or replacement broods ($F_{1,119} = 30.17$, $P < 0.0001$) but not to age of the parent ($F_{1,119} = 0.39$, $P = 0.54$, Figure 3b).

Defense of the brood—small carcasses

To further investigate the effect of age of the resident on defense of the brood, the success of young and old residents against old larger intruders were examined on small carcasses. As before, there was no significant difference between the success rate of young residents (25%) and older residents (34.4%) ($\chi^2 = 0.63$, $P = 0.43$).

DISCUSSION

The present study measured 6 components of reproductive performance, 3 related to the initiation of reproduction (probability of brood failure, latency to oviposition, probability of usurping a resource), and 3 related to the continuance of reproduction (defense of brood, number and mass of offspring reared). Older females were found superior to younger females in each measure of initiating reproduction but in no measure of continuing reproduction. Consideration of the selection hypothesis was minimized by reducing mortality to near zero, and consideration of the constraint hypothesis was minimized by providing young and old females with similar foraging, mating, and breeding experience. The results suggest that younger females were restrained in initiating reproduction, consistent with a lower value of the current brood relative to their higher RRV. A lower expected RRV in older females might be related to age. Alternatively, older females breeding for the first time may have a lower expected RRV because of the longer period of "searching" but not locating a resource for breeding (an expected lower rate of encountering reproductive opportunities). Additional work is necessary to distinguish between these 2 hypotheses.

Three prior studies of *Nicrophorus* spp. are broadly consistent with these findings, and along with the present study, make *Nicrophorus* our best model of the effects of aging on reproduction in an invertebrate with parental care. Nagano and Suzuki (2007) found that older *N. quadripunctatus* Kraatz
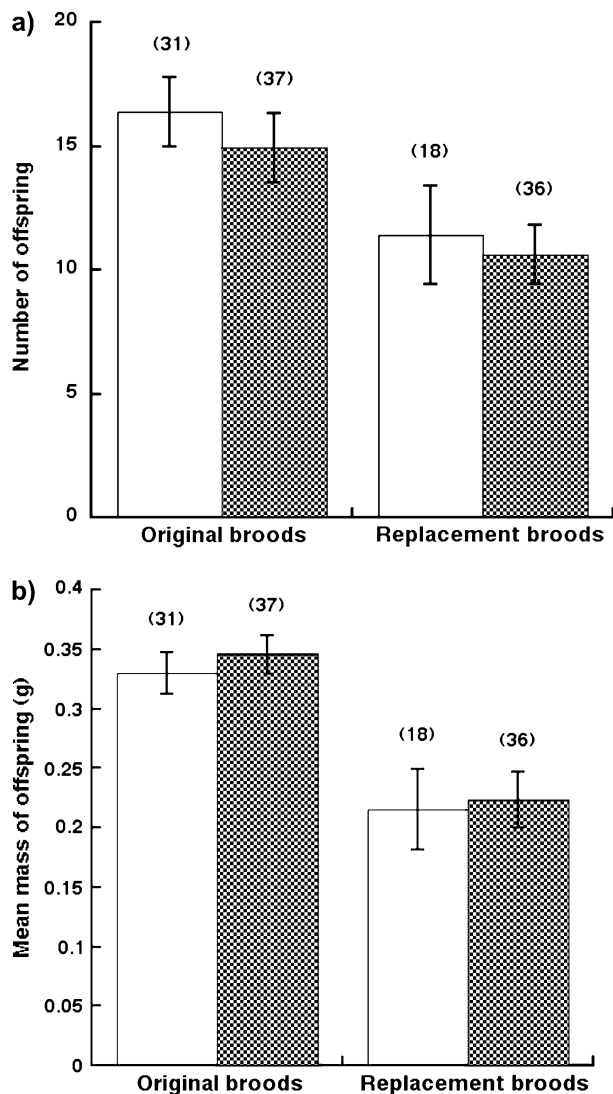

Figure 1
The percentage of trials in which offspring arrived on the carcass on day 4, 5, or 6. Only trials that produced offspring included ($N = 56$ for young residents [open bars], $N = 66$ for old residents [shaded bars]) ($U = 2308.5$, $P = 0.02$, Mann–Whitney U test).

