



Faculty Publications

2014-04-08

Prior experience affects allocation to current reproduction in a burying beetle

Eric J. Billman

Brigham Young University - Provo

J. Curtis Creighton

Purdue University Calumet

Mark C. Belk

Brigham Young University - Provo, mark_belk@byu.edu

Follow this and additional works at: <https://scholarsarchive.byu.edu/facpub>



Part of the [Biology Commons](#)

BYU ScholarsArchive Citation

Billman, Eric J.; Creighton, J. Curtis; and Belk, Mark C., "Prior experience affects allocation to current reproduction in a burying beetle" (2014). *Faculty Publications*. 5428.

<https://scholarsarchive.byu.edu/facpub/5428>

This Peer-Reviewed Article is brought to you for free and open access by BYU ScholarsArchive. It has been accepted for inclusion in Faculty Publications by an authorized administrator of BYU ScholarsArchive. For more information, please contact ellen_amatangelo@byu.edu.

Original Article

Prior experience affects allocation to current reproduction in a burying beetle

Eric J. Billman,^a J. Curtis Creighton,^b and Mark C. Belk^a

^aDepartment of Biology, Brigham Young University, 401 Widtsoe Building, Provo, UT 84602, USA and

^bDepartment of Biological Sciences, Purdue University Calumet, 2200 169th Street, Hammond, IN 46323, USA

Received 13 July 2013; revised 24 February 2014; accepted 5 March 2014; Advance Access publication 8 April 2014.

The cost of reproduction hypothesis predicts that the level of reproductive investment to current reproduction is constrained by an individual's future reproductive potential or residual reproductive value. Therefore, age, or differences between young and old individuals in residual reproductive value, is expected to influence reproductive investment. However, recent theoretical work suggests that residual reproductive value is also influenced by an individual's state or condition which may in part be determined by prior reproductive experience. We evaluated the reproductive investment of same-aged female burying beetles (*Nicrophorus orbicollis*) to determine how prior reproductive experience affects current reproduction. Consistent with previous research, females reproducing on low-quality carcasses allocated more to future reproduction by producing smaller offspring and gaining more mass than females on high-quality carcasses. When prior experience was manipulated, females that initially reproduced on a low-quality resource exhibited an accentuated response to a high-quality carcass by producing significantly larger broods of offspring compared with control females reproducing on high-quality carcasses. Conversely, females that initially reproduced on a high-quality carcass and were subsequently presented a low-quality carcass exhibited a decrease in offspring size and an increase in female mass change, indicative of a switch in allocation from current to future reproduction. The change in carcass quality resulted either in terminal investment or reproductive restraint, dependent on prior experience. Our results combined with those of previous papers demonstrate that the level of reproductive investment in burying beetles is influenced by both age and prior reproductive experience.

Key words: life-history evolution, *Nicrophorus*, reproductive restraint, resource availability, terminal investment.

INTRODUCTION

Organisms exhibit great diversity in their age-related patterns of reproductive investment. Life-history theory accounts for this diversity by predicting that age-specific patterns of fecundity maximize an individual's lifetime fitness (Roff 2002). Due to competing energetic demands, reproductive investment in current reproduction comes at a cost to future reproductive potential (Williams 1966; Reznick 1985). Therefore, organisms determine the level of reproductive investment by balancing the fitness benefits of investment to current reproduction with the potential costs to future reproductive opportunities. The cost of reproduction hypothesis predicts that the level of reproductive investment to current reproduction is constrained by an individual's future reproductive potential or residual reproductive value (Fisher 1930; Williams 1966; Clutton-Brock 1984; Reznick 1985). Young individuals with high residual reproductive value should be

less willing to incur a high reproductive cost and thus have a low level of investment to current reproduction to ensure future reproductive potential. Conversely, old individuals with low residual reproductive value should terminally invest, or have a high level of investment to current reproduction, because future reproductive opportunities are not available (Clutton-Brock 1984).

