

# Contest behavior and other reproductive efforts in aging breeders: a test of residual reproductive value and state-dependent models

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Received: 28 May 2012 / Revised: 21 August 2012 / Accepted: 22 August 2012 / Published online: 2 September 2012  
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**Abstract** Two models have been proposed to explain age-related changes in reproductive performance. State-dependent models predict that reproductive effort depends on the magnitude of surplus energy reserves, which often varies with age. Contrary to this prediction, there was no significant effect of starvation on the outcome of contests for carcasses by female *Nicrophorus orbicollis* despite weight loss by starved females relative to controls. The residual reproductive value (RRV) model predicts that individuals adjust their current reproductive effort based on potential for future reproduction. Younger adults are predicted to restrain reproductive effort because they are less willing to risk their potentially longer reproductive careers. This model was tested empirically for several components of reproduction. Age was found to be strongly correlated with dominance when two similarly sized females discovered a carcass on the same day. Age also had a small positive effect on egg mass and was positively correlated with ovipositing at least one egg. Age did not affect nesting performance (the degree of carcass burial or the value of a prepared carcass for another female). Age also had no effect on fecundity when a female bred alone but was an important factor when two females were in direct competition. Changing RRV related to aging appears to be a robust determinant of contest outcomes in burying beetles, but effects on other components of reproductive effort in the present and previous studies are more variable, perhaps because of effects of changing state.

**Keywords** Aggression · Life history · Asymmetric war · Parental care · Terminal investment · Nutrition

## Introduction

Life history models based on an organism's residual reproductive value (RRV) (Williams 1966; Clutton-Brock 1984) have had some success in predicting increases in age-related reproductive effort and performance (Tallamy 1982; Pärt et al. 1992; Angelier et al. 2007; Hatch and Westneat 2008; Kight et al. 2011). Other studies, however, have found no change, a decrease, or a peaked pattern in reproductive performance with age, even prior to a period of accelerating senescence (Priest et al. 2002; Garel et al. 2009; Cotter et al. 2011). Even more problematical are cases in which some components of reproductive effort seem to increase, while others decrease with age in the same individual (Trumbo 2009). State-dependent models of reproductive effort show promise for predicting when an effort might decrease or increase with age (McNamara et al. 2009; Kindsvater et al. 2011) but do not explicitly address varying responses of different components of reproduction to aging.

Reproductive effort is not a single entity but can be partitioned into components including contest behavior, nesting behavior, the number of eggs produced (Rosenheim et al. 1996), and parental effort (here considered as a subset of reproductive effort; *sensu* Clutton-Brock (1991)). While each component entails some risks to future reproduction (Trivers 1972), these risks are varied and can include wasted time, deterioration of physical condition, loss of energy reserves, increased susceptibility to infection, and increased probability of immediate injury/death (Townsend 1986; Descamps et al. 2009; Bergeron et al. 2011). The different types of risk may be relevant to explain the simultaneous

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Communicated by O. Rueppell

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increase and decrease of different components of reproduction as an individual ages. For example, state-dependent models predict that if older individuals are in poor condition (less surplus state), then they may decrease effort to increase the chance of surviving and reproducing later (McNamara et al. 2009).

While state-dependent models based on energy reserves should apply to provisioning offspring (Spencer and Bryant 2002) or to prolonged contests (wars of attrition; Marden and Waage 1990; Mesterton-Gibbons et al. 1996), they may be less relevant when contests are rapid and severe, and risks are immediate injury or death (Enquist and Leimar 1990). In that case, younger adults may restrain fighting to protect their greater expected future reproductive output as predicted by RRV models (Curio 1983; Clutton-Brock 1984). These types of contests occur in burying beetles, and therefore it was predicted that: (1) the RRV model would be sufficient to explain age-related changes in fighting motivation in this group and (2) manipulation of energy reserves (one measure of state) would not affect contest outcomes. For other components of effort that negatively affect state in a continuous manner (e.g., depletion of energy reserves), however, both RRV and state-dependent models will likely be necessary. Although the direction of effects of age on other components of reproduction could not be predicted *a priori*, more variable responses were expected.

