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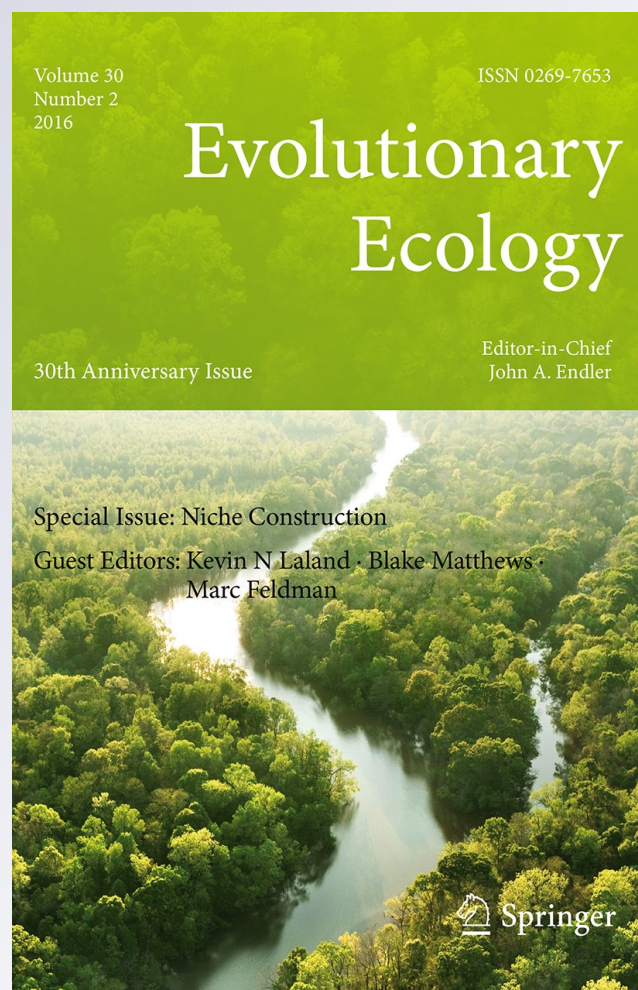
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Effects of parental care on the accumulation and release of cryptic genetic variation: *review of mechanisms and a case study of dung beetles*

Emilie C. Snell-Rood^{1,2} · Melissa Burger^{2,3} · Quinton Hutton² · Armin P. Moczek²

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Abstract Cryptic genetic variation plays an important role in the emergence of disease and evolutionary responses to environmental change. Focusing on parental care behavior, we discuss three mechanisms by which behavior can affect the accumulation and release of cryptic genetic variation. We illustrate how these hypotheses might be tested with preliminary data from *Onthophagus* dung beetles, which provide indirect parental care by provisioning their offspring with dung and sheltering them underground. The *environmental stress hypothesis* states that parental care reduces selection intensity on novel mutations when increased parental care results in a less stressful offspring environment. A review of recent literature, coupled with an irradiation experiment in beetles, suggests this mechanism may operate in some situations, but depends on the types of mutations under consideration. The *relaxed selection hypothesis* states that genes expressed in low care environments should be under weakened selection because their phenotypic manifestations are exposed to selection less frequently, and thus are prone to mutation accumulation. If parental care is reduced, for instance due to population-wide environmental changes, such cryptic variation may exert phenotypic effects, becoming exposed to selection. There is substantial theory in support of this hypothesis, and comparisons between beetle populations that differ in parental care behavior further support this idea. Finally, the *compensation hypothesis* states that organisms with direct parental care may be able to respond to cues or signals from offspring and compensate for genetic variants. We highlight the extensive discussion of this hypothesis with respect to medical care and genetic load in humans and explore invertebrate systems that may constitute powerful models for further

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inquiry. In summary, several mechanisms exist by which care behavior may shape the accumulation and release of cryptic genetic variation, thereby affecting the potential emergence of diseases and the rate and direction of evolutionary responses to novel environments.

Keywords Cryptic genetic variation · Parental care · Life history · Niche construction · Buffering

Introduction

Biologists have long been fascinated by the factors and mechanisms that affect the maintenance of genetic variation within populations. Identifying such mechanisms and characterizing their nature has important implications for understanding and predicting not only the evolutionary responses of populations (Lande and Shannon 1996; Mitchell-Olds and Schmitt 2006), but also the emergence of disease (Chakravarti 1999; Cooper et al. 2010). In recent decades, attention has turned to genetic variation that is “cryptic”—in other words, under normal conditions, the genetic variation has no measurable phenotypic effects and fitness consequences, yet becomes subject to selection when aspects of the environment or genotype changes such that the mutation suddenly has a phenotypic effect (Hermisson and Wagner 2004; Gibson and Dworkin 2004). As such, cryptic genetic variation is thought to impact responses to novel environments (Ledon-Rettig et al. 2010; Masel 2006; McGuigan and Sgro 2009; Schlichting 2008), including the emergence of disease in the face of novel nutritional conditions or the evolution of populations in human altered environments (Ghalambor et al. 2007; Gibson 2009; McGuigan and Sgro 2009; Schlichting 2008).

Several important studies have now demonstrated how genetic “capacitors,” such as the heat shock protein system, can facilitate the accumulation and release of cryptic genetic variation (Rutherford and Lindquist 1998; Rutherford 2000; Bergman and Siegal 2003; Levy and Siegal 2008), yet similar dynamics are likely to emerge as a consequence of behavior. For instance, complex behavior such as medical care or foraging behavior, may weaken selection on a trait through compensatory actions, and thus should result in accumulation of genetic variation in a population (Muller 1950; Williams and Nesse 1991; Crow 1997; Kondrashov and Crow 1993; Lynch et al. 1999; Lynch 2010). Indeed, the term “behavioral inertia” has been used to capture the idea that behavior may buffer selection on genes: for instance, thermoregulatory behavior can compensate for mutations in genes that affect thermal tolerance (Huey et al. 2003). This view of behavior has also been termed “counteractive niche construction,” where organisms neutralize some change in selection through behavior (Odling-Smee et al. 2003).

Here, we give more explicit consideration of the role of behavior, through its effects on the selective environment experienced by an organism, in influencing the accumulation and release of cryptic genetic variation. Such behavioral niche construction influences selection dynamics (Saltz and Foley 2011) and can result in complex evolutionary feedbacks because the niche-constructing behavioral traits that affect selection can themselves co-evolve with “recipient” traits affected by the modified conditions (Laland et al. 1996, 1999; Saltz and Nuzhdin 2014). In this review, we articulate three mechanisms by which behavior may influence the accumulation and release of cryptic genetic variation. We

specifically focus on care behavior, but much of the discussion can apply to other behavioral traits as well. Throughout, we discuss onthophagine dung beetles as a study system to illustrate how these ideas might be tested in the laboratory and natural populations.

