



Plasticity in extended phenotype increases offspring defence despite individual variation in web structure and behaviour

Nicholas DiRienzo ^{a, b, *}, Hitoshi Aonuma ^{b, c}

^a Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, U.S.A.

^b Research Institute for Electronic Science, Hokkaido University, Sapporo, Hokkaido, Japan

^c CREST, Japan Science and Technology Agency, Tokyo, Japan

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Many animals actively defend their offspring using a range of behaviours from calling and mobbing in birds, to physical grappling in crustaceans, and the expression of these behaviours positively scale with offspring value. While this role of behaviour in defence is well studied, very little is known about how other traits, specifically the structure of architectural constructions such as webs and nests, contribute to offspring defence. Additionally, although some taxa show consistent individual differences in offspring defence behaviour, it is completely unknown whether individuals also differ in defensive structures. We addressed these questions in the redback spider, *Latrodectus hasselti*, by measuring how a female laying an eggcase influences female behaviour and web structure, and whether those traits scale with relative reproductive investment. Our results show that females modified web structure in response to an eggcase, but only the protective elements of web structure positively scaled with the relative value of that eggcase. Finally, despite the significant correlations, fixed effects (e.g. eggcase possession/value) in the models explained only 5–23% of the variation in behaviour and web structure, while the random effect of individual identity explained 46–65% of the variation. This variation drove moderate to high repeatability estimates across all traits, suggesting that some individuals consistently invest relatively more in defence, while some invest less. These results highlight that extended phenotypic traits may be a critical component of offspring defence in some taxa. Furthermore, individual variation in these traits suggest that different reproductive strategies may exist, whereby some individuals invest more in reproduction at a cost to safety/foraging and vice versa.

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The juvenile stage of virtually all animals is frequently the most vulnerable to predation. Behavioural defences are one method by which many species with some level of parental care have evolved to protect offspring from predation (Andersson, Wiklund, & Rundgren, 1980; Montgomerie & Weatherhead, 1988). Furthermore, it is hypothesized that organisms should scale their level of defence to the relative value of their offspring, investing more if there are larger brood numbers or as the brood ages (Andersson et al., 1980; Patterson, Petrinoich, & James, 1980). Although both of these points have been the focus of extensive research, virtually all the studies have focused on active behavioural defence mechanisms (e.g. aggression), while overlooking the role architectural constructions may play in defence. Additionally, we now know that almost all taxa show some level of consistent individual differences

in behaviour (e.g. arachnids: Pruitt, DiRienzo, Kralj-Fišer, Johnson, & Sih, 2011; insects: Niemelä, DiRienzo, & Hedrick, 2012; birds: Schuett, Godin, & Dall, 2011; mammals: Guenther, Finkemeier, & Trillmich, 2014; fish: Bell & Sih, 2007), thus prompting the question of whether individuals also vary in how they defend their offspring. Individual variation in structural defences may provide a new level at which fitness trade-offs may occur, while also explaining how trait variation is maintained in populations. Despite these potentially important interactions, to our knowledge no study has investigated the interplay between behaviour, extended phenotypes and individual variation.

Offspring, especially those who are immobile, are vulnerable to a wide variety of biotic threats. The most common of these threats comes from predators, to which parents often defend against using a variety of aggressive behaviours, from mobbing and alarm calling in avian species (Hollander, Van Overveld, Tokka, & Matthysen, 2008; Redondo & Carranza, 1989; Wiklund, 1990), to biting and lunging in fish (Itzkowitz, 1985; Ridgway, 1988), to striking and

* Correspondence: N. DiRienzo, Department of Ecology and Evolutionary Biology, University of Arizona, P.O. Box 210088, Tucson, AZ 85721, U.S.A.

E-mail address: ndirienzo@gmail.com (N. DiRienzo).

grabbing with chelae in crayfish (Figler, Blank, & Peeke, 2001; Martin & Moore, 2010). Similar behaviours are used to counter other biotic threats such as infanticidal females (Wolff & Peterson, 1998) and brood parasites (Trnka, Požgayová, Samaš, & Honza, 2013). Defending against these threats yields obvious fitness benefits in the form of offspring survival, yet comes at a potential cost of injury or death to parents. The reproductive value hypothesis predicts that parents should scale their defensive efforts relative to the value of the offspring (Patterson et al., 1980). Indeed, evidence in support of this hypothesis has been found in a number of species (Greig-Smith, 1980; Redondo & Carranza, 1989; Ridgway, 1988; Wiklund, 1990). For example, in merlins, *Falco columbarius*, female parents increase attack intensity as brood size increases, while also increasing defence for first broods, which have higher survival probability, compared to replacement broods, which have lower survival probability (Wiklund, 1990). Thus, the increased risk of injury associated with vigorous defence is offset by the predicted increase in reproductive fitness.