Fighting is an important component of reproductive behavior for many species, especially those that compete for high-value resources. Contests for resources are affected by asymmetries in the resource-holding potential of combatants such as differences in body size (Otronen 1988; Humphries et al. 2006; Jonart et al. 2007) and differences in fighting experience (Chase et al. 1994). Contests can also be determined by asymmetries in the relative value of the resource for different individuals (Smith and Metcalfe 1997; Mesterton-Gibbons and Adams 1998). Individual motivation may vary because of differences in need or familiarity with a resource, differences in readiness to use a resource or territory (Mohamad et al. 2010; Hollander et al. 2012), or differences in the expectation of locating alternative resources in a timely manner (Cant et al. 2006; Mohamad et al. 2010), a factor that is often age-related for reproductive resources (Papaj and Messing 1998; Kou et al. 2009). In particular, younger adults are expected to show greater reproductive restraint because of their greater RRV, while older adults, especially those close to the period of accelerating senescence, are expected to show near-maximal (terminal) reproductive effort (Issac and Johnson 2005).

Burying beetles are an amenable model for investigating age-related changes in reproductive allocation. First, reproductive efforts are quite varied (fighting, nesting, parental care) and can be manipulated. Second, burying beetles are iteroparous, so younger adults might be expected to exhibit

some restraint, yet they typically attempt to breed only a few times on high-value resources, so intrasexual fights can be severe (Enquist and Leimar 1990; see Eggert and Müller 2011). Third, prior work has established that young and old females have equivalent fighting ability, but that motivation can affect contest outcomes (Trumbo 2009). Fourth, alternative hypotheses for age-related improvements in reproduction can be minimized. In many systems, older individuals may be superior because of more reproductive experience or because less fit individuals are lost from older cohorts (Curio 1983; Forslund and Pärt 1995). Use of a laboratory population of burying beetles where experience and nutrition can be controlled, and where mortality can be reduced to near zero, can minimize the relevance of these alternative hypotheses for age-related improvements in reproduction (Trumbo 2009).

In the present study, it was first confirmed that one important measure of state (energy reserves) does not affect contest outcomes among *N. orbicollis* Say females. Primiparous females of different ages were then placed on a carcass either alone or in competition. Contest winners, egg mass, clutch size, nesting performance, and whether to initiate egg laying were assessed. These data, along with previous studies of burying beetles, suggest that age has different effects on various components of reproduction. While the RRV model alone appears adequate to explain the positive age-related effects on fighting and initiating oviposition, additional models such as state-dependent ones (McNamara et al. 2009; Cotter et al. 2011; Kindsvater et al. 2011) will likely be needed to explain positive, negative, and neutral effects of aging on other components of reproductive effort.

## Methods

### Study animal

Adult burying beetles compete for small, highly valued vertebrate carcasses (Wilson 1971). They respond rapidly to discovery of a carcass, ovipositing in as little as 12 h while carcass preparation is still ongoing (Pukowski 1933). Prepared carcasses are vulnerable to usurpation by rival burying beetles during much of the nesting cycle (Trumbo 2007). The female oviposits in the soil and, after several days, larvae crawl to the carcass to be fed by parents and to feed directly from the resource (Eggert et al. 1998; Smiseth and Moore 2004). Care is provided by a single female or a male–female pair; when biparental, males typically desert first, attributed to their greater RRV (Ward et al. 2009). Females have the potential to breed several times (Scott and Traniello 1990), but whether they do so depends on their body size, carcass availability, and population density (Creighton 2005; Müller et al. 2007).

### Effect of energy reserves on contests

The laboratory population of *N. orbicollis* was derived from wild-caught beetles from Bethany, CT, USA, and kept at 20 °C, 15:9 L/D. Females were isolated immediately after emergence and fed until 25 days of age. At 25 days, females were measured and paired according to pronotal width (<2 % difference) and body mass (<3 % difference). One female from each pair ( $n=42$ ) was selected at random to undergo 7 days of food deprivation (with water provided). Each beetle was weighed again at the start of the trial. Starved females lost between 7.6 and 18.9 % (mean, 14.3 %) of their body mass, while fed females gained an average of 1.8 % in body mass in the 7 days leading up to the trial. Females were mated to a different male on each of 2 days during this 7-day period. Each female was marked by clipping the right or left elytron. Both females were introduced into a breeding container (11×18×33 cm) filled two thirds with soil with a mouse carcass (21–24 g). Breeding containers were kept in the dark. At days 1 and 4, containers were checked to determine which female was on the carcass. On day 4, injuries were assessed (severed legs or antennae) and body mass was re-measured.