Parental care behavior

Parental care affects selection through control of developmental environment

Parental care manifests in diverse ways, yet tends to converge on one function: changing environmental conditions in a manner closer to what is “optimal” for offspring development and survival, for instance by providing food, shelter, and/or protection against thermal variation, predators, and competitors (Silver et al. 1985; Conway and Martin 2000; Scott 1998). In other words, parental care reduces between-offspring variation in environmental conditions relative to conditions where parental care is compromised or absent. For instance, parental thermoregulatory behavior can counteract temperature extremes in both directions (e.g., brooding or fanning offspring). Parental provisioning increases the changes that offspring have adequate resources for growth, and offspring defense improves the likelihood offspring are not directly exposed to predators.

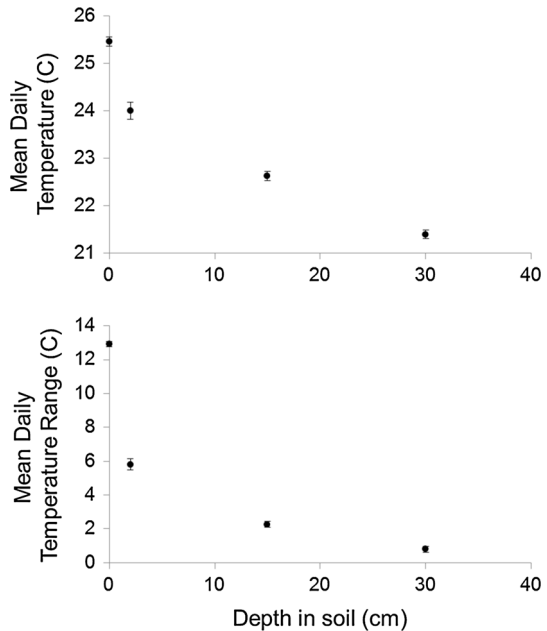
Systems for the study of parental care and cryptic genetic variation

Parental care can be direct, such as delivery of food to offspring or defense of vulnerable young, or indirect, such as any behaviors that bias the conditions experienced by offspring towards those that are favorable (Fox and Czesak 2000; Thompson and Pellmyr 1991; Royle et al. 2012; Clutton-Brock 1991). Such indirect forms of care include placement of eggs in safe locations with optimal thermal conditions or provisioning of eggs with extra yolk or food (e.g., dung, paralyzed prey). These forms of indirect care are ideal for examining the role of behavior in cryptic genetic variation because they tend to be more discrete in space and time, and more easily quantified and manipulated in contrast to direct forms of care, which occur over extended periods of time, often require multiple measures, and are more difficult to reliably manipulate.

Insect systems are particularly promising in this context because they are easy to rear in large numbers and the effects of parental care—and experimental manipulations thereof—manifest over relatively short generation times. While most model invertebrate systems have relatively low levels of parental care, many non-model species engage in diverse forms of parental care, even direct care of offspring (reviewed in Costa 2006; Choe and Crespi 1997; Wong et al. 2013; Trumbo 2012; Smiseth 2014). Many insects provide indirect care through greater egg size (Wheeler 1996; Fox and Czesak 2000), placement of eggs on particularly nutritious food sources (Renwick and Chew 1994; Thompson and Pellmyr 1991), or the transmission of microbial partners that aid in digestion or protection while feeding on challenging resources (Feldhaar 2011; Douglas 2009).

Here, we highlight horned beetles in the genus *Onthophagus*, which exhibit remarkable parental care behavior (Emlen 1997; Moczek 1998, 1999; Hunt and Simmons 2000, 2002; Estes et al. 2013). Specifically, adult beetles provision each offspring with a brood ball, a spherical to ovoid mass of dung processed and constructed by adult females. Females oviposit one egg per brood ball, which provides the total amount of

Fig. 1 Brood ball burial depth affects temperature conditions during development. We used ibutton temperature probes buried at the soil surface, and at various depths within the natural range of *Onthophagus taurus* brood ball burial depth (see Fig. 2), to measure soil temperature in the field. Mean daily temperature decreased with soil depth; daily temperature variation (the difference between maximum and minimum temperature within a 24 h period) also decreased with soil depth



food that larvae need to complete larval development and metamorphosis. As such, the construction of brood balls buffers offspring against nutritional stress (Hunt and Simmons 2000, 2002, 2004) and enables parents to adjust brood ball size in proportion to the quality of the food resource (Moczek 1998; Kishi and Nishida 2006). Lastly, beetles invest heavily in the construction of deep burrows or tunnels where they bury brood balls, which in turn protect offspring from competitors, predators, parasites, and temperature fluctuations throughout larval development (Fig. 1, Halfter and Matthews 1966; Halffter and Edmonds 1982). While it is not clear for what function brood ball burial originally evolved, it clearly shapes the developmental environment of offspring in several different ways.

Importantly, parental care in *Onthophagus* is not fixed at a particular level, but instead exhibits experimentally exploitable variation over a range of phylogenetic distances. For example, indirect parental care (e.g., brood ball size) exhibits genetic variation within populations of *Onthophagus taurus* (Hunt and Simmons 2000, 2002). Furthermore, populations and species have diverged in both brood ball size and nesting depth (Fig. 2, Macagno et al. 2016), and in *O. taurus*, some females and populations produce larger brood balls, burying them deeper in the soil, more sheltered from temperature fluctuations (Fig. 2). Increased care behavior represents part of a life history strategy where increased investment per offspring comes at a cost of survival (Hunt et al. 2002); it is also likely that the time associated with constructing larger, more deeply buried brood balls comes at the expense of lifetime fecundity, although this remains to be tested.

