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Effects of mothers' and fathers' experience with predation risk on the behavioral development of their offspring in threespined sticklebacks

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Stressors experienced by parents can influence the behavioral development of their offspring. Here, we review recent studies in threespined sticklebacks (a species in which males are the sole providers of parental care) showing that when parents are exposed to an ecologically relevant stressor (predation risk), there are consequences for offspring. For example, female sticklebacks exposed to predation risk produce eggs with higher concentrations of cortisol, a stress hormone, and offspring with altered behavior and physiology. Male sticklebacks exposed to predation risk produce offspring that are less active, smaller, and in poorer condition. The precise mechanisms by which maternal and paternal experiences with predators affect offspring phenotypes are under investigation, and could include steroid hormones, olfactory cues and/or parental behavior. As in other species, some of the consequences of parental exposure to predation risk for offspring in sticklebacks might be adaptive, but depend on the stressor, the reliability of the parental and offspring environments and the evolutionary history of the population.

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Introduction

There is growing evidence that parents' experiences can influence the next generation. For example, female crickets exposed to cues of predatory spiders produced offspring with heightened antipredator behavior that were more likely to survive encounters with predators [1]. Indeed, offspring of stressed parents differ from offspring of unstressed parents in many respects, including morphology [2], physiology [3], and behavior [1,4]. Because paternal care is relatively rare among taxa, and because mothers often have intimate contact with their developing embryos and offspring, most studies to date have focused on the consequences of maternal stress for offspring. However, there is growing appreciation that stressors experienced by fathers can also affect the next generation [5–7]. For example, stressors experienced by fathers before mating influence offspring via effects on seminal fluid [8] and sperm [7,9•]. There is also evidence that stressors experienced by fathers *post*-fertilization can affect offspring — the mechanisms underlying post-fertilization paternal effects are less understood, but could be mediated indirectly through changes in maternal care [10] or could reflect direct effects of fathers on offspring via, for example, changes in paternal provisioning behavior.

Recent work in our lab has investigated the effects of maternal and paternal stress on offspring phenotypes in threespined sticklebacks (*Gasterosteus aculeatus*). Sticklebacks are a small fish distributed throughout the northern hemisphere that are renowned for their geographic variation in behavior [11]. For example, sticklebacks from populations that are subject to strong predation have morphological, behavioral and physiological adaptations for coping with predators [12]. Another important feature of the stickleback system is that like many other fish species, sticklebacks exhibit paternal care, where the father is solely responsible for providing care that is necessary for offspring survival. In this paper, we summarize the effects of maternal and paternal exposure to predation risk on offspring in sticklebacks, discuss their potential adaptive significance and mechanisms, and outline several key areas for future work. While we focus on sticklebacks, it is worth pointing out that many of our findings are similar to studies on mammals and other taxa, which suggests that the way parental stress can affect offspring extends across systems that differ dramatically in parental investment (placentas versus eggs, maternal versus paternal care, etc.).

Effects of maternal stress on offspring outcomes in sticklebacks

In a wide range of organisms, mothers that experience predation risk improve the antipredator defenses of their offspring [1–4]. These studies suggest that when females can detect reliable environmental cues of predation risk, natural selection favors adaptive maternal 'programming' of offspring behavior to match the anticipated environment [13]. However, a large literature in diverse vertebrate species has shown that maternal stress can have deleterious consequences for offspring, often mediated by glucocorticoid stress hormones (reviewed in [14–16]). We hypothesize that adaptive maternal effects are more likely to be observed when natural selection has had an opportunity to produce them, therefore we are more likely to detect adaptive maternal effects in response to an ecologically relevant stressor as opposed to a stressor that animals in natural populations are unlikely to encounter.

We examined the consequences of maternal exposure to predation risk in a series of studies in sticklebacks. The experimental protocol involves exposing female sticklebacks to predation risk during the time when they are yolking eggs (pre-fertilization), and comparing their offspring to offspring of females that were not exposed to predation risk (control females). Females are chased by a model of a predator at an unpredictable time of day once a day for 30–40 seconds per day. This regime is meant to simulate experience in a high-predation locality.