These predicted patterns of allocation to current versus future reproduction assume that same-aged individuals are equivalent in quality or state (McNamara and Houston 1996; Wilson and Nussey 2010). We refer to state as a suite of traits that contributes to reproductive success including but not limited to body size, immune function, fat reserves, parasite load, foraging skills, territory size, prior experience, etc. Differences that occur in state among individuals are important for determining reproductive success and result in variation in reproductive success among individuals (Wendeln and Becker 1999; Beauplet and Guinet 2007; Hamel et al. 2009; McNamara et al. 2009; Lescroëil et al. 2010; Trumbo 2012). Variation in individual state may have a genetic basis, may be environmentally induced, or may be the result of an individual's genotype and the unique combination of environments experienced over the individual's lifetime (Wilson and Nussey 2010).

Address correspondence to E.J. Billman who is now at Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA. E-mail: eric.billman@oregonstate.edu.

Early life conditions and prior reproductive experience can greatly influence state-based cues that will influence an individual's reproductive investment for current and future reproductive bouts (Creighton et al. 2009; Cotter et al. 2011; Trumbo 2012). In general, age and state should be correlated because older individuals are likely to have had more breeding opportunities and to have been exposed to other stressors that reduce body condition. Therefore, age- and state-based life-history models should have similar predictions for life-history patterns across an organism's life. However, the correlation between age and state may be weaker in opportunistic breeders because the passage of time does not accurately predict the extent of prior reproductive investment (i.e., number of reproductive bouts) and the consequent deterioration in state. Thus, state-based cues may have greater influence than age-based cues for determining the extent of reproductive investment in opportunistic breeders (Cotter et al. 2011; Trumbo 2012).

Burying beetles (Coleoptera: Silphidae) are an excellent model system for evaluating the effect of state-based cues on current reproductive investment. These beetles are opportunistic breeders utilizing the carcasses of small vertebrates to breed. Biparental care is provided to offspring by burying and preserving the carcass, which serves as the sole food source for parents and offspring during the reproductive bout (Scott and Traniello 1990). Thus, carcass size represents resource quality or the amount of resource that is available to allocate to current reproduction and for somatic investment for future reproduction by the parents. During burial, parents estimate carcass size by assessing carcass volume and regulate brood size to match carcass size through filial cannibalism (Trumbo and Fernandez 1995; Trumbo 2006). These behaviors result in a positive correlation between brood size and carcass size (Creighton 2005) and a positive correlation between carcass size and costs of reproduction (Creighton et al. 2009). Because carcasses become available at unpredictable intervals, reproductive opportunities are unpredictable both in terms of carcass availability and quality. Therefore, burying beetles that are the same age will have potentially experienced different levels of reproductive investment and consequent deterioration in state.

Reproductive patterns in the burying beetle *Nicrophorus orbicollis* allow us to predict expected levels of reproductive investment on the current bout given previous experience (Creighton 2005; Creighton et al. 2009). Female *N. orbicollis* increase allocation to offspring with age. Additionally, females breeding for the first time respond differently to carcasses of different size. On small carcasses (which represent lower quality resources) females demonstrate reproductive restraint (allocation to future vs. current reproduction) (Creighton et al. 2009). This restraint on poor carcasses may be an adaptive response for females in an attempt to increase potential of future reproduction assuming more and larger carcasses will be available. On larger carcasses (which represent higher quality resources), females do not demonstrate the same level of restraint and instead, allocate resources at a higher rate to their current attempt (Creighton et al. 2009). Therefore, females from these 2 types of carcasses beginning a second reproductive attempt enter with different experience and level of investment, that is different states. We predict that a female first given a small carcass and subsequently a large carcass will increase her level of reproductive investment to current reproduction relative to females that were given 2 small or 2 large carcasses. Conversely, we predict that a female first given a large carcass and subsequently a small carcass will decrease her level of reproductive investment relative to females that were given 2 small or 2 large carcasses to conserve her state given the possibility

of finding another high-quality carcass in the future. We conducted an experiment on the burying beetle *N. orbicollis* to test these predictions. Specifically, we manipulated the order and quality of available resources for female *N. orbicollis* to test the effect of prior reproductive experience on current levels of reproductive investment.