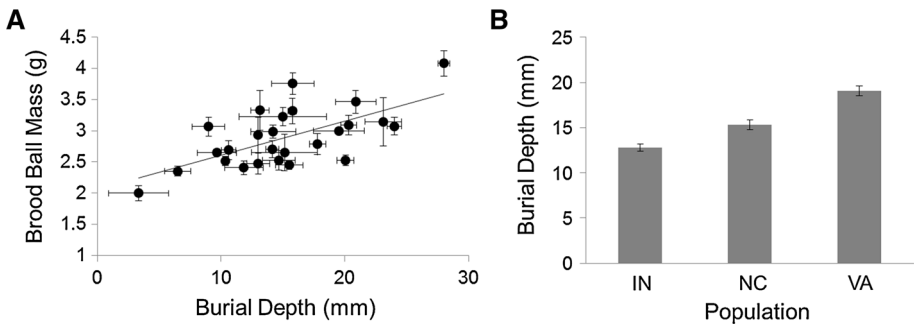


Fig. 2 Variation within and between populations in parental care. Brood ball burial depth was measured by allowing females to make brood balls in 60 cm tall 10 cm diameter PVC pipes; soil was sifted in 2 cm depth increments to measure burial depth. **a** There were significant differences between females in brood ball burial depth ($F_{23,146} = 12.9$, $P < 0.0001$); this measure of care was positively correlated with the mass of individual brood balls (Spearman's $\rho = 0.37$, $P < 0.0001$, $N = 192$), which also varied between individuals and populations (population: $F_{2,139} = 32.1$, $P < 0.0001$; individual: $F_{22,139} = 3.98$, $P < 0.0001$). Shown are mean and standard error for females that constructed at least three brood balls in the lab. **b** Female beetles from different populations showed significant variation in brood ball burial depth in the lab ($F_{2,146} = 41.6$, $P < 0.0001$)

Mechanism 1: the stress hypothesis

Theory

Several mechanisms have been proposed by which behavior may affect the accumulation and release of cryptic genetic variation. First, behavioral traits may affect the degree of stress experienced during development, which, in turn could affect the phenotypic consequences of underlying genetic variation and subsequent selection on those genes. It has been suggested that the effects of mutations, and thus selection, are generally stronger in stressful environments (Martin and Lenormand 2006; Kondrashov and Houle 1994). Thus, in the presence of care, any new mutation would be predicted to have, on average, a lesser phenotypic effect. Subsequent bouts of relaxed selection on such genes may thus result in their retention and accumulation in a population until the buffering capacity of parental care is reached or when care behaviors are compromised.

Although the idea linking stress and selection intensity is prevalent in the literature, recent meta-analyses have more generally called into question whether the effects of mutations are truly more pronounced in stressful environments (Halligan and Keightley 2009; Agrawal and Whitlock 2010). Indeed, there appears to be remarkable system-specificity in whether this notion is supported: most studies on insects support such a connection, while data on birds (Hoffmann and Merila 1999) and prokaryotes (Agrawal and Whitlock 2010) provide mixed support. Consequently, whether or not stress heightens selection on new mutations may thus be best determined on a system by system basis, and the same would be true for the hypothesized role of parental care in shaping these interactions.

Case study in dung beetles

We used dung beetles to provide a preliminary test of the role of indirect parental care in influencing the phenotypic effects, and subsequent selection on, new mutations. We introduced novel mutations in paternal *Onthophagus gazella* by exposing beetles to 1 or 2 krad of irradiation. Offspring were split between rearing treatments that simulated high or low levels of parental care and several measures of body size were used as phenotypic

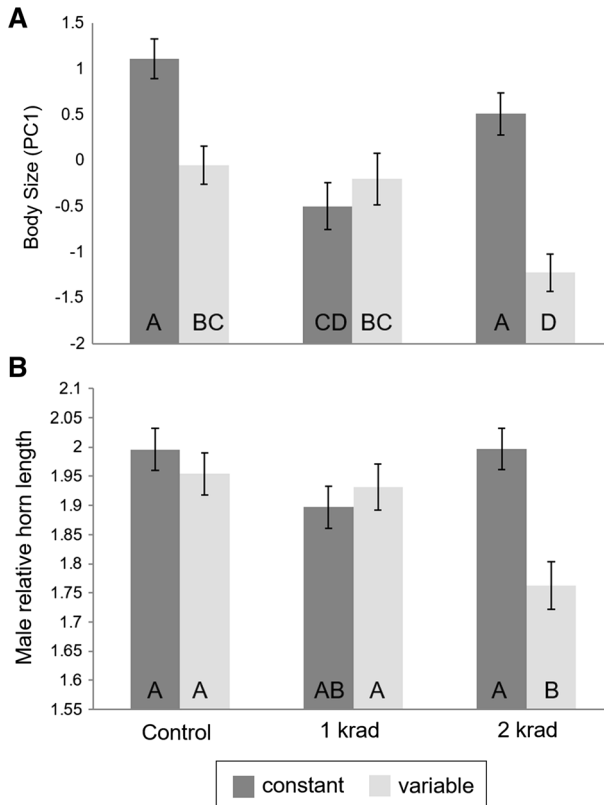


Fig. 3 Effects of novel mutations depend on conditions simulating different levels of parental care. Paternal *Onthophagus gazella* ($N > 5$) were treated at day 5 of adulthood (when spermatogenesis is actively occurring) with 1 or 2 krad irradiation using a $^{137}\text{Cesium}$ source and offspring were reared under constant or variable temperature conditions. Based on the literature on sterilization of beetle pest species (e.g., *Tribolium*, Pajni and Virk 1978; Tuncbilek and Kansu 1996), these levels have negative effects on beetles, but are not lethal. Body size was measured as PC1 from a PCA that included thoracic width and the length of two pairs of legs. **a** The effects of irradiation on body size depended on not just the irradiation levels, but also the temperature rearing treatment (irradiation \times temperature: $F_{2,65} = 7.95$; $P = 0.0008$; in a model that includes irradiation, temperature and sex). Letters indicate significant differences between categories as estimated using a Tukey–Kramer HSD test. **b** Male horn length was analyzed in a model that also included body size (PC1 from a PCA that included thoracic width and the length of two pairs of legs) because relative horn length is an important determinant of contest outcome (Snell-Rood and Moczek 2013). The effects of irradiation on male horn length depended on not just irradiation levels, but also the temperature rearing treatment (irradiation \times temperature: $F_{2,31} = 4.41$; $P = 0.02$; in a model that includes irradiation, temperature and body size). Letters indicate significant differences between categories as estimated using a Tukey–Kramer HSD test

measures of developmental stress. In particular, high daily temperature variation during development (19–31 °C) was used to simulate shallow brood ball burial depth and thus low parental care, whereas a consistent rearing temperature of the same mean (25 °C) was used to simulate deep burial and thus high parental care. The degree of temperature variation was based on field observations at of brood balls placed at different soil depths (see Fig. 1) at either extreme of variation in beetle burial depth (see Fig. 2). We found a significant interaction between rearing conditions simulating different levels of care and radiation treatment (Fig. 3): in the 2 krad treatment, the effects of irradiation on body size and relative horn length were most pronounced in the treatment simulating compromised parental care (variable rearing temperatures, corresponding to shallow burial depth). However, we did not see this effect in the 1 krad treatment.