Being chased by predators alters the composition of a female's eggs, and thus, the future developmental environment her offspring experience. Eggs of females exposed to predation risk are larger and have higher cortisol content than the eggs of control females [17], and an RNASeq study showed that maternal predator exposure influences the expression of hundreds of genes in embryos, including noncoding RNAs, genes involved in epigenetic modifications and genes involved in neural growth [18]. Moreover, there are long-lasting consequences of maternal stress for stickleback offspring. For example, maternal predator exposure influences the development of the offspring stress axis [19]. In addition, having a predator-exposed mother affects how offspring react to a predator later in life. Offspring of predator-exposed mothers are less likely to orient to a live predatory Northern pike (*Esox luscius*) than offspring of unexposed mothers [20]. This seemingly slight behavioral difference has serious survival consequences: offspring of predator-exposed mothers are captured more quickly by the predator compared to offspring of unexposed mothers [21]. Additionally, offspring of predator-exposed mothers show deficits in their ability to learn a color-reward association compared to offspring of unexposed mothers [21]. However, some of these learning deficits might be overcome by the increased tendency of offspring of predator-exposed mothers to use social information from shoalmates [22] and shoal more closely with one another than offspring of control mothers [17].

We originally hypothesized that the effects of maternal stress on offspring were mediated by glucocorticoids, specifically cortisol. Glucocorticoids have been implicated with the maladaptive consequences of maternal stress for offspring in many taxa [14–16,23]. Consistent with this literature, female sticklebacks mount a cortisol response to predation risk [24] and this results in eggs with a higher cortisol content [25]. However, subsequent studies found that egg cortisol content drops quickly after fertilization (within 72 h [25]), and experimental application of exogenous cortisol to developing eggs fails to affect offspring development (Paitz *et al.*, in preparation). These results suggest that predator-induced maternal effects on offspring in sticklebacks are not directly caused by cortisol, a result consistent with the emerging literature in other organisms showing that the mechanisms underlying the effects of maternal stress on offspring are complex and often include more than just the HPA axis [23].

Effects of paternal stress on offspring outcomes in sticklebacks

While maternal effects are well-documented in a diverse array of species (reviewed in [14–16]), paternal effects are less studied, even though it has been suggested that paternal effects may be similar in magnitude to maternal effects [26•]. The stickleback system provides an excellent opportunity to examine post-fertilization paternal effects, as fathers are the sole providers of parental care that is necessary for offspring survival, and early studies suggested that paternal behavior shapes offspring behavior in this species [27]. During the breeding season, males defend their breeding territory from intruders and predators and attract females to spawn in their nests. After spawning, the female leaves the male's territory and the male is solely responsible for the care of the eggs. During the ~6-day incubation period, the male 'fans' (oxygenates) the eggs, removes rotten eggs and debris, and defends the territory. After embryos hatch, father sticklebacks continue to tend their newly hatched offspring for ~7 days, chasing and retrieving fry that stray from the nest and spitting them back into the nest.

Stickleback nests are highly susceptible to predation, and fathers are constantly vigilant toward intruders. We hypothesized that fathers adjust their behavior in response to predation risk, and that such adjustments might have consequences for offspring. To test this hypothesis, male sticklebacks were either briefly exposed to predation risk by a model of a common nest predator (sculpin, *Cottus asper*) or were unexposed to predation risk while they were caring for embryos in their nest. Males were presented with a model sculpin for three minutes on the day after fertilization. This treatment was designed to simulate the types of conditions males in high-predation environments might encounter — brief but dangerous encounters with local predators that regularly predate nests. Adult offspring of predator-exposed fathers were smaller, in poorer condition and less active than offspring of unexposed fathers [28•]. Interestingly, sticklebacks that were reared with predation risk [29], or have evolved with predation risk [12], also have these characteristics. These data are consistent with the hypothesis that fathers alter their paternal behavior in response to predation risk, and that fathers can 'program' their offspring for living in a high-predation environment. These findings are important because while we know that the care provided by mothers early in life can have a long-lasting influence on offspring [30], these are some of the first data to suggest that fathers can do the same. While recent studies are documenting the important consequences of paternal stress before conception on offspring brain development [31] and HPA axis regulation [32,33] potentially via changes in DNA methylation in sperm [34], these are some of the first data to show that fathers, like mothers, can influence their offspring *post-fertilization*. Furthermore, we have found that father care alters expression of a gene responsible for de novo methylation (DNMT3a) in offspring brains [35•], suggesting that paternal care might have long-lasting effects on offspring behavior via DNA methylation.