METHODS

Nicrophorus orbicollis reproduces on small vertebrate carcasses, which serve as the sole food source for both parents and offspring during the reproductive bout. Adults fight for possession of the carcass, with the largest male and female eventually monopolizing it (Scott 1998). Once a carcass is secured, parents prepare the carcass by burying it, cleaning it of fur or feathers, shaping it into a ball, and preserving it with oral and anal secretions. Females lay eggs in the surrounding soil; first instar larvae usually arrive at the carcass 5 days after carcass burial. After larvae arrive at the carcass, parental care continues in the form of feeding larvae regurgitated carcass tissue, maintenance of the carcass, and defense of the carcass and young from predators. Parental care is provided until larvae disperse into the soil to pupate, which can be 15–20 days after carcass burial. In the laboratory, females compensate for the absence of males when caring for young, which allows us to measure individual reproductive investment and costs (Creighton 2005; Creighton et al. 2009).

Wild burying beetles were captured in central Wisconsin during summer 2008, using pitfall traps baited with aged chicken. Male–female pairs were placed on 30-g mouse carcasses and allowed to reproduce to generate a laboratory population at Purdue University Calumet, Hammond, Indiana. First-generation beetles ($n = 65$ individuals) representing 13 wild-pairs were transported to the Evolutionary Ecology Laboratory at Brigham Young University in Provo, Utah. Individuals were reared individually in small plastic containers (14.7 cm \times 10.3 cm \times 6.9 cm), fed raw chicken liver twice per week, and maintained on a 14L:10D light cycle. For age determination of adult beetles, the date of eclosion was designated as day 0.

We evaluated the effects of prior reproductive experience on current reproduction using the following experimental design. When 28-days-old virgin females were randomly assigned to 1 of 4 treatments (2 experimental treatments and 2 control treatments); treatments differed in the order of carcass sizes presented to females over 2 reproductive bouts. For the experimental treatments, females were given either a 20-g or 30-g (± 1 -g) carcass for the first reproductive bout, and the carcass size was switched for the second reproductive bout (20-30 treatment and 30-20 treatment, respectively). For control treatments, females were given either 20-g or 30-g carcasses for both the first and second reproductive bouts (20-20 control and 30-30 control, respectively).

At the start of each reproductive bout, females were weighed, and then paired with a randomly selected male that was virgin, sexually mature, and unrelated to the female. Breeding pairs were placed in a plastic container (21.1 cm \times 14.8 cm \times 9.6 cm) with 6 cm of moist commercially purchased topsoil and provided with a newly defrosted mouse carcass. After carcass preparation (48 h), males were removed to isolate reproductive patterns of females. Females were removed when the larvae dispersed from the burial chamber into the surrounding soil to pupate. Females were weighed and returned to individual small plastic containers and provided raw chicken liver. After 72 h, the female was placed on a new carcass, again with a male that was virgin, sexually mature, and unrelated to the female. Pupae from each reproductive bout were checked daily until eclosion, at which point the offspring were counted and weighed.

Life-history traits were compared among treatments using an analysis of covariance (ANCOVA; Proc GLM, SAS Institute Inc. 2008). Response variables for 4 separate analyses were brood size (number of adult offspring produced), mean offspring mass (g), total brood mass (g), and female mass change (g). Female mass change was determined by subtracting the mass of the female at the start of a reproductive bout from her mass at larval dispersal. We assumed that a gain in mass by the female represents investment to her future reproduction because any mass increase represents food not available to current offspring. Prior to analyses, we transformed life-history traits to accommodate for potential nonlinear relationships between variables; final brood size was square root transformed, offspring size and total brood mass were \log_{10} transformed, and female mass change was $\log_{10}(x+1)$ transformed. For each analysis, female body size (mass at start of reproductive bout, \log_{10} transformed) was the covariate. The main effects in the model were prior carcass size, current carcass size, and their interaction. Post hoc mean comparisons were made using Tukey's honestly significant difference test.