These preliminary analyses support the idea that indirect parental care can indeed buffer the effects of novel mutations, at least in some cases: phenotypic effects of irradiation were more pronounced in the “low care” treatment, but only for one of the two irradiation treatments. These results also suggest that the buffering capacity of parental care may differ greatly depending on the mutational target involved. While our experimental manipulation afforded us control over irradiation intensity, we had no control over exactly where in the genome mutations would occur. For instance, it is conceivable that mutations in genes involved in axis patterning during appendage formation manifest phenotypically regardless of the degree of parental care. On the other hand, mutations in genes underlying growth regulation (such as insulin signaling), with multiple redundant pathway components, may be more conducive to buffering, or in fact may even be more pronounced under benign conditions when growth rates are greater (Jasnos et al. 2008).

These data, coupled with recent meta-analyses, suggest that the *environmental stress hypothesis* provides a mechanism linking behavior to the accumulation and release of genetic variation only for some taxa, genes, and conditions, and that its applicability needs to be determined on a case-by-case basis.

Mechanism 2: *the relaxed selection hypothesis*

Theory

Parental care influences the environments offspring experience during development. At the same time, it is well established that the phenotypic and fitness effects of mutations are sensitive to the environment (Kondrashov and Houle 1994; Fry et al. 1996; Fernandez and Lopez-Fanjul 1997; Shabalina et al. 1997; Vassilieva et al. 2000; Szafraniec et al. 2001). This environmental sensitivity of selection is not surprising given that gene expression itself often depends on environmental conditions (Snell-Rood et al. 2010; Aubin-Horth and Renn 2009; Hodgins-Davis and Townsend 2009).

A well-established theoretical literature links the frequency of environmental exposure to selection intensity on genes with effects in those environments (Van Dyken and Wade 2010; Kawecki 1994; Whitlock 1996; Snell-Rood et al. 2010). If parental care increases the likelihood offspring experience environment “*P*” (parental environment) but not environment “*S*” (solitary environment), selection on genes with effects in *S* is relaxed relative to populations that experience these environments at similar frequencies. In other words, purifying selection (on deleterious genes) and positive selection (on beneficial genes) are both less pronounced for genes with an effect in environment *S*.

These interactions between parental behavior, offspring developmental environment and selection can create evolutionary feedbacks that accelerate adaptation to the parental care environment P (Drown and Wade 2014; Wade 1998). Over time, care behavior also affects the evolution of what constitutes “stressful” versus “optimal” environments for offspring development. In particular, initial asymmetries in what are “favorable” environments may quickly become amplified by relaxed selection. As offspring experience an environment less frequently, mutations with deleterious effects in that environment should accumulate at an increasing rate; at the same time, fixation is more likely for mutations with positive effects in the environments chosen more frequently by parents.

Relaxed selection on genes with effects in environment S should thus lead to the accumulation of cryptic genetic variation. As long as parents are able to generally choose environment P for their offspring, the effects of this cryptic genetic variation will not be seen by selection. However, a change in parental care, for instance due to the change in the availability of environments S and P may expose this variation to selection.

Case study in dung beetles

As above, we used dung beetles to test the idea that parental care behavior is correlated with the accumulation of mutations with effects in “low care” conditions. We focused on indirect care behavior in *O. taurus*—specifically, variation in brood ball burial depth and its consequences for developmental temperature experienced by offspring (see Figs. 1, 2). Beetles from two natural populations that heritably differed in average brood ball burial depth were reared in common garden conditions meant to simulate either high care (stable temperature conditions, 25 °C) or low care conditions (variable temperature conditions, fluctuating daily between 19 to 31 °C; see Fig. 1).

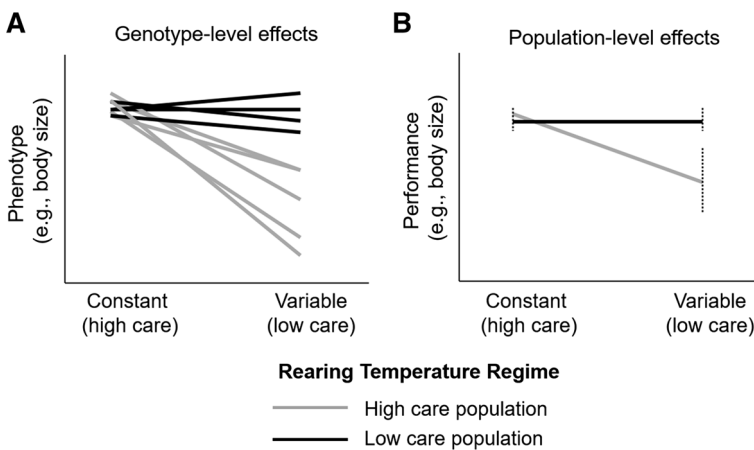


Fig. 4 General predictions for a quantitative genetics approach to the relaxed selection hypothesis. Two populations that differed in parental care were reared in conditions that simulated either high care (constant rearing temperature) or low care (variable daily temperature). **a** If genes expressed in the low care conditions harbor more underlying genetic variation, we would predict greater phenotypic variation in those rearing conditions, but more so for the high care population. A greater contribution of genetic variation to this phenotypic variation (as assessed by full sibling lines, represented by reaction norms) would be consistent with underlying genetic variation rather than phenotypic plasticity. **b** If the underlying cryptic variation harbors more deleterious variation, we expect the high care populations to show a relatively greater decline in performance than the low care population when reared under low care conditions

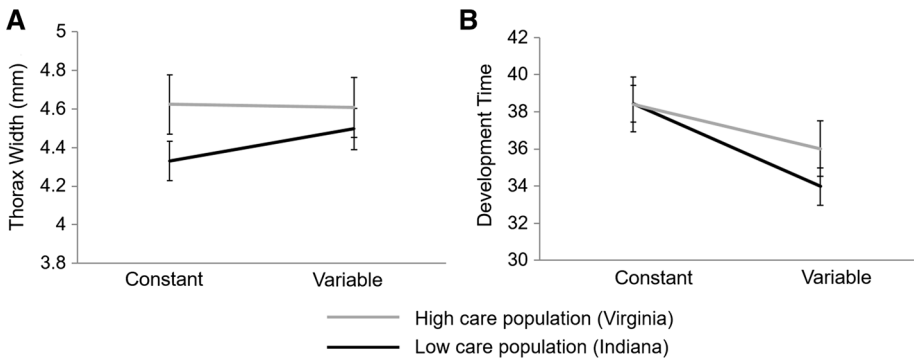


Fig. 5 Cryptic genetic variation across populations that vary in parental care. There were no significant differences between populations in body size in the two temperature rearing conditions ($F_{1,13} = 1.34$; $P = 0.26$). However, the high care population (Virginia) showed greater overall phenotypic variation than the low care population (Indiana) in the variable temperature environment (shown are population least square means and standard error bars from a mixed-effects ANOVA on 93 individuals that included mother as a random effect; F test for equality of variance between populations—constant environment: $F_{13,35} = 1.02$, $P = 0.91$; variable environment: $F_{13,28} = 2.89$, $P = 0.02$). **b** There was a significant effect of rearing temperature condition on development time ($F_{1,76} = 37.9$; $P < 0.0001$), although this effect was more pronounced for the low care population in a marginally significant manner (population \times temperature interaction: $F_{1,76} = 3.38$; $P = 0.07$). A Tukey–Kramer HSD test revealed significant differences in development time for the two temperature treatments for the Indiana population, but not the Virginia population