Although these behavioural mechanisms yield fitness benefits in the form of increased offspring survival, there are other forms of defence that may provide similar protection and potentially interact with behavioural mechanisms. Animal constructions, which are extended phenotypic traits that include structures such as spider webs, ant and bee nests and beaver dams, mediate a number of fitness-related processes (e.g. foraging, mating, defence; Doucet & Montgomerie, 2003; Pinter-Wollman, 2015; Smith, Ostwald, & Seeley, 2015), including, potentially, offspring defence. To date, much of the work has focused on how factors such as nest site selection, density and conspicuousness of the construction may aid in defence (for review see Mainwaring, Hartley, Lambrechts, & Deeming, 2014), while overlooking how the architecture itself may do so. Certain features may be more effective at defence than others. For example, male sand gobys, *Pomatoschistus minutus*, were shown to reduce the size of their nest opening, which is used to aerate their brood, when predators are present, suggesting a defensive function of altering opening size (Lissåker & Kvarnemo, 2006). Such variation in architecture in response to investing in reproduction may be common, while also interacting with behaviour. Furthermore, given that these structures are costly to produce, both energetically and in terms of consequences for the offspring (Ford, 1977; Jakob, 1991; Lissåker & Kvarnemo, 2006), they also may be subject to the reproductive value hypotheses, whereby individuals scale the protective capability of their structure in accordance with the value of their offspring (Patterson et al., 1980).

While animals should increase their defensive efforts, both behaviourally and structurally, when they have offspring, as well as scale those defences with offspring value, extensive research has shown that animals are often limited in their plasticity. Such limits result in individuals displaying consistently different responses to the same context or situation (Sih, Bell, & Johnson, 2004). Some spiders are consistently more aggressive towards prey (DiRienzo & Montiglio, 2016a), mosquito fish and social spiders vary in how social they are (Cote, Fogarty, & Sih, 2012; Pruitt, Riechert, & Jones, 2008), and field crickets vary in their boldness (DiRienzo, Niemelä, Skog, Vainikka, & Kortet, 2015). Such individual differences may also occur in the context of nest defence, whereby some individuals invest more in protecting their offspring than others (Burtka & Grindstaff, 2013). Recently, a number of studies on avian species have demonstrated such individual differences in behavioural nest defences, measured by repeatability, whereby individual females are consistent across breeding seasons in how intensely they defend their nests (Burtka & Grindstaff, 2013; Hollander et al., 2008; Trnka et al., 2013). This raises the question of how those individuals who consistently invest less in behavioural defence compensate for the potential fitness losses. One hypothetical

explanation for the maintenance of nonaggressive females in this population is that they build different structures that better protect their offspring, thus reducing the need for behavioural defence. The implications of individual differences in behavioural and structural defence are significant, as different relative investments in each may allow equal fitness outcomes for different behavioural or structural phenotypes. To our knowledge, no study has explicitly considered this question. Collectively, it highlights the need to better understand the role of structure in nest defence, while also focusing how individuals within a population vary in this defence.

Here we used redback spiders, *Latrodectus hasselti*, to study how web structure is affected by reproductive investment and the relative value of that investment, as well as whether individuals consistently vary in their investment in protective structures. Widow spiders (*Latrodectus* spp.) are ideal for this study as they build complex three-dimensional webs, which have distinct features that are used for foraging (gumfooted) as well as safety (structural lines) (Blackledge, Coddington, & Gillespie, 2003; Zevenbergen, Schneider, & Blackledge, 2008). Female spiders face predation pressure from conspecifics as well as from lizards and wasps (Blackledge et al., 2003; Trubl, Gburek, Miles, & Johnson, 2012), against which the dense three-dimensional webs are thought to defend against (Blackledge et al., 2003). And, while mature females have few parasites, eggcase parasites are common to widow spiders (Marie & Vetter, 2015; Pemberton & Rosa, 1940; Vetter et al., 2012) and spiders in general (Austin, 1985). Many widow spiders build a funnel-shaped retreat where they lay their eggcases (Shulov & Weissman, 1959), yet females appear to vary in the density of the retreat (N. DiRienzo, personal observation), or whether they even build a retreat (Barrantes & Eberhard, 2010). Thus, denser, more robust funnels may provide additional protection from parasitoids. Furthermore, although females respond to changes in body condition by altering their relative investment in different aspects of web structure for foraging (gumfooted lines) and safety (structural lines and web density), individual differences are still maintained across state differences (DiRienzo & Aonuma, 2017; DiRienzo & Montiglio, 2016b). These individual differences, coupled with limited plasticity, suggest that females may also show consistent differences in how they protect their reproductive investments.

In this study we asked the following three questions. (1) Do females increase investment in protective structures when they have an eggcase? (2) Does the level of protection provided structurally scale with the relative investment in the eggcase? (3) Are there consistent individual differences in web structure, including protective elements, when an eggcase is present versus absent. We predicted that females would increase funnel density, web mass (a proxy for web density), the number of structural lines, and become more aggressive when they have an eggcase versus when they do not. We also predicted that these same measures would positively scale with eggcase mass. Finally, we predicted that females would show consistent individual differences in all measures across eggcase status, thus suggesting they consistently vary in protective strategy.

METHODS

We collected mature ($N = 24$) and immature ($N = 7$) female *L. hasselti* spiders in Fukuoka, Japan in the summer of 2015. The spiders were brought into the laboratory at Hokkaido University in Sapporo, Japan, after which they were assigned a unique identity number and placed in individual containers (7 cm high, 9 cm diameter). The spiders were provided two *Acheta domesticus* crickets per week, each approximately the same size as the spider. The spiders were maintained at 27 °C on a 12:12 h light:dark cycle.

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