By analyzing the data with this design, we are able to clearly predict and interpret the results. We predict that reproductive allocation will be significantly affected by current carcass size based on previous research (Creighton 2005; Creighton et al. 2009). If prior experience affects current reproductive allocation, then either prior carcass size or its interaction with current carcass size will significantly affect life-history traits. Prior carcass size will be significant if it has a similar effect on current reproductive allocation regardless of the current carcass size. However, the interaction of prior carcass size and current carcass size will be significant if females respond differently to the current carcass size based on prior experience. Thus, this design provides a clear test of the effect of state, or prior experience, on reproductive investment of burying beetles.

RESULTS

Brood size was significantly affected by prior carcass size, and current carcass size was marginally significant (Table 1). However, the

interaction between the 2 factors was not significant (Table 1). Prior experience affected brood size; females originally reproducing on a 20-g carcass had larger broods on both carcass sizes in the current bout (Figure 1). For the current bout, females given 30-g carcasses tended to have larger broods than females given 20-g carcasses as predicted under a response to resource availability (Figure 1).

Offspring size was significantly affected by current carcass size, but prior carcass size and the interaction of the 2 factors were not significant (Table 1). Females reproducing on 30-g carcasses in the current reproductive bout had larger offspring than females given 20-g carcasses (Figure 1). This pattern is consistent with a response to resource availability with no effect of prior experience.

Total brood mass was significantly affected by prior carcass size, current carcass size, and their interaction (Table 1). These results suggest that reproductive allocation to the current bout is affected by prior experience and resource availability. Females that were switched from a 20-g carcass to a 30-g carcass had a significantly greater total brood mass than all other treatment combinations ($P < 0.001$). Total brood mass was similar for females in all other treatment combinations ($P > 0.167$).

Female mass change was significantly affected by current carcass size, but prior carcass size and the interaction of the 2 factors were not significant (Table 1). Females given 20-g carcasses for the current reproductive bout had significantly larger increase in mass during the bout indicative of reduced costs of reproduction (Figure 1). This pattern is consistent with a response in female mass change due to resource availability with no effect of prior experience.

DISCUSSION

Variation in age-specific fecundity may be determined by age-based cues, that is the time remaining for future reproduction (Williams 1966), or by state-based cues, that is the level of deterioration that has resulted from previous reproductive experience or other biological causes (e.g., injuries, immune function, etc.; McNamara and Houston 1996; McNamara et al. 2009). However, age- and

Table 1

Analysis of covariance tables for comparisons of brood size, offspring mass, total brood mass, and female mass change of female burying beetles as a function of prior carcass size, current carcass size, and their interaction, and the covariate female mass

Effect	Num DF	Den DF	F-statistic	P value
Brood size				
Prior carcass	1	51	8.10	0.006
Current carcass	1	51	3.56	0.065
Female mass	1	51	0.52	0.475
Prior carcass × current carcass	1	51	2.47	0.122
Offspring mass				
Prior carcass	1	51	0.81	0.372
Current carcass	1	51	9.21	0.004
Female mass	1	51	0.00	0.969
Prior carcass × current carcass	1	51	0.16	0.688
Total brood mass				
Prior carcass	1	51	15.64	<0.001
Current carcass	1	51	38.31	<0.001
Female mass	1	51	1.45	0.234
Prior carcass × current carcass	1	51	10.36	0.002
Female mass change				
Prior carcass	1	51	0.44	0.508
Current carcass	1	51	4.62	0.036
Female mass	1	51	11.21	0.002
Prior carcass × current carcass	1	51	0.16	0.689

DF, degrees of freedom.