The relaxed selection hypothesis makes several key predictions for such a design (Fig. 4). First, in populations with a history of high levels of care, deleterious mutations should accumulate in genes with effects specific to the low care conditions more so than in a population that historically experienced lower levels of care. Such a prediction could be measured directly, by sequencing genes of known environmental effects, or indirectly, by using a quantitative genetics approach that screens for the phenotypic manifestations of cryptic genetic variation. A family-level design predicts in part that greater phenotypic variation should be present in the low care environment for the higher care population relative to the low care population. Measuring the contribution of genetic variation to this phenotypic variation can determine whether such phenotypic variation stems from underlying genetic variation or developmental plasticity (see Fig. 4). Using this quantitative genetics approach, we see provisional support for the first part of this prediction with respect to variation in body size: offspring derived from the population with greater parental care were more variable in size (thorax width) if reared in the variable temperature treatment (Fig. 5) relative to offspring from the population with lower levels of parental care (shallower burial depth and smaller brood balls). A full sibling design was used to test the contribution of genetic variation to overall phenotypic variation. For development time, “family” explained more variation in the variable temperature environment (88 %) than the constant temperature environment (55 %), consistent with the release of cryptic genetic variation rather than simply a plastic developmental response to the variable temperature conditions.

Second, if mutations with effects specific to the low care environment are deleterious, we predicted that the performance of the high care population would be relatively more compromised under the variable temperature (low care) conditions (Fig. 4). We see partial support for this prediction with respect to development time: offspring derived from the

lower care population sped up development time in the variable temperature condition, whereas offspring from the higher care population were unable to do so (Fig. 5). This is consistent with the idea that the high care population may harbor deleterious mutations that affect development time under variable temperature conditions that they experience less frequently.

While these data provide preliminary support for the relaxed selection hypothesis, they are severely limited by sample size ($N = 2$ populations and 7 full sibling lines with adequate sample size for the genetic variation analysis). A more extensive quantitative genetic experiment is clearly needed to adequately test and expand upon these ideas. Combining such a quantitative genetics approach with a re-sequencing approach would be especially informative to assess standing levels of sequence variation in natural populations, and relative sensitivity of mutational variation of a given gene to the high or low care environments.

Mechanism 3: *the compensation hypothesis*

In systems with direct care, involving prolonged physical contact between parents and offspring, it is possible that more complex, responsive behaviors may directly compensate for new, deleterious mutations. As before, the resulting weakened selection is predicted to lead to the accumulation of mutations which would be cryptic under normal care conditions, but would be exposed to selection if care is removed or reduced. For instance, genes with deleterious effects on vision would be compensated for by eye care in humans and genes with negative effects on early life foraging ability might be compensated for by parents delivering more food to their offspring. While this idea has been discussed extensively with respect to “mutation load” in humans (Muller 1950; Williams and Nesse 1991; Crow 1997; Kondrashov and Crow 1993; Lynch et al. 1999; Lynch 2010), it is unclear to what extent it applies to direct care in non-human animals. Here, the *Onthophagus* dung beetle system falls short as an empirical system as parents only provide indirect care for offspring and there are no opportunities for parents to assess their offspring’s phenotype and compensate. However, a subset of closely related dung beetle species exist that provide more direct care for offspring, such as attendance of single offspring throughout their development in the genus *Kheper* (Edwards 1988). A particularly promising, but more distantly related, beetle system is the genus *Nicrophorus* (burying beetles), which not only provide their offspring with a subterranean “cake” made of a cleaned and embalmed small mammal carcass, but also feed their larvae regurgitated and partially processed food in response to “begging” cues (Smiseth and Moore 2007, 2008). Such systems where parents assess their performance of their offspring through cues or signals are ideal for testing the “compensation” hypothesis. Indeed, *Nicrophorus* mothers can increase provisioning intensity for low mass offspring (Lock et al. 2007).

Implications and future directions

In this review, we have considered several mechanisms by which behavior in general, and parental care in particular, can influence the accumulation and release of cryptic genetic variation. Specifically, care behavior has the potential to create relaxed selection in less stressful environments, on genes with effects specific to low care environments, or through

direct compensation for a mutation effect. Such relaxed selection can result in the accumulation of mildly deleterious mutations in populations with high care. While care behavior causes the phenotypic effects of these mutations to remain cryptic under most circumstances, a change in environmental conditions (e.g., due to prolonged resource scarcity) has the potential to expose the underlying genetic variation to selection. While we have treated these three mechanisms separately, it is important to note that they are not mutually exclusive. Indeed, in many systems, all three may be at work simultaneously, further amplifying relaxed selection due to care behavior. We conclude this review by highlighting several interesting implications of these ideas and open areas of future research.

Complex evolutionary feedbacks with parental care

When behavioral traits affect the selective environment, a form of niche construction, this creates the potential for complex feedbacks between the evolution of behavior and dynamics of natural selection on recipient traits (Laland et al. 1996, 1999). Parental care varies enormously within and across species. Theory has shown that genetic variation in parental care behavior (e.g., maternal effects) can result in runaway evolutionary processes, where the match between the parental care and offspring environment evolve rapidly (Drown and Wade 2014; Wade 1998). The present discussion suggests additional complex feedbacks. In particular, positive feedback cycles between buffering mechanisms and selection intensity may amplify buffering mechanisms over evolutionary time as seen in more general models (Rajon and Masel 2011). As deleterious genes specific to the low care environment accumulate, there should be greater and greater selection for care behavior, further relaxing selection on the no care environment. Indeed, this positive feedback cycle could explain why loss of parental care tends to be rare relative to the evolutionary origins of care (Mank et al. 2005; Reynolds et al. 2002; Brown et al. 2010).

