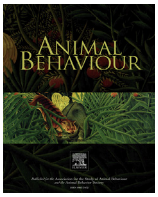
Animal Behaviour 104 (2015) 115–122

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Egg cortisol treatment affects the behavioural response of coho salmon to a conspecific intruder and threat of predation

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ARTICLE INFO

Article history:
Received 23 October 2014
Initial acceptance 8 December 2014
Final acceptance 18 February 2015
Available online 11 April 2015
MS. number: A14-00858R

Keywords:
activity
aggression
antipredator
fish
foraging
glucocorticoid
personality

Knowledge continues to emerge on how maternally derived egg hormones influence progeny behaviour in oviparous taxa. Of particular interest is how glucocorticoids (GCs) in eggs, as a signal of maternal stress, affect offspring behavioural traits. To date, research has focused on effects of egg GCs on offspring behaviours within a single experimental context. Little is known regarding how egg GCs affect relationships among behaviours and across ecological contexts (i.e. behavioural syndromes). We explored how exogenously increased egg cortisol shapes behavioural syndromes of juvenile coho salmon, *Oncorhynchus kisutch*. Social dominance during a territory intrusion and boldness following a simulated predator attack were recorded for juvenile coho salmon reared from cortisol-treated and untreated eggs. When exposed to a conspecific intruder, coho salmon treated with cortisol in ovo increased dominance behaviours, whereas coho salmon reared from untreated eggs reduced these behaviours. Following exposure to a simulated predator attack, coho salmon reared from cortisol-treated eggs increased boldness (i.e. increased activity and feeding; reduced shelter use), whereas coho salmon reared from untreated eggs reduced boldness. A dominance–boldness relationship was observed for coho salmon reared from cortisol-treated, but not untreated, eggs; dominance during the territory intrusion positively correlated with boldness under threat of predation. Our results highlight the complex influence of egg GCs on offspring behaviour and behavioural syndromes. Continued investigation into the outcomes of egg GCs on offspring will broaden our understanding of intergenerational components of the hormone–behaviour nexus.

How elevated egg hormone levels modify progeny, and whether these effects are adaptive, is an emerging topic of interest in behavioural and evolutionary ecology (reviewed in Dufty et al., 2002; Meylan, Miles, & Clobert, 2012). Among oviparous taxa, maternal hormones are thought to be passively absorbed into developing eggs (birds, Groothuis, Müller, von Engelhardt, Carere, & Eising, 2005; reptiles, Radder, 2007; fishes, Mommer, 2013; but see Groothuis & Schwabl, 2008; Moore & Johnston, 2008 for discussion on maternal and embryonic control of yolk hormone deposition). Maternal stressor exposure can elevate concentrations of stress hormones, or glucocorticoids (GCs), in eggs (McCormick, 2006; Saino, Romano, Ferrari, Martinelli, & Møller, 2005). Exogenous elevation of egg GCs is used to mimic predicted outcomes of maternal stress. When egg GCs are experimentally elevated, behavioural effects on offspring can be profound, and also variable. Yellow-legged gulls, *Larus michahellis*, reared from GC-treated eggs did not beg as loudly or as frequently (Rubolini et al., 2005). In another species, European starlings, *Sturnus vulgaris*, chicks reared from GC-treated eggs begged at a higher intensity (Love & Williams, 2008). Running speeds of lizards (*Amphibolurus muricatus* and *Bassiana duperreyi*) were not affected by manipulation of egg GCs (Warner, Radder, & Shine, 2009). In brown trout, *Salmo trutta*, exogenously elevating egg GC concentration can increase juvenile aggression toward a mirror image (Sloman, 2010) and decrease aggression toward a conspecific (Burton, Hoogenboom,

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http://dx.doi.org/10.1016/j.anbehav.2015.03.011

Armstrong, Groothuis, & Metcalfe, 2011). Although much is gleaned from studies to date that exogenously elevate egg GCs and quantify behavioural effects in a single environmental context, it is unclear how fluctuations in maternally derived egg GCs may be influencing correlations between behaviours displayed under different ecological contexts (i.e. behavioural syndromes sensu Sih & Bell, 2008; Sih, Bell, & Johnson, 2004).

There is now an intensifying interest in the proximate mechanisms underlying behavioural syndromes (Bell & Aubin-Horth, 2010; Careau & Garland, 2012; Coppens, de Boer, & Koolhaas, 2010). Of particular interest is how the production and regulation of GCs contribute to behavioural syndromes, given that hormones can modulate ‘suites of correlated traits’ (McGlothlin & Ketterson, 2008). In fishes, for example, endogenous GC synthesis in response to a stressor has an instrumental role in predicting an array of correlated behavioural traits (e.g. competitive ability, foraging, locomotion; reviewed in Øverli et al., 2007). Rainbow trout, *Oncorhynchus mykiss*, with an attenuated plasma GC stress response tended to be more dominant displaying increased aggression, activity levels and feeding (Pottinger & Carrick, 2001). Similar relationships between stressor-induced plasma GCs and correlated behaviours are also observed in birds (reviewed in Cockrem, 2007). Great tits, *Parus major*, with lower GC responses to stressors explored a novel environment more quickly and were more aggressive toward an intruder (Cockrem, 2007). Do maternally inherited GCs have a role in programming behavioural syndromes as well? Examination of how maternally derived egg GCs influence behavioural syndromes in progeny would complement the advances in our understanding of how circulating, stressor-induced GCs predict behavioural coupling.