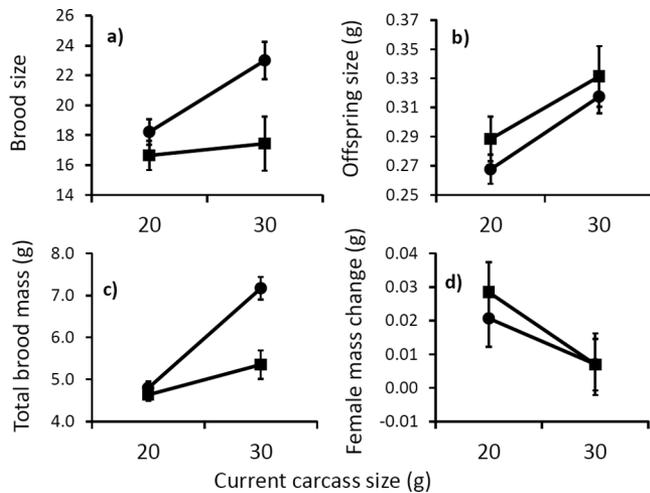


Figure 1

Mean (\pm SE) life-history traits for female burying beetles given 20-g or 30-g carcasses for the current bout. Females had previously been given a 20-g carcass (circles) or 30-g carcass (squares). The 4 life-history traits are (a) brood size, (b) offspring mass, (c) total brood mass, and (d) female mass change.

state-based hypotheses are not mutually exclusive. Instead, individuals likely assess multiple cues to determine the level of reproductive investment to balance the benefits of current reproduction with costs to future reproductive opportunities (Cotter et al. 2011; Trumbo 2012). By manipulating the quality and order of carcasses, we demonstrated that a female's previous reproductive experience influences the level of reproductive investment to current reproduction.

The interactive effect of prior experience and current carcass size on total brood mass was consistent with our predictions. Females that were switched from a low-quality carcass (i.e., 20-g carcass) to a high-quality carcass (i.e., 30-g carcass) responded by having higher reproductive investment to current reproduction compared with all other treatment combinations. The apparent reproductive restraint by females on low-quality resource allowed females to respond to a high-quality carcass by having greater allocation to current reproduction compared with other females given a high-quality resource. Females that experienced a reduction in carcass size did not exhibit a greater reduction in total brood mass than expected based on patterns observed in the treatment group receiving 2 low-quality carcasses. Prior experience also affected brood size, with females originally given low-quality resources producing larger broods on the current reproductive bout.

This study demonstrates that an individual's state as determined by prior experience affects reproductive allocation to current reproduction and likely interacts with age-based cues. Previous experience therefore affects how an organism assesses the balance of fitness benefits from investment to current reproduction with costs to future reproduction. For females in the 20–30 treatment, the balance shifts towards the benefits from increased investment to current reproduction. Similar patterns are predicted for old individuals with a low reproductive value (Williams 1966; Clutton-Brock 1984) or for individuals with a perceived decrease in reproductive value (e.g., individuals presented with an immune challenge; Norris and Evans 2000; Bonneaud et al. 2004; Velando et al. 2006; Cotter et al. 2011; Trumbo 2012). Reproductive patterns of females in the 30–20 treatment suggest that the benefits from increased investment

to current reproduction are not high enough to outweigh the costs to future reproduction; therefore, the balance shifts towards a reduced investment to current reproduction, or reproductive restraint. Organisms are predicted to exhibit reproductive restraint early in life when reproductive value is high (Williams 1966). Additionally, recent research has demonstrated that reproductive restraint late in life is a mechanism to reduce damage accumulation and deterioration of somatic condition to gain further breeding attempts (McNamara et al. 2009; Cotter et al. 2011; Trumbo 2012).