Throughout this review, we have generally assumed organisms are responding to environmental changes through compensatory, buffering behavior. This has been termed a form of “counteractive” niche construction whereby individuals act to offset environmental change, thereby stabilizing their environment, or that of their offspring (Odling-Smee et al. 2003). However, these ideas also apply to “inceptive” niche construction, where individuals initiate environmental change through dispersal or modification of their environment. Parents may modify their environment in ways to make them more productive or stable, such as habitat modifications made by ants that affect colony performance (Frederickson et al. 2005). This distinction is especially relevant in the context of cryptic genetic variation, because both forms of niche construction could interact in interesting ways. For example, movement or habitat modification (inceptive niche construction) could expose populations to novel environments that reveal underlying genetic variation, whereas behavioral changes (counteractive niche construction) may then compensate or buffer against the phenotypic effects of these genetic variants. Indeed, such counteractive niche construction has been proposed to enable organisms to tolerate otherwise maladaptive consequences of inceptive niche construction (Odling-Smee et al. 2003).

The evolutionary significance of cryptic genetic variation

In this review, we have mostly considered the mechanisms by which care behavior may lead to the accumulation of cryptic genetic variation. However, the consequences of such genetic variation for the direction and speed of evolution remain largely unclear. Theory

modeling the evolution of environment-dependent gene expression suggests that much of this genetic variation will be deleterious relative to species without environment-dependent gene expression (Van Dyken and Wade 2010). However, other models suggest that cryptic genetic variation will be enriched for beneficial mutations (relative to random mutations) because the pool of variants is periodically exposed to selection, resulting in the loss of extremely deleterious variants (Masel 2006). Either way, when cryptic genetic variation is exposed to selection, it has the potential to fuel rapid responses to selection, enable population differentiation, and facilitate the evolution of local adaptation.

Cryptic genetic variation is likely to be exposed to selection when care behavior is compromised. This may be rather common as parental care is costly, part of a life history strategy where total investment in each offspring trades off with total fecundity. If a parent cannot afford the cost of care and invests less in each offspring, underlying genetic variation may exert phenotypic effects. For instance, in *Onthophagus* beetles, optimal provisioning and burial depth depends on population density, dung type and soil conditions (Buzatto et al. 2012; Hunt and Simmons 2004) and in *Nicrophorus* beetles, the amount of care varies with resource quality (Scott and Traniello 1990). Moreover, environmental conditions may vary in a way that overwhelms parental care at least occasionally, for instance in periods of exceptional climate fluctuations or resource scarcity. Consequently, cryptic variation is especially likely to be exposed to selection in novel, variable or rapidly changing environments. Thus, the present discussion is particularly relevant to understanding the emergence of disease and predicting how populations may adapt to anthropogenic change—this is an exciting area wide open for future research. Overall, this discussion joins a broader appreciation of how behavior can have drastic effects on selection and evolution, whether it's parental care affecting thermal environments, self-medication affecting disease exposure (de Roode et al. 2013), or changes in locomotor behavior affecting aquatic versus terrestrial environments (Standen et al. 2014).

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References

- Agrawal AF, Whitlock MC (2010) Environmental duress and epistasis: how does stress affect the strength of selection on new mutations? *Trends Ecol Evol* 25(8):450–458. doi:10.1016/j.tree.2010.05.003
- Aubin-Horth N, Renn SCP (2009) Genomic reaction norms: using integrative biology to understand molecular mechanisms of phenotypic plasticity. *Mol Ecol* 18(18):3763–3780. doi:10.1111/j.1365-294X.2009.04313.x
- Bergman A, Siegal ML (2003) Evolutionary capacitance as a general feature of complex gene networks. *Nature* 424(6948):549–552
- Brown JL, Morales V, Summers K (2010) A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *Am Nat* 175(4):436–446. doi:10.1086/650727
- Buzatto BA, Tomkins JL, Simmons LW (2012) Maternal effects on male weaponry: female dung beetles produce major sons with longer horns when they perceive higher population density. *BMC Evol Biol*. doi:10.1186/1471-2148-12-118

- Chakravarti A (1999) Population genetics—making sense out of sequence. *Nat Genet* 21:56–60
- Choe J, Crespi B (1997) The evolution of social behaviour in insects and Arachnids. Cambridge University Press, New York
- Clutton-Brock T (1991) The evolution of parental care. Princeton University Press, Princeton
- Conway CJ, Martin TE (2000) Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* 54(2):670–685
- Cooper DN, Chen JM, Ball EV, Howells K, Mort M, Phillips AD et al (2010) Genes, mutations, and human inherited disease at the dawn of the age of personalized genomics. *Hum Mutat* 31(6):631–655. doi:10.1002/humu.21260
- Costa J (2006) The other insect societies. Harvard University Press, Cambridge
- Crow JF (1997) The high spontaneous mutation rate: is it a health risk? *Proc Natl Acad Sci USA* 94(16):8380–8386
- de Roode JC, Lefevre T, Hunter MD (2013) Self-medication in animals. *Science* 340(6129):150–151. doi:10.1126/science.1235824
- Douglas AE (2009) The microbial dimension in insect nutritional ecology. *Funct Ecol* 23(1):38–47. doi:10.1111/j.1365-2435.2008.01442.x
- Drown DM, Wade MJ (2014) Runaway coevolution: adaptation to heritable and nonheritable environments. *Evolution* 68(10):3039–3046. doi:10.1111/evo.12470
- Edwards PB (1988) Field ecology of a brood-caring dung beetle *Kheper nigroaeneus*—habitat predictability and life history strategy. *Oecologia* 75(4):527–534
- Emlen DJ (1997) Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera:scarabaeidae). *Behav Ecol Sociobiol* 41(5):335–341
- Estes AM, Hearn DJ, Snell-Rood EC, Feindler M, Feeser K, Abebe T et al (2013) Brood ball-mediated transmission of microbiome members in the dung beetle, *Onthophagus taurus* (Coleoptera: Scarabaeidae). *PLoS ONE*. doi:10.1371/journal.pone.0079061
- Feldhaar H (2011) Bacterial symbionts as mediators of ecologically important traits of insect hosts. *Ecol Entomol* 36(5):533–543. doi:10.1111/j.1365-2311.2011.01318.x
- Fernandez J, LopezFanjul C (1997) Spontaneous mutational genotype-environment interaction for fitness-related traits in *Drosophila melanogaster*. *Evolution* 51(3):856–864
- Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. *Annu Rev Entomol* 45:341–369
- Frederickson ME, Greene MJ, Gordon D (2005) Ecology: ‘Devil’s gardens’ bedevilled by ants. *Nature* 437:495–496
- Fry JD, Heinsohn SL, Mackay TFC (1996) The contribution of new mutations to genotype-environment interaction for fitness in *Drosophila melanogaster*. *Evolution* 50(6):2316–2327
- Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct Ecol* 21:394–407
- Gibson G (2009) Decanalization and the origin of complex disease. *Nat Rev Genet* 10(2):134–140. doi:10.1038/nrg2502
- Gibson G, Dworkin I (2004) Uncovering cryptic genetic variation. *Nat Rev Genet* 5(9):681–690. doi:10.1038/nrg1426
- Halfpeter G, Edmonds WD (1982) The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutionary approach. *Publicaciones Instituto de Ecología Mexico. Instituto de Ecología, Mexico DF*, pp 1–176
- Halfpeter G, Matthews E (1966) The natural history of dung beetles of the subfamily Scarabaeinae. *Folia Entomologica Mexicana* 12–14:1–312
- Halligan DL, Keightley PD (2009) Spontaneous mutation accumulation studies in evolutionary genetics. *Annu Rev Ecol Syst* 40:151–172. doi:10.1146/annurev.ecolsys.39.110707.173437
- Hermisson J, Wagner GP (2004) The population genetic theory of hidden variation and genetic robustness. *Genetics* 168(4):2271–2284. doi:10.1534/genetics.104.029173
- Hodgins-Davis A, Townsend JP (2009) Evolving gene expression: from G to E to GxE. *Trends Ecol Evol* 24(12):649–658
- Hoffmann AA, Merila J (1999) Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol Evol* 14(3):96–101
- Huey RB, Hertz PE, Sinervo B (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am Nat* 161(3):357–366. doi:10.1086/346135
- Hunt J, Simmons LW (2000) Maternal and paternal effects on offspring phenotype in the dung beetle *Onthophagus taurus*. *Evolution* 54(3):936–941