Conclusions and future directions

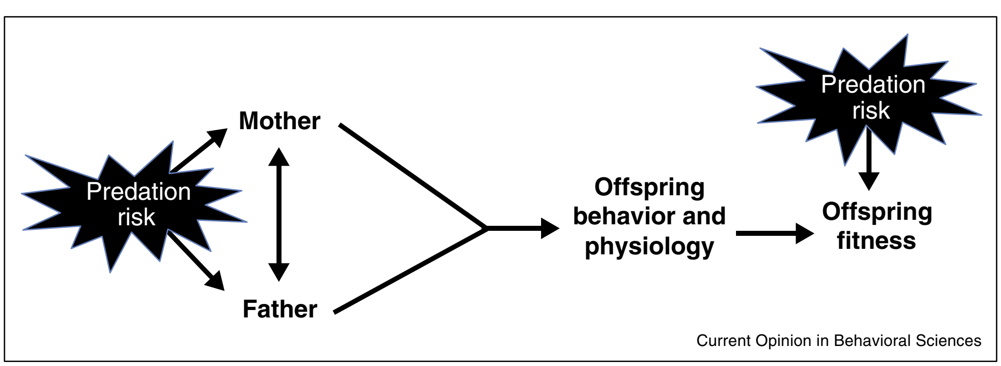
Are there interactions between maternal and paternal effects?

Maternal and paternal effects on offspring are often studied in isolation of each other, even though it is likely that they frequently co-occur and interact with one another [36•]. For example, in sticklebacks, the previous predator experiences of a mother affects the amount of paternal care males provide to her offspring, with fathers providing less care, both pre-hatching and post-hatching, to offspring of predator-exposed mothers [37]. Such examples of differential allocation are common [5,6]. For example, a parent might compensate or differentially allocate care based on the behavior of its partner. Teasing apart the influence of fathers from the influence of mothers can be challenging, but can be facilitated by studying a diverse array of species that exhibit different forms of parental care (exclusive maternal care, exclusive paternal care or biparental care). For example, in species such as sticklebacks with exclusive paternal care, we can ask if attentive paternal care can compensate for the effects of maternal stress on offspring. Moreover, it is likely that both mothers and fathers in natural populations experience stressors such as predation risk, therefore examining the consequences for offspring of simultaneously exposing both mothers and fathers to stressors will move us toward a more complete understanding of the role parental effects play in nature (Figure 1).

Are predator-induced parental effects adaptive?

Determining whether parental effects are adaptive can be challenging. A recent meta-analysis by Uller and colleagues [38•] argued that the most convincing test involves comparing the fitness of parental effects in two environments: one where offspring fitness is measured in the type of environment that resembles their parent ('matched'), the other where offspring fitness is measured in an environment different from their parents' ('mismatched'). Strong evidence for an adaptive parental effect would occur if offspring fitness (survival and reproductive success) is highest in the 'matched' environment [13,38•]. Other considerations when examining the adaptive significance of predator-induced parental effects are the reliability of the environment within and across generations [13,38•,39] and the evolutionary history of the population [27,40•]. For example, if the environment is so variable that the likelihood that the parental and offspring environments will match is low, then selection should not favor parental effects. Instead, selection might favor adaptive parental effects if offspring are likely to encounter the same environment as their parents. However, if the environment is highly predictable across generations, we may instead predict selection to favor genetic adaptation over parental effects. In this way, genetic adaptation may allow offspring to be 'buffered' from the noise experienced by their parents.

Figure 1



Model conceptualizing the direct and indirect effects of predation risk to mothers and fathers on offspring.

Can parental effects facilitate evolution?

If parental effects can be adaptive, that opens the possibility that they might evolve and even facilitate adaptation [41,42•]. Parental effects might play an important role in adaptive radiations, if, for example, parents can prepare their offspring for the type of environment they are likely to encounter as populations move into new habitats or niches. Such transgenerational plasticity could allow an initial colonizing population to persist in a novel environment, and allow it to persist until genetic adaptation can occur [43–45]. Determining whether predator-induced parental effects might allow populations to cope with novel predator regimes would help us understand how particular species might become successful invaders or cope with changing environmental conditions.

Conflict of interest statement

Nothing declared.

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References

1. Storm JJ, Lima SL: **Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior**. *Am Nat* 2010, **175**:382-390.

2. Agrawal AA, Laforsch C, Tollrian R: **Transgenerational induction of defences in animals and plants**. *Nature* 1999, **401**:60-63.

3. Sheriff MJ, Krebs CJ, Boonstra R: **The ghosts of predators past: population cycles and the role of maternal programming under fluctuating predation risk**. *Ecology* 2010, **91**:2983-2994.