An organism that exhibits reproductive restraint must assume that the future will be at least as good as current conditions. For organisms such as burying beetles that reproduce on discrete resources, reproductive restraint will allow those individuals that initially secure suboptimal carcasses to conserve energy and condition so they can capitalize on high-quality resources in future reproductive bouts. Some observations of female reproductive behavior (e.g., utilization of suboptimal carcasses and satellite females) suggest that opportunities to secure a carcass for reproduction are limited (Müller et al. 1990; Trumbo 1990, 2006; Trumbo 2009). However, evidence of carcass availability for *N. investigator* support the assumption of the reproductive restraint hypothesis that burying beetles will have future reproductive opportunities. Densities of small rodents are sufficient such that only a small percentage (1–2%) would be required to die to support the beetle population (Smith and Merrick 2001). Additionally, observed reproductive patterns in this study and in others (Creighton et al. 2009; Cotter et al. 2011) suggest that beetles may have a high probability of future reproduction; otherwise the response to resource acquisition should be to maximize reproduction on the current bout despite reproductive costs. For example, in some arthropods, the probability of successfully mating is sufficiently low such that an individual will maximize investment on the current reproductive bout despite the high survival costs (Toda and Kimura 1997; Andrade 2003; Barry and Kokko 2010). An extreme example is the male redback spider (*Latrodectus hasselti*) that exhibits an adaptive behavior of offering itself as a nuptial gift to his mate who cannibalizes the male during copulation; high mortality during mate searching and increased paternity assurance ensures that self-sacrifice is an adaptive strategy (Andrade 2003).

Offspring size and female mass change were not affected by prior experience, but instead were affected by current carcass size or resource availability. Offspring size increased on high-quality resources whereas female mass change decreased; this pattern suggests that female had higher quality offspring but at greater somatic costs. This response may provide a lifetime fitness advantage to females under conditions of variable resource availability despite the increased cost incurred. Similar increases in reproductive investment as a response to resource availability have been demonstrated in other organisms as well. Other insect species that reproduce on a discrete resource exhibit similar patterns of increased allocation to current reproduction on high-quality resources (Heimpel and Rosenheim 1995; Heimpel and Collier 1996). For some bird species, high resource availability increases reproductive investment in the current reproductive period manifest either in larger clutch sizes and/or more broods within the reproductive season (Martin 1987; Grant et al. 2000; Christman 2002; Preston and Rotenberry 2006). In fishes, in the family Poeciliidae, incipient matrotrophy allows small females to have larger broods and offspring under high resource availability, but the pattern is less obvious for large females presumably because greater energy reserves in larger

fish allow them to sufficiently provision embryos even under low resource availability (Reznick and Yang 1993; Trexler 1997; Marsh-Matthews and Deaton 2006). Thus, a variety of taxonomically distant species exhibit increased investment to current reproduction during periods of high resources; future research should examine lifetime fitness to determine if these patterns represent adaptive responses or simply constraints imposed by limited resources.

This study successfully demonstrated that burying beetles exhibit a response to carcass size based on their previous reproductive experience. However, because we only tested for the response over 2 reproductive bouts, it is unclear what the consequence will be for the lifetime fitness of a female burying beetle. When provided a constant supply of carcasses for reproduction, female *N. orbicollis* exhibit different life-history strategies depending on carcass quality (Creighton et al. 2009). Despite the different life-history strategies, females in the 2 controls (20-g or 30-g carcasses for each reproductive bout, respectively) produced the same number of offspring over their lifetime (Creighton et al. 2009). This pattern occurred because females reproducing on 20-g carcasses had smaller brood sizes but more reproductive attempts due to greater allocation to future reproduction. Under variable resource availability, females that initially reproduce on a suboptimal carcass and subsequently on an optimal carcass may receive a lifetime fitness advantage by exhibiting an accentuated reproductive investment as observed in this study. However, the increased reproductive costs incurred could limit the number of reproductive attempts such that the lifetime number of offspring would not be significantly different than for females reproducing continually on suboptimal carcasses (Creighton et al. 2009; McNamara et al. 2009). Why then would the response observed in this study be exhibited? Under laboratory conditions, costs of reproduction are reduced compared with natural conditions because we remove the costs of securing a carcass; burying beetles compete for the opportunity to reproduce on a carcass, receiving injuries that reduce their state and probability of future reproduction (Cotter et al. 2011). Additionally, burying beetles under laboratory conditions do not have to search for food or carcasses, both of which can be spatially and temporally variable, further reducing costs to somatic conditions in laboratory studies. Therefore, measures of lifetime fitness from laboratory studies represent the maximum potential an individual can achieve. Under natural conditions, we predict that the responses observed in this study will provide a lifetime fitness advantage for burying beetles; however, this prediction has not been tested.