- Hunt J, Simmons LW (2002) The genetics of maternal care: direct and indirect genetic effects on phenotype in the dung beetle *Onthophagus taurus*. Proc Natl Acad Sci USA 99(10):6828–6832. doi:[10.1073/pnas.092676199](https://doi.org/10.1073/pnas.092676199)
- Hunt J, Simmons LW (2004) Optimal maternal investment in the dung beetle *Onthophagus taurus*? Behav Ecol Sociobiol 55(3):302–312. doi:[10.1007/s00265-003-0705-1](https://doi.org/10.1007/s00265-003-0705-1)
- Hunt J, Simmons LW, Kotiaho JS (2002) A cost of maternal care in the dung beetle *Onthophagus taurus*? J Evol Biol 15(1):57–64. doi:[10.1046/j.1420-9101.2002.00374.x](https://doi.org/10.1046/j.1420-9101.2002.00374.x)
- Jasnos L, Tomala K, Paczesniak D, Korona R (2008) Interactions between stressful environment and gene deletions alleviate the expected average loss of fitness in yeast. Genetics 178(4):2105–2111. doi:[10.1534/genetics.107.08453.1](https://doi.org/10.1534/genetics.107.08453.1)
- Kawecki TJ (1994) Accumulation of deleterious mutations and the evolutionary cost of being a generalist. Am Nat 144(5):833–838
- Kishi S, Nishida T (2006) Adjustment of parental investment in the dung beetle *Onthophagus atripennis* (Col., Scarabaeidae). Ethology 112(12):1239–1245. doi:[10.1111/j.1439-2006.01284.x](https://doi.org/10.1111/j.1439-2006.01284.x)
- Kondrashov AS, Crow JF (1993) A molecular approach to estimating the human deleterious mutation rate. Hum Mutat 2(3):229–234
- Kondrashov AS, Houle D (1994) Genotype-environment interactions and the estimation of the genomic mutation rate in *Drosophila melanogaster*. Proc R Soc Lond Series B Biol Sci 258(1353):221–227
- Laland KN, Odling-Smee FJ, Feldman MW (1996) The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. J Evol Biol 9(3):293–316
- Laland KN, Odling-Smee FJ, Feldman MW (1999) Evolutionary consequences of niche construction and their implications for ecology. Proc Natl Acad Sci USA 96(18):10242–10247
- Lande R, Shannon S (1996) The role of genetic variation in adaptation and population persistence in a changing environment. Evolution 50(1):434–437. doi:[10.2307/2410812](https://doi.org/10.2307/2410812)
- Ledon-Rettig CC, Pfennig DW, Crespi EJ (2010) Diet and hormonal manipulation reveal cryptic genetic variation: implications for the evolution of novel feeding strategies. Proc R Soc Lond Series B Biol Sci 277(1700):3569–3578. doi:[10.1098/rspb.2010.0877](https://doi.org/10.1098/rspb.2010.0877)
- Levy SF, Siegal ML (2008) Network hubs buffer environmental variation in *Saccharomyces cerevisiae*. PLoS Biol 6(11):e264. doi:[10.1371/journal.pbio.0060264](https://doi.org/10.1371/journal.pbio.0060264)
- Lock JE, Smiseth PT, Moore PJ, Moore AJ (2007) Coadaptation of prenatal and postnatal maternal effects. Am Nat 170(5):709–718. doi:[10.1086/521963](https://doi.org/10.1086/521963)
- Lynch M (2010) Rate, molecular spectrum, and consequences of human mutation. Proc Natl Acad Sci USA 107(3):961–968. doi:[10.1073/pnas.0912629107](https://doi.org/10.1073/pnas.0912629107)
- Lynch M, Blanchard J, Houle D, Kibota T, Schultz S, Vassilieva L et al (1999) Perspective: spontaneous deleterious mutation. Evolution 53(3):645–663
- Macagno A, Moczek A, Pizzo A (2016) Rapid divergence of nesting depth and digging appendages among tunneling dung beetle populations and species. Am Nat (in press)
- Mank JE, Promislow DEL, Avise JC (2005) Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. Evolution 59(7):1570–1578. doi:[10.1554/04-734](https://doi.org/10.1554/04-734)
- Martin G, Lenormand T (2006) The fitness effect of mutations across environments: a survey in light of fitness landscape models. Evolution 60(12):2413–2427
- Masel J (2006) Cryptic genetic variation is enriched for potential adaptations. Genetics 172(3):1985–1991. doi:[10.1534/genetics.105.051649](https://doi.org/10.1534/genetics.105.051649)
- McGuigan K, Sgro CM (2009) Evolutionary consequences of cryptic genetic variation. Trends Ecol Evol 24(6):305–311. doi:[10.1016/j.tree.2009.02.001](https://doi.org/10.1016/j.tree.2009.02.001)
- Mitchell-Olds T, Schmitt J (2006) Genetic mechanisms and evolutionary significance of natural variation in *Arabidopsis*. Nature 441(7096):947–952. doi:[10.1038/nature04878](https://doi.org/10.1038/nature04878)
- Moczek AP (1998) Horn polyphenism in the beetle *Onthophagus taurus*: larval diet quality and plasticity in parental investment determine adult body size and male horn morphology. Behav Ecol 9(6):636–641
- Moczek AP (1999) Facultative paternal investment in the polyphenic beetle *Onthophagus taurus*: the role of male morphology and social context. Behav Ecol 10(6):641–647
- Muller HJ (1950) Our load of mutations. Am J Hum Genet 2(2):111–176
- Odling-Smee F, Laland K, Feldman M (2003) Niche construction: the neglected process in evolution monographs in population biology 37. Princeton University Press, Princeton
- Pajni HR, Virk N (1978) Irradiation induced sterility in males and females of *Tribolium castaneum* Herbst (Tenebrionidae: Coleoptera). Curr Sci 47(5):175
- Rajon E, Masel J (2011) Evolution of molecular error rates and the consequences for evolvability. Proc Natl Acad Sci USA 108(3):1082–1087. doi:[10.1073/pnas.1012918108](https://doi.org/10.1073/pnas.1012918108)
- Renwick JAA, Chew FS (1994) Oviposition behavior in Lepidoptera. Annu Rev Entomol 39:377–400