4. Bestion E, Teyssier A, Aubret F, Clobert J, Cote J: **Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal**. *Proc R Soc B Biol Sci* 2014:281.

5. Braun K, Champagne FA: **Paternal influences on offspring development: behavioural and epigenetic pathways**. *J Neuroendocrinol* 2014, **26**:697-706.

6. Curley JP, Mashoodh R, Champagne FA: **Epigenetics and the origins of paternal effects**. *Horm Behav* 2011, **59**:306-314.

7. Dias BG, Ressier KJ: **Parental olfactory experience influences behavior and neural structure in subsequent generations**. *Nat Neurosci* 2014, **17**:89-96.

8. Sirot LK, Lapointe SL, Shatters R, Bausher M: **Transfer and fate of seminal fluid molecules in the beetle, *Diaprepes abbreviatus*: implications for the reproductive biology of a pest species**. *J Insect Physiol* 2006, **52**:300-308.

9. • Crean AJ, Dwyer JM, Marshall DJ: **Adaptive paternal effects? Experimental evidence that the paternal environment affects offspring performance**. *Ecology* 2013, **94**:2575-2582.
One of the first examples of an adaptive paternal effect; effects mediated by sperm.

10. Mashoodh R, Franks B, Curley JP, Champagne FA: **Paternal social enrichment effects on maternal behavior and offspring growth**. *Proc Natl Acad Sci U S A* 2012, **109(Suppl. 2)**:17232-17238.

11. Bell MA, Foster SA: *The Evolutionary Biology of the Threespine Stickleback*. Oxford: Oxford University Press; 1994.

12. Reimchen TE: **Predators and morphological evolution in threespine stickleback**. In *The Evolutionary Biology of the Threespine Stickleback*. Edited by Bell MA. Foster, SA: Oxford; 1994:240-273.

13. Marshall DJ, Uller T: **When is a maternal effect adaptive?** *Oikos* 2007, **116**:1957-1963.

14. Weinstock M: **The long-term behavioural consequences of prenatal stress**. *Neurosci Biobehav Rev* 2008, **32**:1073-1080.

15. Maccari S, Krugers HJ, Morley-Fletcher S, Szyf M, Brunton PJ: **The consequences of early-life adversity: neurobiological, behavioural and epigenetic adaptations**. *J Neuroendocrinol* 2014, **26**:707-723.

16. Schoech SJ, Rensel MA, Heiss RS: **Short and long-term effects of developmental corticosterone exposure on avian physiology, behavioral phenotype, cognition, and fitness: review**. *Curr Zool* 2011, **57**:514e530.

17. Giesing E, Suski C, Warner R, Bell A: **Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring**. *Proc R Soc B Biol Sci* 2011, **278**:1753-1759.

18. Mommer BC, Bell AM: **Maternal experience with predation risk influences genome-wide embryonic gene expression in threespined sticklebacks (*Gasterosteus aculeatus*)**. *PLOS ONE* 2014:9.

19. Mommer BC, Bell AM: **A test of maternal programming of offspring stress response to predation risk in threespine sticklebacks**. *Physiol Behav* 2013, **122**:222-227.

20. McGhee KE, Pintor L, Suhr E, Bell AM: **Maternal exposure to predation risk decreases offspring antipredator behaviour and survival in threespined stickleback**. *Funct Ecol* 2012, **26**:932-940.

21. Roche D, McGhee K, Bell AM: **Maternal predator-exposure has lifelong consequences for offspring learning in sticklebacks**. *Biol Lett* 2012, **6**:932-935.

22. Feng S, McGhee KAMB: **Effect of maternal predator exposure on the ability of stickleback offspring to generalize a learned colour-reward association**. *Anim Behav* 2015, **107**:61-69.

23. Beijers R, Buitelaar JK, de Weerth C: **Mechanisms underlying the effects of prenatal psychosocial stress on child outcomes: beyond the HPA axis**. *Eur Child Adolesc Psychiatry* 2014, **23**:943-956.

24. Bell AM, Backstrom T, Huntingford FA, Pottinger TG, Winberg S: **Variable neuroendocrine responses to ecologically-relevant challenges in sticklebacks**. *Physiol Behav* 2007, **91**:15-25.

25. Paitz RT, Mommer BC, Suhr E, Bell AM: **Changes in the concentrations of four maternal steroids during embryonic development in the threespined stickleback**. *J Exp Zool A* 2015, **323**:422-429.