Figure 3
Mean (±standard error) (a) number of offspring and (b) mass of offspring produced by young (open bars) and old (shaded bars) females in original and replacement broods. Sample sizes are shown above the bars.

females oviposited faster than younger females, although the number of reproductive attempts was varied intentionally. Scott (1998) and Lock et al. (2007) measured a number of components of reproductive performance in females of different age, controlling for the number of breeding attempts, although it was not clear if body mass or differential mortality between cohorts was controlled. Scott (1998) reported that age had no effect on the duration of care of female *N. orbicollis* (although there was a positive effect on males). *Nicrophorus vespilloides* Herbst increased egg mass with age (Lock et al. 2007). The effect of age on parental feedings was less clear in *N. vespilloides,* older females spending more time in proximity to offspring without feeding (a negative effect on offspring fitness), but more time provisioning young (a positive effect). In summary, age has clear positive effects on initiating reproduction, whereas the effects on continuing reproduction and parental care are either substantially less or zero. These studies point out the importance of measuring multiple components of reproductive performance at different stages of the reproductive cycle.

For insects without parental care, there is a curious dichotomy of results related to age-related patterns of reproductive performance. Many studies have found that egg mass or offspring survivability decrease with age (Mousseau and Dingle 1991; Fox 1993; Hercus and Hoffman 2000; McIntyre and Gooding 2000; Kern et al. 2001; Priest et al. 2002). Studies of reproductive agonistic behavior, however, have generally found that competitive ability in contests increases with age (Papaj and Messing 1998; Kemp 2002; Humphries et al. 2006), consistent with theory that younger adults pay a greater lifetime cost for injury or death (Enquist and Leimar 1990). The contrasting findings between studies of egg mass/offspring survivorship and studies of contests have not been resolved. Differences in the choice of model organisms and whether the focus was on age-related improvements in performance or on senescence may explain some of the variation. Comparative work within a taxon might uncover life history differences to explain age-related variation of reproductive effort (Stegmann and Linsenmair 2002; Kemp et al. 2006).

The possibility that components of reproductive effort do not change in concert with age was not given much consideration by early modelers of reproductive effort. There are at least 3 hypotheses to explain why age affects the initiation but not the continuance of reproduction in burying beetles. Reproductive effort among individuals is theorized to vary according to the expression:

Value of current brood/RRV (Curio 1983)

On finding a suitable carcass for breeding, the value of the incipient reproductive attempt is modest because of the high loss of carcasses to scavengers, invertebrate competitors, microbes (Scott et al. 1987; Trumbo 1990c; Hoback et al. 2004; Rozen et al. 2008), and to other burying beetles (Trumbo 1990a; Trumbo 1992; Suzuki 2000; Müller et al. 2007). For an organism that has an extremely limited number of opportunities to breed on a high-risk, high-reward resource, the value of the current reproduction relative to RRV can increase significantly as the resource is prepared and offspring develop. If a burying beetle is able to safely bury a carcass, strip off the hair or feathers, and control carrion fly larvae and microbes, the probability of completing reproduction improves dramatically. Similarly, the threat from other burying beetles decreases after burial, and is near zero by the time larvae reach the third day (Robertson 1993; Trumbo 2006). The sizes of original broods in this experiment (mean of 16.6) may well have been greater than the RRV of both young and old females, although there is still a critical lack of information on the availability of carcasses for burying beetles in the field. Although the ratio (Value of current brood/RRV) during an ongoing reproductive cycle should increase similarly for young and old females, the relationship between effort and benefit may not be linear. Older females may begin a reproductive attempt with close to maximal (terminal) reproductive effort (Issac and Johnson 2005), and any increase in effort as offspring develop may produce diminishing returns. Younger females, on the other hand, may begin a reproductive attempt with a lower level of effort and the increase in effort as the current brood becomes more valuable may produce a substantial return. This scenario would be more likely when there is an S-shape benefit to effort curve (e.g., see Trivers 1972). Older females might then give greater effort than younger females throughout the reproductive cycle but the effects of that greater effort would be increasingly difficult to detect as younger females increase effort during the cycle. The follow-up experiment with small carcasses was designed to reduce the value of the current brood to determine if it was possible to detect an age-related difference in reproductive performance at the parental stage. As was found using larger

carcasses, there was no significant difference between young and old resident in defending a brood. It appears clear that the differences in reproductive performance of young and old females were more substantial at the initiation of reproduction than during parental care; this result cannot be completely aligned with a simple application of the RRV hypothesis.