- Reynolds JD, Goodwin NB, Freckleton RP (2002) Evolutionary transitions in parental care and live bearing in vertebrates. *Philos Trans R Soc B Biol Sci* 357(1419):269–281. doi:[10.1098/rstb.2001.0930](https://doi.org/10.1098/rstb.2001.0930)
- Royle N, Smiseth P, Kolliker M (2012) The evolution of parental care. Oxford University Press, New York
- Rutherford SL (2000) From genotype to phenotype: buffering mechanisms and the storage of genetic information. *BioEssays* 22:1095–1105
- Rutherford SL, Lindquist S (1998) Hsp90 as a capacitor for morphological evolution. *Nature* 396(6709):336–342
- Saltz JB, Foley BR (2011) Natural genetic variation in social niche construction: social effects of aggression drive disruptive sexual selection in *Drosophila melanogaster*. *Am Nat* 177(5):645–654. doi:[10.1086/659631](https://doi.org/10.1086/659631)
- Saltz JB, Nuzhdin SV (2014) Genetic variation in niche construction: implications for development and evolutionary genetics. *Trends Ecol Evol* 29(1):8–14. doi:[10.1016/j.tree.2013.09.011](https://doi.org/10.1016/j.tree.2013.09.011)
- Schlichting CD (2008) Hidden reaction norms, cryptic genetic variation, and evolvability. In *Year in evolutionary biology 2008* (Vol. 1133, pp 187–203, *Annals of the New York Academy of Sciences*). Oxford: Blackwell Publishing
- Scott MP (1998) The ecology and behavior of burying beetles. *Annu Rev Entomol* 43:595–618
- Scott MP, Traniello JFA (1990) Behavioral and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp). *Anim Behav* 39:274–283
- Shabalina SA, Yampolsky LY, Kondrashov AS (1997) Rapid decline of fitness in panmictic populations of *Drosophila melanogaster* maintained under relaxed natural selection. *Proc Natl Acad Sci USA* 94(24):13034–13039
- Silver R, Andrews H, Ball GF (1985) Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *Am Zool* 25(3):823–840
- Smiseth P (2014) Parental Care. In: Shuker D, Simmons L (eds) *The evolution of insect mating systems*. Oxford University Press, Oxford, pp 221–241
- Smiseth PT, Moore AJ (2007) Signalling of hunger by senior and junior larvae in asynchronous broods of a burying beetle. *Anim Behav* 74:699–705. doi:[10.1016/j.anbehav.2006.09.022](https://doi.org/10.1016/j.anbehav.2006.09.022)
- Smiseth PT, Moore AJ (2008) Parental distribution of resources in relation to larval hunger and size rank in the burying beetle *Nicrophorus vespilloides*. *Ethology* 114(8):789–796. doi:[10.1111/j.1439-0310.2008.01516.x](https://doi.org/10.1111/j.1439-0310.2008.01516.x)
- Snell-Rood E, JD Van Dyken, Cruickshank T, Wade M, Moczek A (2010) Toward a population genetic framework of developmental evolution: costs, limits, and consequences of phenotypic plasticity. *BioEssays*, 32, 71–81
- Snell-Rood E, Moczek A (2013) Horns and the role of development in the evolution of beetle contests. In: Hardy I, Briffa M (eds) *Animal contests*. Cambridge University Press, Cambridge, pp 178–198
- Standen EM, Du TY, Larsson HCE (2014) Developmental plasticity and the origin of tetrapods. *Nature* 513(7516):54. doi:[10.1038/nature13708](https://doi.org/10.1038/nature13708)
- Szafraniec K, Borts RH, Korona R (2001) Environmental stress and mutational load in diploid strains of the yeast *Saccharomyces cerevisiae*. *Proc Natl Acad Sci USA* 98(3):1107–1112
- Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. *Annu Rev Entomol* 36:65–89
- Trumbo S (2012) Patterns of parental care in invertebrates. In: Royle N, Smiseth P, Kolliker M (eds) *The evolution of parental care*. Oxford University Press, Oxford, pp 81–100
- Tunçbilek AS, Kansu IA (1996) The influence of rearing medium on the irradiation sensitivity of eggs and larvae of the flour beetle, *Tribolium confusum* J. du Val. *J Stored Prod Res* 32(1):1–6. doi:[10.1016/0022-474x\(95\)00039-a](https://doi.org/10.1016/0022-474x(95)00039-a)
- Van Dyken JD, Wade MJ (2010) The genetic signature of conditional expression. [Research Support, N.I.H., Extramural; Research Support, Non-U.S. Gov't]. *Genetics* 184(2):557–570
- Vassilieva LL, Hook AM, Lynch M (2000) The fitness effects of spontaneous mutations in *Caenorhabditis elegans*. *Evolution* 54(4):1234–1246
- Wade MJ (1998) The evolutionary genetics of maternal effects. In: Mousseau TA, Fox CW (eds) *Maternal effects as adaptations*. Oxford University Press, New York, pp 5–21
- Wheeler D (1996) The role of nourishment in oogenesis. *Annu Rev Entomol* 41:407–431. doi:[10.1146/annurev.ento.41.1.407](https://doi.org/10.1146/annurev.ento.41.1.407)
- Whitlock MC (1996) The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *Am Nat* 148:S65–S77
- Williams GC, Nesse RM (1991) The dawn of Darwinian medicine. *Q Rev Biol* 66(1):1–22
- Wong JWY, Meunier J, Kolliker M (2013) The evolution of parental care in insects: the roles of ecology, life history and the social environment. *Ecol Entomol* 38(2):123–137. doi:[10.1111/een.12000](https://doi.org/10.1111/een.12000)