### Effect of age on contests, clutch failure, egg number, and nesting behavior

The reproductive performance of young and old females was compared both when breeding alone and when in direct competition. Females were isolated in smaller containers (9 cm in diameter, 5 cm in depth) 10 days after adult emergence. Young females were kept in these individual containers for 10–12 days and were 20–22 days old at the start of the experiment. Old females were kept in individual containers for 42–50 days and were 52–60 days old at the start of the experiment. For a 24-h period, both 10 and 2–3 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 sexed groups and two 24-h exposures to a single male. Because all food was provided (small pieces of chicken liver or ground beef, <1 g), older females were not able to gain an advantage in foraging experience. By rearing in isolation, mortality was reduced to near zero (Trumbo 2009). At 7 days prior to the onset of trials, females were fed a diet of ground beef suffused with either Solvent Blue 35 (400 mg per 20 g of meat) or Red Sudan Red 7B dye (200 mg per 20 g of meat) (Sigma) so that the eggs of young and old females could be distinguished (see Eggert and Müller 2000). Color differences also allowed the identification of the young or old female on the carcass by examination of the soft tissue between sclerotized segments on the underside of the

thorax. Food was withheld from all females at 24 h prior to the start of a trial to reduce differences in body mass (see Trumbo (2009)). There was no mortality prior to the start of the experimental trials.

To begin each trial, a single female ( $n=23$  young,  $n=23$  old) or a young–old matched pair of females ( $n=28$ ) was placed in a translucent breeding container (11×18×33 cm) filled two thirds with soil with a mouse carcass (27–30.5 g) that was covered with a paper towel (15:9 L/D). The mean pronotal widths of young and old females in trials with a single breeder were not significantly different, and the pronotal widths of the paired females in competition trials differed by <2 %. 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. Two measures of nesting performance were assessed: degree of burial after 24 h and re-use of a carcass prepared for 4 days. After 24 h, the container was checked to determine the degree of burial (1—not moved or buried, 2—approximately 25 % of carcass covered by soil, 3—50 % covered by soil, 4—75 % covered by soil, 5—100 % covered by soil). At this time, the carcass was inspected to determine whether each female was on or off the carcass. On day 4, the trial was terminated and the location of females, injuries, and number of red and blue eggs were recorded. The carcasses prepared by single females were then provided to primiparous middle-aged females (34 days old) to assess whether differences in preparation by young and old females would affect the re-use of the carcass. All carcasses from rearing containers with eggs (thereby excluding abandoned carcasses) were removed and placed into new breeding containers with new soil. The mass of the brood produced by these middle-aged females was determined at the time of larval dispersal.

### Egg mass

Additional young (22 days old,  $n=17$ ) and old (53 days old,  $n=19$ ) *N. orbicollis* females were individually provided a 21–24-g mouse carcass as cited earlier. At 84 h, the trials were terminated and the soil was inspected for eggs. The first five eggs uncovered for each trial were weighed together to obtain a mean score for egg mass for each female.

### Statistical analyses

In trials with two females, the effects of treatment on contest outcomes were determined by the binomial test (excluding cases in which both or neither female were on the carcass). *P* values represent the probability of an equal or greater number of wins by one of the treatments (two-tailed). The frequency of clutch failure (no eggs oviposited) was examined using a 2×2×2 log-linear analysis of frequency data

(clutch failure or success, young or old female, alone or in competition). Interactive effects were included in the analysis whether or not they were significant as suggested by Cox and Snell (1989). Effects on fecundity and burial of the carcass were assessed by nonparametric Wilcoxon's two-sample tests because of the non-normal distribution (fecundity) or ordinal nature of the data (burial). Clutch size data were analyzed from all trials and from just those trials in which at least one egg was produced (*t* tests). The results were qualitatively the same, so only the results for trials excluding clutch failures are reported. All analyses were two-tailed and performed using SAS (2007).