26. • Head ML, Berry LK, Royle NJ, Moore AJ: **Paternal care: direct and indirect genetic effects of fathers on offspring performance**. *Evolution* 2012, **66**:3570-3581.
Evaluates direct and indirect genetic effects of fathers on offspring performance, and suggests that maternal and paternal effects might be of similar magnitude.

27. Tulley JJ, Huntingford FA: **Paternal care and the development of adaptive variation in anti-predator responses in sticklebacks**. *Anim Behav* 1987, **35**:1570-1572.

28. • Stein LR, Bell AM: **Paternal programming in sticklebacks**. *Anim Behav* 2014, **95**:165-171.
Exposing fathers to predation risk while providing care caused them to produce offspring with phenotypes associated with high predation risk.

29. Bell AM, Dingemanse NJ, Hankison SJ, Langenhof MBW, Rollins K: **Early exposure to nonlethal predation risk by size-selective predators increases somatic growth and decreases size at adulthood in threespined sticklebacks**. *J Evol Biol* 2011, **24**:943-953.

30. Weaver ICG, Cervoni N, Champagne FA, D'Alessio AC, Sharma S, Seckl JR, Dymov S, Szyf M, Meaney MJ: **Epigenetic programming by maternal behavior**. *Nat Neurosci* 2004, **7**:847-854.

31. Harker A, Raza S, Williamson K, Kolb B, Gibb R: **Preconception paternal stress in rats alters dendritic morphology and**

connectivity in the brain of developing male and female offspring. *Neuroscience* 2015, **303**:200-210.

32. Yehuda R: **Are different biological mechanisms involved in the transmission of maternal versus paternal stress-induced vulnerability to offspring?** *Biol Psychiatry* 2011, **70**:402-403.

33. Rodgers AB, Morgan CP, Bronson SL, Revello S, Bale TL: **Paternal stress exposure alters sperm microRNA content and reprograms offspring HPA stress axis regulation**. *J Neurosci* 2013, **33**:9003-9012.

34. Mychasiuk R, Harker A, Ilnytskyy S, Gibb R: **Paternal stress prior to conception alters DNA methylation and behaviour of developing rat offspring**. *Neuroscience* 2013, **241**:100-105.

35. • McGhee KE, Bell AM: **Paternal care in a fish: epigenetics and fitness enhancing effects on offspring anxiety**. *Proc R Soc B Biol Sci* 2014:281.
Paternal care influences offspring behavioral development, possibly via changes in DNA methylation.

36. • Crean AJ, Bonduriansky R: **What is a paternal effect?** *Trends Ecol Evol* 2014, **29**:554-559.
Articulates experimental designs for teasing apart maternal and paternal effects and the different evolutionary implications of maternal and paternal effects.

37. McGhee KE, Feng S, Leasure S, Bell AM: **A female's past experience with predators affects male courtship and the care her offspring will receive from their father**. *Proc R Soc B Biol Sci*, in press.

38. • Uller T, Nakagawa S, English S: **Weak evidence for anticipatory parental effects in plants and animals**. *J Evol Biol* 2013, **26**:2161-2170.
Meta-analysis showing that evidence for adaptive parental programming is weak.

39. English S, Pen I, Shea N, Uller T: **The information value of non-genetic inheritance in plants and animals**. *PLOS ONE* 2015, **10**:e0116996.

40. • Stamps JA, Krishnan VV: **Combining information from ancestors and personal experiences to predict individual differences in developmental trajectories**. *Am Nat* 2014, **184**:647-657.
Uses a Bayesian model to show when we should expect offspring to ignore or pay attention to information provided by their parents.

41. Kirkpatrick M, Lande R: **The evolution of maternal characters**. *Evolution* 1989, **43**:485-503.

42. • Duckworth RA, Belloni V, Anderson SR: **Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird**. *Science* 2015, **347**:875-877.
Strong consequences of maternal effects for population dynamics in the wild.

43. West-Eberhard MJ: *Developmental Plasticity and Evolution*. Oxford: Oxford University Press; 2003.

44. Ghalambor CK, McKay JK, Carroll S, Reznick DN: **Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation to new environments**. *Funct Ecol* 2007, **21**:394-407.

45. Badyaev AV, Uller T: **Parental effects in ecology and evolution: mechanisms, processes and implications**. *Philos Trans R Soc Lond B Biol Sci* 2009, **364**:1169-1177.