A second explanation for the finding that younger females perform more poorly at nest initiation but that young and old females perform similarly during later stages of a reproductive cycle is the "targeted reproductive effort" hypothesis (Cameron et al. 2000). This hypothesis proposes that greater effort will be given when care is more valuable for offspring. If we take it as given that young females produce later (this study) and/or smaller eggs (Lock et al. 2007, for *N. vespilloides*), then it is possible that younger females would provide more care at a later stage of the parental cycle because of greater need. In this case, there might be a negative correlation of effort between the initiation phase of reproduction and the parental phase (prenatal and postnatal effects, Lock et al. 2007). Although Lock et al. (2007) did not find unambiguous evidence that younger parents were providing greater care-giving effort, they did find that weight gain in larvae of young and old females was equivalent, suggesting that young females had somehow compensated for their poor start. Offspring behavior might then be selected to be plastic to respond to the form of care given by parents. On its own, the targeted reproductive effort hypothesis does not explain why the performance of younger females in *N. vespilloides* is initially lower or why age affects intruder but not resident contest performance in *N. orbicollis*. The targeted reproductive effort hypothesis makes it clear that not only must multiple components of reproductive performance be assessed but that differences in 1 component of care might also affect subsequent effort for other components of care.

A third hypothesis to explain poor reproductive performance of young females is a nonadaptive limit to optimal reproductive maturation. It is impossible for an organism to instantly switch from a nonreproductive state to a fully reproductive state. Although the timing and rate of maturation should respond to natural selection and should reflect changing RRV, the transition period cannot be reduced to zero even if a reproductive opportunity with a potentially high payoff is encountered. There are costs to entering a reproductive state at an earlier age, some of which may be irreversible and accumulate over the entire postmaturational period (Zwaan 1999; Harshman and Zera 2006). For young organisms, the presence of a good reproductive opportunity may be an important signal to alter reproductive physiology. Once the transition has been made, reproductive effort may then reflect brood value and RRV. It has been noted in a number of iteroparous organisms that the most significant change in reproductive performance comes between the first and second reproductive attempts (examples in Angelier et al. 2007) when the RRV hypothesis predicts the greatest change just prior to senescence, and the experience hypothesis predicts a gradual (although perhaps diminishing) improvement in performance with an increasing number of reproductive attempts. The maturational limits hypothesis should be most applicable where maintaining a reproductive-ready state is costly, the timing of first reproduction is uncertain, and the initial breeding season (or attempt) can generate a substantial fraction of an organism's expected lifetime reproductive success. For organisms with a short lifespan and few reproductive attempts such as burying beetles, this transition might occur in the course of a single reproductive attempt.

These hypotheses are not mutually exclusive. For example, either the RRV or maturational limits hypotheses might explain the initial slower response of younger females, and the targeted reproductive effort hypothesis may then explain equal or greater effort of young females during parental care because of the greater need of offspring. Study of age-related reproductive performance of burying beetles makes it clear that even when the constraint (experience) hypothesis and the selection (differential mortality) hypothesis can be minimized, the RRV hypothesis will not be easily applied to explain age-related variation in reproductive performance in organisms with complex parental care.

REFERENCES

Angelier F, Weimerskirch H, Dana S, Chastel O. 2007. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. Behav Ecol Sociobiol. 61:611–621.

Ardia DR, Clotfelter ED. 2006. Individual quality and age affects responses to an energetic constraint in a cavity-nesting bird. Behav Ecol. 18:259–266.

Cameron EZ, Linklater WL, Stafford KJ, Minot EO. 2000. Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? Behav Ecol Sociobiol. 47:243–249.

Clutton-Brock TH. 1984. Reproductive effort and terminal investment in iteroparous animals. Am Nat. 123:212–229.

Cox DR, Snell EJ. 1989. The analysis of binary data. New York: Chapman & Hall.

Curio E. 1983. Why do young birds reproduce less well? Ibis. 125:400–404.

Eggert A-K, Reinking M, Müller JK. 1998. Parental care improves offspring survival and growth in burying beetles. Anim Behav. 55:97–107.

Enquist M, Leimar O. 1990. The evolution of fatal fighting. Anim Behav. 39:1–9.

Field J, Turner E, Fayle T, Foster WA. 2007. Costs of egg-laying and offspring provisioning: multifaceted parental investment in a digger wasp. Proc Roy Soc Ser B—Biol Sci. 274:445–451.