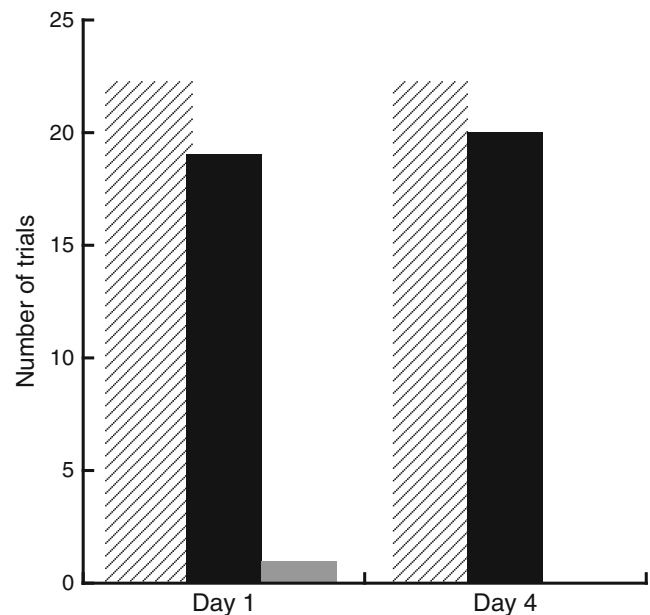
## Results

### Effect of energy reserves on contests

The starvation treatment had no detectable effect on contest outcomes on day 1 ( $p=0.78$ , binomial test) or on day 4 ( $p=0.88$ ; Fig. 1). There were only three changes in carcass ownership in 42 trials between days 1 and 4 (two from the fed female to the starved female, one from starved to fed). Injuries to one or both females occurred in 11 of 42 trials (26.2 %), including three deaths. During the 4 days with the carcass, dominant females gained a mean ( $\pm$  SD) of 9.9 ( $\pm 3.7$  %) while subordinate females lost a mean of 15.3 ( $\pm 5.6$  %) of their body mass compared to the start of the contest. This occurs because the dominant female feeds on the resource and restricts the subordinate's access (Eggert et al. 2008). The female in possession of the carcass on day 4 was always heavier than the subordinate female ( $n=42$ ), regardless of the nutritional treatment prior to the trial ( $p<0.001$ ). Therefore, in every trial, the body mass difference on day 4 confirmed the dominance status indicated by the observation.

### Effect of age on contests, clutch failure, egg number, and nesting behavior

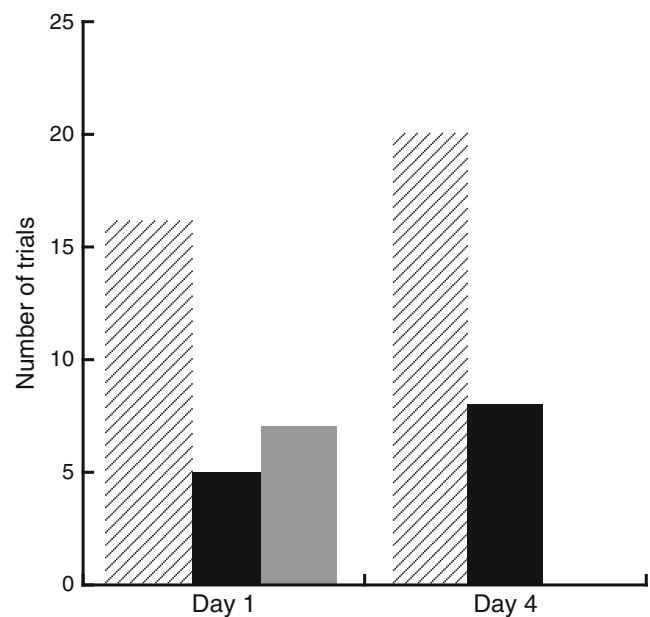
In contests, older females were more likely to be in sole possession of the carcass on day 1 (binomial test,  $p=0.03$ ) and on day 4 ( $p=0.04$ ) compared to younger females (Fig. 2). Age, but not whether the female attempted to breed alone or in competition, had an effect on the frequency of clutch failure ( $G_{\text{age}}^2=7.38$ , 2 df,  $p=0.025$ ,  $G_{\text{competition}}^2=0.68$ , 2 df,  $p=0.71$ ; Fig. 3). The interaction between age and treatment on clutch failure was not significant ( $G^2=7.40$ , 4 df,  $p=0.11$ ). In trials excluding clutch failures, the number of eggs produced by young and old females when breeding alone was not different ( $t=0.34$ , 1 df,  $p=0.37$ ; Fig. 4). In competition trials, on the other hand, old females produced over twice as many eggs as young females ( $t=3.77$ , 1 df,  $p<0.001$ ). For both breeding