In fishes, behavioural traits incorporated into behavioural syndromes commonly include dominance over conspecifics and boldness under threat of predation (reviewed in Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011). Social dominance and boldness are commonly reported to be positively correlated within individuals (Aubin-Horth, Deschênes, & Cloutier, 2012; Bell, 2005; Bell & Sih, 2007; Dingemanse et al., 2007; Huntingford, 1976). In three-spined sticklebacks, *Gasterosteus aculeatus*, the dominance–boldness syndrome is evident in high- but not low-predation populations (Dingemanse et al., 2007). Furthermore, within a generation, this behavioural syndrome manifests following exposure to a predator (Bell & Sih, 2007). Ecological stressors can thus select for the coupling of behaviours if adaptive under particular environmental conditions (Dall, Houston, & McNamara, 2004). Between generations, elevated egg GCs, as a maternal signal of a challenging environment, could be another potential driver of the dominance–boldness syndrome. Social dominance in brown trout (Burton et al., 2011; Sloman, 2010) and predator avoidance in three-spined sticklebacks (McGhee, Pintor, Suhr, & Bell, 2012) appear to be influenced by egg GC levels, which can be elevated following maternal exposure to a stressor (McCormick, 2006; Stratholt, Donaldson, & Liley, 1997). However, how inherent hormonal properties of eggs shape coupling of these behaviours within individuals remains largely unknown. We experimentally increased the concentration of cortisol (the primary GC in fishes) in coho salmon, *Oncorhynchus kisutch*, eggs, mimicking the predicted outcomes of maternal stressor exposure. We examined how elevated egg cortisol influenced social dominance in response to a conspecific intruder, boldness under threat of predation, and the relationship between interindividual differences in dominance and boldness (i.e. presence or absence of a behavioural syndrome).

The early life history of coho salmon provides an ideal opportunity to investigate how egg hormones affect the occurrence of behavioural syndromes. Following emergence from spawning ground gravel, juvenile coho salmon inhabit freshwater streams for 1–2 years before migrating out to the ocean as smolts (Sandercock, 1991). During this rearing period the threat of predation by avian (e.g. great blue heron, *Ardea herodias*) and piscivorous predators is significant (Clements, Stahl, & Schreck, 2012; Sandercock, 1991). While evading predators, juvenile coho salmon must acquire sufficient resources to fuel growth necessary for successful downstream migration to sea. In contrast to other juvenile Pacific salmon (e.g. sockeye salmon, *Oncorhynchus nerka*, chum salmon, *Oncorhynchus keta*, pink salmon, *Oncorhynchus gorbuscha*), juvenile coho salmon do not readily school, are more aggressive toward conspecifics and defend feeding territories in streams (Dill, Ydenberg, & Fraser, 1981; Hutchison & Iwata, 1997). The two ecological scenarios (i.e. predator evasion and territory defence) theoretically require an individual to be behaviourally plastic; increased activity and feeding can assert dominance in a competitive interaction (Abbott & Dill, 1985), but such behaviours would increase predation risk in the presence of a predator (reviewed in Lima & Dill, 1990). Increased shelter occupancy is suitable for both competitive (Faria, Almada, & do Carmo Dunes, 1998) and predatory (Lima & Dill, 1990) scenarios. Behavioural syndromes can thus constrain this behavioural plasticity if dominance and boldness are coupled within an individual (Sih et al., 2004). However, behavioural syndromes can emerge if the coupled behaviours confer a fitness advantage in a particular environment (Dall et al., 2004).

We predicted that coho salmon reared from cortisol-treated eggs would (1) be less socially dominant (reduced activity, feeding, shelter occupancy and aggression) when interacting with a conspecific intruder (Burton et al., 2011) and (2) act in a bold or risk-taking manner following a simulated predator attack (increased activity and feeding, reduced shelter occupancy; McGhee et al., 2012). Elevations in egg cortisol as a signal of a challenging maternal environment (e.g. high predation pressure) could be a selective factor for behavioural syndromes (Bell, 2005; Bell & Sih, 2007; Dingemanse et al., 2007). We predicted that correlational strength between dominance and boldness would be greater in coho salmon reared from cortisol-treated eggs.

METHODS

Egg Exposure and Offspring Rearing

Sperm and eggs were taken from 15 ripe male and 15 ripe female coho salmon that had migrated to the Fisheries and Oceans Canada (DFO) Chilliwack River Hatchery in Chilliwack, British Columbia, Canada. Sperm and eggs were then transported to the University of British Columbia (UBC) within ~2 h. In duplicate, 15 g of eggs from each female were fertilized with sperm from a male to create full-sibling crosses (i.e. each female was paired once with a male). Facility water (30 ml) was added to the sperm–egg mixture to activate sperm motility. Four hundred millilitres of water dosed with 1000 ng/ml cortisol (H4001; Sigma) dissolved in 95% ethanol (0.002% final concentration) was then added to one replicate and 400 ml of control water (0 ng/ml cortisol) was added to the other replicate with the same concentration of ethanol as cortisol-treated eggs. The concentration of cortisol was chosen based on plasma concentrations detected in mature female Pacific salmon (Hruska et al., 2010), and has been used previously to exogenously elevate salmonid egg GCs (Auperin & Geslin, 2008). Using enzyme immunoassay (EIA; see Sopinka, Hinch, Middleton, Hills, & Patterson, 2014 for protocols), egg cortisol concentrations 2 and 24 h post-fertilization were determined for each full-sibling cross and each hormone treatment (untreated, 0 ng/ml; cortisol-treated, 1000 ng/ml). Intra- and interplate variability was 5.3% and 8.6%, respectively. Egg cortisol concentrations were significantly higher after 2 h