Forslund P, Pärt T. 1995. Age and reproduction in birds—hypotheses and tests. Tr Ecol Evol. 10:374–378.

Fox CW. 1993. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). Oecologia. 96:139–146.

Garel M, Solberg EJ, Saether B-E, Grøtan V, Tufto J, Helm M. 2009. Age, size, and spatiotemporal variation in ovulation patterns of a seasonal breeder, the Norwegian moose (*Alces alces*). Am Nat. 173:89–104.

Harshman LG, Zera AJ. 2006. The cost of reproduction: the devil in the details. Tr Ecol Evol. 22:80–86.

Hercus MJ, Hoffman AA. 2000. Maternal and grandmaternal age influence offspring fitness in *Drosophila serrata*. Proc Roy Soc Ser B—Biol Sci. 267:2105–2110.

Hoback WW, Bishop AA, Kroemer J, Scalzitti J, Shaffer JJ. 2004. Differences among antimicrobial properties of carrion beetle secretions reflect phylogeny and ecology. J Chem Ecol. 30:719–729.

Humphries EL, Hebblethwaite AJ, Batchelor TP, Hardy ICW. 2006. The importance of valuing resources: host weight and contender age as determinants of parasitoid wasp contest outcomes. Anim Behav. 72:891–898.

Issac JL, Johnson CN. 2005. Terminal reproductive effort in a marsupial. Biol Lett. 1:271–275.

Kemp DJ. 2002. Butterfly contests and flight physiology: why do older males fight harder? Behav Ecol. 13:456–461.

Kemp DJ, Wiklund C, Gotthard K. 2006. Life history effects upon contest behaviour: age as a predictor of territorial contest dynamics in two populations of the Speckled Wood butterfly, *Pararge aegeria* L. Ethology. 112:471–477.

Kern S, Ackermann M, Stearns SC, Kawecki TJ. 2001. Decline in offspring viability as a manifestation of aging in *Drosophila melanogaster*. Evolution. 55:1822–1831.

Laaksonen T, Korpimaki E, Hakkarainen H. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. J Anim Ecol. 71:23–31.

Lock JE, Smiseth PT, Moore PJ, Moore AJ. 2007. Coadaptation of prenatal and postnatal maternal effects. Am Nat. 170:709–718.

McIntyre GS, Gooding RH. 2000. Effects of maternal age on larval competitiveness in house flies. Heredity. 85:480–489.

Mousseau TA, Dingle H. 1991. Maternal effects in insect life histories. Ann Rev Entomol. 36:511–534.

Müller JK. 1987. Replacement of a lost clutch: a strategy for optimal resource utilization in *Necrophorus vespilloides* (Coleoptera: Silphidae). Ethology. 76:74–80.

Müller JK, Braunisch V, Hwang W, Eggert A-K. 2007. Alternative tactics and individual reproductive success in natural associations of the burying beetle, *Nicrophorus vespilloides*. Behav Ecol. 18:196–203.

Müller JK, Eggert A-K, Dressel J. 1990. Intraspecific brood parasitism in the burying beetle, *Nicrophorus vespilloides* (Coleoptera: Silphidae). Anim Behav. 40:491–499.

Müller JK, Eggert A-K, Furlkröger E. 1990. Clutch size regulation in the burying beetle *Necrophorus vespilloides* Herbst (Coleoptera: Silphidae). J Insect Behav. 3:265–270.

Nagano M, Suzuki S. 2007. Effects of carrion size and male presence on the clutch size in *Nicrophorus quadripunctatus* (Coleoptera: Silphidae). Entomol Sci. 10:245–248.

Papaj DR, Messing RH. 1998. Asymmetries in physiological state as a possible cause of resident advantage in contests. Behaviour. 135:1013–1030.

Pearson J, Nisbet ICT, Ottinger MA. 2005. Age-related differences in nest defense in common terns: relationship to other life-history parameters. AGE. 27:297–305.

Priest NK, Mackowiak B, Promislow DEL. 2002. The role of parental age effects on the evolution of aging. Evolution. 56:927–935.

Pukowski E. 1933. Ökologische Untersuchungen an *Necrophorus* F. Zeitschr Morph Ökol Tiere. 27:518–586.