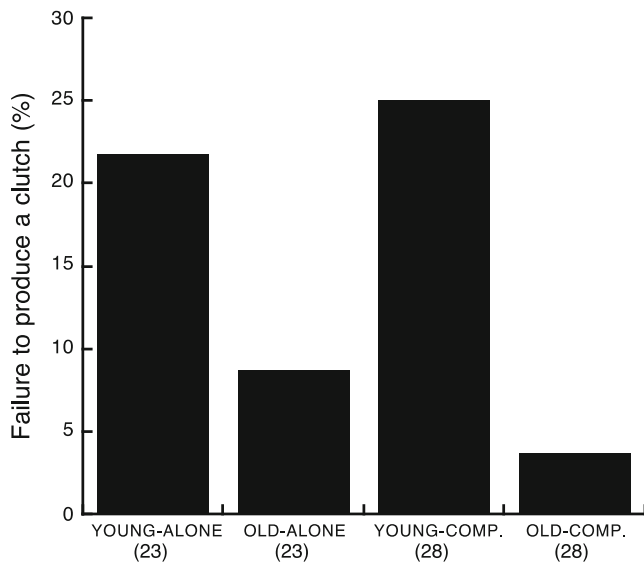
**Fig. 1** Number of trials in which the fed (hatched bars) or starved (black bars) female was present on the carcass on day 1 and on day 4. Gray bar indicates trial in which both or no females were on the carcass

alone and competition trials, results for egg production were qualitatively the same if trials with clutch failures are included in the analysis (Fig. 4).

Age did not affect either measure of quality of nesting behavior. The burial score (mean  $\pm$  SE) for young ( $3.30 \pm$

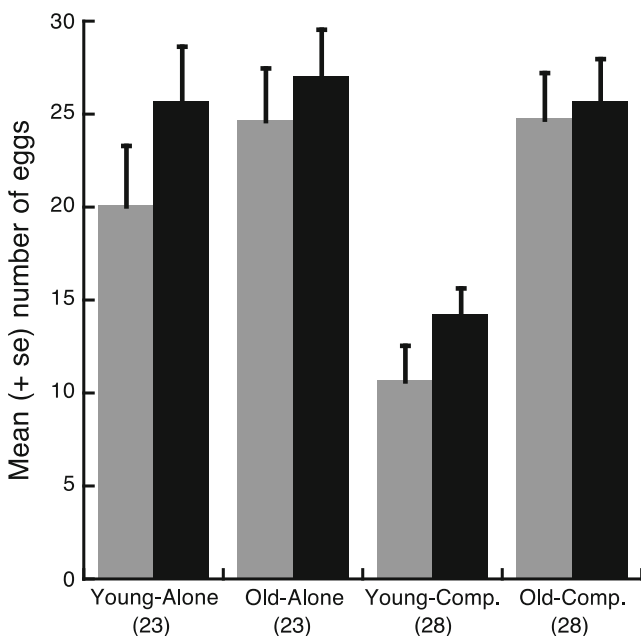


**Fig. 2** Number of trials in which the younger (black bars) or older (hatched bars) *N. orbicollis* female was present on the carcass on day 1 and on day 4. Gray bar indicates trial in which both or no females were on the carcass



**Fig. 3** Percentage of trials in which young and old female *N. orbicollis* failed to produce eggs. Sample sizes are in parentheses

0.35) and old ( $3.65 \pm 0.26$ ) females breeding alone did not differ (Wilcoxon's test,  $z=0.59$ ,  $p=0.55$ ). There was no evidence of cooperation during burial as the mean burial score was not greater when two females were present on one carcass (all singles  $3.48 \pm 0.22$ , pairs  $2.82 \pm 0.26$ ; Wilcoxon's test,  $z=1.85$ ,  $p=0.06$ ). A second measure of nesting performance (carcass preparation) also showed no difference. Middle-aged females produced a similar mean ( $\pm$  SE) brood mass when re-using a carcass previously prepared by a



**Fig. 4** Mean number of eggs produced by young and old *N. orbicollis* females when breeding alone and in competition. Gray bars represent all trials; black bars represent only trials in which at least one egg was produced. Sample sizes are in parentheses

young ( $3.23 \pm 0.34$  g) or old ( $3.33 \pm 0.28$  g) female ( $t=0.23$ , 1 df,  $p=0.82$ ).