Life-history theory provides predictions for the patterns of life-history allocation. Previous research has demonstrated that burying beetles use both age- and state-based cues to determine the extent of reproductive investment (Creighton et al. 2009; Trumbo 2009; Cotter et al. 2011; Trumbo 2012). In this study, we also demonstrated that burying beetles use previous experience and current carcass size to determine reproductive investment. Thus, individuals use a variety of cues to adjust their schedule of reproduction, and predictions of reproductive investment across an organism's lifetime must account for the interaction of these cues.

FUNDING

Funding was provided to M.C.B. through a Mentoring Environment Grant from Brigham Young University.

We are grateful to Stefan and Jane Shoup who provided access to their property to allow us to collect beetles. We are grateful to Peter Meyers who helped

care for beetles and collect data and to Sandra Garrett and Megan Durrant of Central Animal Care at Brigham Young University for providing mouse carcasses (IACUC number 080403). Jerry Johnson, Steve Peck, Russ Rader, and Bruce Schaalje provided reviews of earlier drafts of the manuscript.

Handling editor: Nick Royle

REFERENCES

- Andrade MCB. 2003. Risky mate search and male self-sacrifice in redback spiders. *Behav Ecol.* 14:531–538.
- Barry KL, Kokko H. 2010. Male mate choice: why sequential choice can make its evolution difficult. *Anim Behav.* 80:163–169.
- Beauplet G, Guinet C. 2007. Phenotypic determinants of individual fitness in female fur seals: larger is better. *Proc Biol Sci.* 274:1877–1883.
- Bonneaud C, Mazuc J, Chastel O, Westerdahl H, Sorci G. 2004. Terminal investment induced by immune challenge and fitness traits associated with major histocompatibility complex in the house sparrow. *Evolution.* 58:2823–2830.
- Christman BJ. 2002. Extreme between-year variation in productivity of a bridled titmouse (*Baeolophus wollweberi*) population. *Auk.* 119:1149–1154.
- Clutton-Brock TH. 1984. Reproductive effort and terminal investment in iteroparous animals. *Am Nat.* 123:212–229.
- Cotter SC, Ward RJS, Kilner RM. 2011. Age-specific reproductive investment in female burying beetles: independent effects of state and risk of death. *Funct Ecol.* 25:652–660.
- Creighton JC. 2005. Population density, body size, and phenotypic plasticity of brood size in a burying beetle. *Behav Ecol.* 16:1031–1036.
- Creighton JC, Heflin ND, Belk MC. 2009. Cost of reproduction, resource quality, and terminal investment in a burying beetle. *Am Nat.* 174:673–684.
- Fisher RA. 1930. *The genetical theory of natural selection.* Oxford: Oxford University Press.
- Grant PR, Grant BR, Keller LF, Petren K. 2000. Effects of El Niño events on Darwin's finch productivity. *Ecology.* 81:2442–2457.
- Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. *J Anim Ecol.* 78:143–151.
- Heimpel GE, Collier TR. 1996. The evolution of host-feeding behavior in insect parasitoids. *Biol Rev.* 71:373–400.
- Heimpel GE, Rosenheim JA. 1995. Dynamic host feeding by the parasitoid *Aphytis melinus*: the balance between current and future reproduction. *J Anim Ecol.* 64:153–167.
- Lesacroël A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver PO, Ainley DG. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology.* 91:2044–2055.