Rauter CM, Moore AJ. 2002. Quantitative genetics of growth and development time in the burying beetle *Nicrophorus pustulatus* in the presence and absence of post-hatching parental care. Evolution. 56:96–110.

Robertson IC. 1993. Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera: Silphidae). J Zool Lond. 231:583–593.

Robertson RJ, Rendell WB. 2001. A long-term study of reproductive performance in tree swallows: the influence of age and senescence on output. J Anim Ecol. 70:1014–1031.

Rozen DE, Engelmoer DJP, Smiseth PT. 2008. Antimicrobial strategies in burying beetles breeding on carrion. Proc Natl Acad Sci. 105:17890–17895.

SAS. 2007. JMP statistics and graphics guide. Version 7. Cary (NC): SAS Institute, Inc.

Schnell GD, Hiott AE, Creighton JC, Smyth VL, Komendat A. 2008. Factors affecting overwintering survival of the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae). J Ins Cons. 12:483–492.

Scott MP. 1998. Facultative adjustment of the duration of parental care by burying beetles. J Insect Behav. 11:597–603.

Scott MP, Gladstein DS. 1993. Calculating males? An empirical and theoretical examination of the duration of paternal care in burying beetles. Evol Ecol. 7:362–378.

Scott MP, Traniello JFA. 1987. Behavioural cues trigger ovarian development in the burying beetle, *Nicrophorus tomentosus*. J Insect Physiol. 33:693–696.

Scott MP, Traniello JFA. 1990. Behavioural and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). Anim Behav. 39:274–283.

Scott MP, Traniello JFA, Fetherston IA. 1987. Competition for prey between ants and burying beetles (*Nicrophorus* spp): differences between northern and southern temperate sites. Psyche. 94:325–332.

Smith RJ. 2002. Effect of larval body size on overwinter survival and emerging adult size in the burying beetle, *Nicrophorus investigator*. Can J Zool. 80:1588–1593.

Stegmann UE, Linsenmair E. 2002. Assessing the semelparity hypothesis: egg-guarding and fecundity in the Malaysian treehopper *Pyrgauchenia tristaniopsis*. Ethology. 108:857–869.

Steiger S, Richter K, Müller JK, Eggert A-K. 2007. Maternal nutritional condition and genetic differentiation affect brood size and offspring body size in *Nicrophorus*. Zoology. 110:360–368.

Suzuki S. 2000. Changing dominant-subordinate relationships during carcass preparation between burying beetle species (*Nicrophorus*: Silphidae: Coleoptera). J Ethol. 18:25–28.

Tallamy DW. 1982. Age specific maternal defense in *Gargaphia solani* (Hemiptera: Tingidae). Behav Ecol Sociobiol. 11:7–11.

Tallamy DW, Brown WP. 1999. Semelparity and the evolution of maternal care in insects. Anim Behav. 57:727–730.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago (IL): Aldine. p. 136–179.

Trumbo ST. 1990a. Interference competition among burying beetles (Silphidae, *Nicrophorus*). Ecol Entomol. 15:347–355.

Trumbo ST. 1990b. Reproductive benefits of infanticide in a biparental burying beetle *Nicrophorus orbicollis*. Behav Ecol Sociobiol. 27:269–273.

Trumbo ST. 1990c. Reproductive success, phenology, and biogeography of burying beetles (Silphidae, *Nicrophorus*). Am Midl Nat. 124:1–11.

Trumbo ST. 1992. Monogamy to communal breeding: exploitation of a broad resource base by burying beetles (*Nicrophorus*). Ecol Entomol. 17:289–298.

Trumbo ST. 2006. Infanticide, sexual selection and task specialization in biparental burying beetles. Anim Behav. 72:1159–1167.

Trumbo ST, Borst DW, Robinson GE. 1995. Rapid elevation of juvenile hormone titer during behavioral assessment of the breeding resource by the burying beetle, *Nicrophorus orbicollis*. J Insect Physiol. 41:535–543.

Trumbo ST, Valletta RC. 2007. The costs of confronting infanticidal intruders in a burying beetle. Ethology. 113:386–393.

Williams GC. 1966. Natural selection, costs of reproduction and a refinement of Lack's principle. Am Nat. 100:687–690.

Wilson EO. 1971. The insect societies. Cambridge (MA): Harvard University Press.

Zwaan BJ. 1999. The evolutionary genetics of ageing and longevity. Heredity. 82:589–597.