The frequency of injury in competition trials was not great enough to permit a detailed analysis. One pattern that was apparent post hoc was that injury to one or both females was more frequent when the younger female was dominant on day 4 (six of eight) than when the older female was dominant (four of 20) (Fisher's exact test,  $p=0.011$ ). The five trials in which the older female was injured all occurred during the eight trials when the younger female was dominant (binomial test,  $p=0.002$ ), suggesting a greater intensity of conflict where the typical age asymmetry was not upheld.

#### Egg mass

The mean ( $\pm$  SE) egg mass was 6.2 % greater for older females ( $27.3 \pm 0.4$  mg) compared to younger ( $25.7 \pm 0.5$  mg) females ( $t=2.70$ , 1 df,  $p=0.01$ ).

#### Discussion

The RRV model was sufficient to predict the greater success of older *N. orbicollis* females in contests where different-aged females discovered a carcass at the same time (a similar result has been found for the smaller congener, *Nicrophorus defodiens* Mannerheim, Trumbo, unpublished data). State-dependent models can also predict an increase in reproductive performance with age in an alternative manner than RRV models. If older individuals have built up larger energy reserves or can replenish reserves more quickly because of greater foraging experience, they would be expected to allocate much of their surplus state to current reproduction (Kindsvater et al. 2011). This is unlikely to explain the greater success of older burying beetles in the present study. Females of different ages were of similar size and mass and had similar foraging experience. The starvation experiment also demonstrated that energy reserves had little effect on fighting motivation in this species.

In addition to the effect on fighting, older females produced eggs of slightly greater mass, an effect also seen in *Nicrophorus vespilloides* (Lock et al. 2007). Older females of *N. orbicollis* were also more likely to produce a clutch, an effect seen in a prior study (Trumbo 2009). In species that produce broods of variable size as in burying beetles, RRV models may be sufficient to predict whether reproduction is attempted, while condition (state) may affect brood size. In species that produce a fixed brood size, state-dependent models should affect whether reproduction is attempted (Cook et al. 2004). In the present study, effects of age on other components of reproduction were more variable. Age had no effect on nesting performance (quality of the burial or the value of a prepared resource for re-use) or fecundity

for females breeding alone. In competition trials, young females produced significantly fewer eggs. Age, dominance status, and injury might well have independent effects on fecundity when two females compete, but the small sample size for some combinations of variables did not permit a more detailed analysis. Using *N. vespilloides*, Eggert et al. (2008) demonstrated that limited access to the resource negatively affected fecundity in subordinate females. In previous works on *Nicrophorus* spp., the effects of age on food provisioning and the total mass of the brood were likewise variable and sometimes negative (Scott 1998; Lock et al. 2007; Creighton et al. 2009; Trumbo 2009; Cotter et al. 2011).

### Two models of reproductive effort

Can a joint consideration of the RRV and state-dependent models explain why some components of effort consistently increase with age, while other components show variable patterns in the same organism? Consider a scenario in which an individual will sometimes need to win a contest to reproduce and at other times may reproduce where there is limited competition. If the outcome of a fight is either to win and reproduce, or lose with a significant probability of injury, then it is expected that younger individuals with more future opportunities to reproduce uncontested would risk less. In this case, age-related effects of a declining RRV should predominate over effects of the level of surplus state. An individual near the end of life should not pass up an opportunity to reproduce, even if fighting is required, if it is unlikely to find another reproductive opportunity. In a similar manner, when the probability of survival is low, individuals of diverse taxa are known to expose themselves to greater risks of predation to prepare to breed (Lafaille et al. 2010; Kuriwada et al. 2011; Schwanz et al. 2012) or to greater risks in defending young (Pavel and Bures 2008; Steinhart et al. 2008), consistent with RRV models.