- Marsh-Matthews E, Deaton R. 2006. Resources and offspring provisioning: a test of the Trexler-DeAngelis model for matrotrophy evolution. *Ecology.* 87:3014–3020.
- Martin TE. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu Rev Ecol Syst.* 18:453–487.
- McNamara JM, Houston AI. 1996. State-dependent life histories. *Nature.* 380:215–221.
- McNamara JM, Houston AI, Barta Z, Scheuerlein A, Fromhage L. 2009. Deterioration, death and the evolution of reproductive restraint in late life. *P Roy Soc B: Proc Biol Sci.* 276:4061–4066.
- Müller JK, Eggert AK, Furlkröger E. 1990. Clutch size regulation in the burying beetle *Necrophorus vespilloides* Herbst (Coleoptera: Silphidae). *J Insect Behav.* 3:265–270.
- Norris K, Evans MR. 2000. Ecological immunology: life history trade-offs and immune defense in birds. *Behav Ecol.* 11:19–26.
- Preston KL, Rotenberry JT. 2006. Independent effects of food and predator-mediated processes on annual fecundity in a songbird. *Ecology.* 87:160–168.
- Reznick D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos.* 44:257–267.
- Reznick D, Yang AP. 1993. The influence of fluctuating resources on life history: patterns of allocation and plasticity in female guppies. *Ecology.* 74:2011–2019.
- Roff DA. 2002. *Life history evolution.* Sunderland (MA): Sinauer Associates.
- SAS Institute Inc. 2008. SAS 9.2 help and documentation. Cary (NC): SAS Institute Inc.
- Scott MP. 1998. The ecology and behavior of burying beetles. *Annu Rev Entomol.* 43:595–618.

- 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.
- Smith RJ, Merrick MJ. 2001. Resource availability and population dynamics of *Nicrophorus investigator*, an obligate carrion beetle. *Ecol Entomol.* 26:173–180.
- Toda MJ, Kimura MT. 1997. Life-history traits related to host selection in mycophagous drosophilids. *J Anim Ecol.* 66:154–166.
- Trexler JC. 1997. Resource availability and plasticity in offspring provisioning: embryo nourishment in sailfin mollies. *Ecology.* 78:1370–1381.
- Trumbo ST. 1990. Interference competition among burying beetles (Silphidae, *Nicrophorus*). *Ecol Entomol.* 15:347–355.
- Trumbo ST. 2006. Infanticide, sexual selection, and task specialization in biparental burying beetles. *Anim Behav* 72:1159–1167.
- Trumbo ST. 2009. Age-related reproductive performance in the parental burying beetle, *Nicrophorus orbicollis*. *Behav Ecol.* 20:951–956.
- Trumbo ST. 2012. Contest behavior and other reproductive efforts in aging breeders: a test of residual reproductive value and state-dependent models. *Behav Ecol Sociobiol.* 66:1511–1518.
- Trumbo ST, Fernandez AG. 1995. Regulation of brood size by male parents and cues employed to assess resource size by burying beetles. *Ethol, Ecol Evol.* 7:313–322.
- Velando A, Drummond H, Torres R. 2006. Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. *P Roy Soc B: Proc Biol Sci.* 273:1443–1448.
- Wendeln H, Becker PH. 1999. Effects of parental quality and effort on the reproduction of common terns. *J Anim Ecol.* 68:205–214.
- Williams GC. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am Nat.* 100:687–690.
- Wilson AJ, Nussey DH. 2010. What is individual quality? An evolutionary perspective. *Trends Ecol Evol.* 25:207–214.