A state-dependent model is highly relevant, however, for investment such as producing eggs or provisioning offspring. According to this model of continuous breeding, the individuals' reproductive effort depends on the surplus in state over a minimum needed to ensure survival. Individuals with a large surplus invest more, while individuals with a small surplus, closer to the critical minimum, invest less to increase the chance of survival (McNamara et al. 2009). For example, European earwig mothers in a poor state provide less food to offspring (energy intensive) but do not decrease attendance of offspring (less energy intensive) (Wong and Kölliker 2012). Consideration of the physical state of females may explain a negative association of parental age and offspring performance as parents in declining condition limit reproductive effort (Mousseau and Dingle 1991; Reid et al. 2003; Baudisch 2008), although it is difficult to

disentangle the effects of senescence. RRV models alone cannot explain the diminished effort by a prime-aged adult that experiences a temporary but recoverable decline in body condition (e.g., Reaney and Knell 2010). The energy intensity of different components of reproductive effort may also influence variable age-related changes in male reproductive effort (De Luca and Coccoft 2011).

For organisms with a lengthy, discrete, terminal reproductive bout, an extension of state-dependent models might predict less-than-maximum investment at the beginning of the reproductive attempt to increase the chance that internal resources will not run out before the young reach independence. For burying beetles, the most energetically demanding stage of reproduction is the first 48 h when larvae are on the carcass (about 5 days after discovery of the resource). Increased care-giving behavior (Fetherston et al. 1990), elevated levels of juvenile hormone (Trumbo 1997), rapid loss of body weight (Creighton et al. 2009), and higher CO<sub>2</sub> production (Rauter, personal communication) all indicate that the ability of females to invest at this stage might limit reproductive output and affect decisions about brood size. Investment at this stage may be most relevant for application of modified state-dependent models. Production of a smaller brood that enhances the chance that offspring will reach independence in good condition may be a common response to age-related declines in breeder condition (Reid et al. 2003). In *N. orbicollis*, older females that have previously bred are in a diminished physical state, and these females produce fewer offspring but with the same body mass as offspring produced by younger females (Creighton et al. 2009).

An older breeder in marginal condition is not likely to improve its condition by refraining from fighting, as might occur by refraining from provisioning offspring. When contests are short in duration and involve substantial physical contact, the RRV model may be sufficient to explain age- and season-related changes in fighting motivation (Papaj and Messing 1998; Humphries et al. 2006; Kou et al. 2009). Where contests over reproductive opportunities, however, are prolonged and energetically demanding with little direct combat (Kemp et al. 2006), state-dependent models should be more important. In such wars of attrition, the level of surplus energy is often a good predictor of contest outcome (Marden and Waage 1990; Mesterton-Gibbons and Adams 1998).

In addition to the different responses of various components of reproductive effort to aging, the present study also demonstrates that the effect of age can depend on the competitive environment. Because dominance is often age-related (Piper and Wiley 1989; Wittemyer and Getz 2007), the density and age structure of populations will need to be incorporated in models to predict age-related changes in effort and their effects on the evolutionary ecology of species (Cant et al. 2006).

An empirical examination of the multiple components of reproductive performance, such as of digger wasps (Field et al. 2007) and burying beetles, makes it clear that components of effort have different costs and do not respond similarly to changes in age or state. One source of variation in patterns of reproduction may be explained by whether the costs of reproduction are fixed (e.g., whether to attempt reproduction) or graded (e.g., how many offspring to rear, how much to provision). A second source of variation can occur because different components of reproductive effort have varied negative effects on state. A third source of variation may occur because the effects of state may become less important as an organism approaches terminal investment for reasons unrelated to state (e.g., imminent environmental deterioration). An ongoing challenge is to understand the complex interplay of choice of reproductive effort and state on mortality (McNamara et al. 2009) and to integrate these with environmental (extrinsic) effects on mortality that are known to be major determinants of age-related patterns of reproductive investment.

**Acknowledgments** I thank Lutz Fromhage and Holly Kindsvater for insight into state-dependent models and Eldridge Adams for discussion of contest behavior and review of the manuscript. The Southern Connecticut Regional Water Authority granted permission to collect beetles. The University of Connecticut provided financial support for this work.

**Ethical standards** This study complied with current laws of the USA. The author declares no conflict of interest.

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