State-dependent changes in risk-taking behaviour as a result of age and residual reproductive value

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Animals are able to modify their behaviour in response to changes in their internal and environmental state. The asset protection principle predicts that an animal's risk-taking behaviour should vary as a result of its residual reproductive value (RRV); animals with greater RRV would incur a greater cost if injured or killed and should therefore take fewer risks than those with low RRV. Despite the intuitive appeal of this hypothesis, few studies have effectively separated the effects of RRV on behaviour from those of age. We addressed this weakness in the widely invoked hypothesis by measuring the risk-taking behaviour of female Australian field crickets, *Teleogryllus oceanicus*, at various points in the animal's lifetime. We found significant effects of age on risk-taking behaviour: older females emerged from a shelter sooner after a simulated predation threat and exhibited greater mobility in an open arena. Importantly, there was also a significant marginal effect of RRV on risk-taking behaviour. Females with lower RRV displayed greater levels of risk taking than females with high RRV. Our results thereby offer support for the asset protection principle as an explanation for state-dependent variation in risk-taking behaviour.

The optimal behaviour of an animal is expected to vary according to its internal and environmental state (Houston, Clark, McNamara, & Mangel, 1988; Mangel & Clark, 1988). The trade-off between the potential costs and benefits of a particular behaviour are believed to inform the behavioural decisions of individuals (McNamara & Buchanan, 2005); but the payoffs of these behaviours vary according to the individuals' life history and environmental conditions (Dosmann & Mateo, 2014; Kolodny & Stern, 2017). Consequently, animals often modify their behaviour so as to maximize the benefits and minimize the costs of that behaviour (Briffa, Rundle, & Fryer, 2008; Carter, Goldizen, & Heinsohn, 2012; Hazlett, 1995). This alteration in an individual's behaviour is referred to as state-dependent behavioural plasticity.

There is a vast body of literature on the effect of state in driving behavioural changes. Much of this research has focused on the state dependency involved in risky foraging attempts (Brown & Kotler, 2004; McNamara & Houston, 1994; Schmitz & Trussell, 2016). For example, Olsson, Brown, and Smith (2002) observed the behavioural consequences of the trade-off between the costs of predation and the benefits of foraging in starlings, *Sturnus vulgaris*. They found that due to the potential for greater foraging benefits, starlings behaved more cautiously and took fewer risks in areas with abundant food supplies than starlings in low-quality food patches. Additionally, state-dependent changes in behaviour have been seen in response to variation in multiple environmental conditions such as temperature and season (Betini & Norris, 2012; Briffa, Bridger, & Biro, 2013; Carter et al., 2012; Eccard & Herde, 2013; Mcnamara, Houston, & Lima, 1994), predation risk (Lima, 1998; Lima & Bednekoff, 1999; Martin & Lopez, 1999), food availability (Shuai, Zhang, & Zeng, 2017), and as a result of the interactive effect of mating opportunities, foraging, temperature and predation (Dosmann & Mateo, 2014; Stahlschmidt & Adamo, 2013). Alternatively, alterations in risk-taking behaviour have been observed in response to a wide range of internal states and life history strategies such as nutritional state (Sherratt, 2003), changing social dominance (Rudin, Tomkins, & Simmons, 2017), survival probability (Nicolaus et al., 2012), body condition (Heithaus et al., 2007; Seltmann et al., 2012) and internal thermal state (Godfrey & Bryant, 2000; Martin & Lopez, 1999). These results imply that variation in state causes a shift in the balance of costs and benefits associated with a particular behaviour which leads to state-dependent behavioural plasticity. However, less common is

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research that has focused on observing state-dependent changes in behaviour that are due directly to natural alterations in future reproductive potential, rather than manipulation of their state or environmental conditions. Here, we examined behavioural plasticity in response to fluctuations in residual reproductive value (RRV) and ageing.

Residual reproductive value is defined as an organism's potential for future reproduction (Williams, 1966); a young individual is therefore expected to have a higher RRV than an older individual that has already invested in reproduction. The trade-off between RRV and risky behaviour, commonly referred to as the asset protection principle (Clark, 1994) or the life history trade-off hypothesis (Wolf, van Doorn, Leimar, & Weissing, 2007), predicts that an individual's risky behaviour, such as mate searching in the face of a predatory threat, should depend upon the relative reproductive costs and benefits of that behaviour. The hypothesis proposes that because individuals of high RRV will pay a greater reproductive cost from injury or death than individuals with low RRV, they should engage less in risky behaviour (Clark, 1994; Kemp, 2006; Luttbeg, 2017; Wolf et al., 2007). Therefore, as an individual's RRV declines, it is expected that they will display greater levels of risk-taking behaviour.

Despite increasing theoretical expectation (Dingemanse & Wolf, 2010; Wolf et al., 2007), there is a lack of empirical studies testing the relationship between future reproductive assets and risk-taking behaviour, and their potential to induce behavioural plasticity (Nicolaus et al., 2012). However, in grey mouse lemurs, *Microcebus murinus*, Dammhahn (2012) found that young individuals with low current but high expected future fitness were less bold than older individuals. This finding has been supported by a small number of additional studies where individuals with low reproductive potential were seen to take more risks than those with greater reproductive assets (Ory, van Son, & Thiel, 2015; Wilson, Godin, & Ward, 2010). Collectively, these studies lend correlational support for the asset protection principle acting as a source of state-dependent behavioural plasticity.

A potential limitation of many of the studies discussed above is their use of age as a proxy for RRV. Age and RRV will be correlated but many studies have treated the two as the same trait (see Dammhahn, 2012; Ory et al., 2015; Takata, Doi, Thomas, & Koyama, 2016). For example, the values of RRV calculated in Dammhahn (2012) and Ory et al. (2015) were based either predominantly or solely on the current and expected age of the study population. This raises the question of whether changes in behaviour are adaptive responses to fluctuations in RRV or occur in response to ageing alone. Fisher, David, Tregenza, and Rodríguez-Muñoz (2015) found that among wild-collected field crickets, *Gryllus campestris*, the age of an individual was significantly correlated with its risk-taking behaviour. When an individual was young, it took longer to emerge from a shelter and moved throughout an arena at a slower rate than when it was older, thus offering an alternative explanation to Dammhahn (2012) and Ory et al. (2015), that ageing itself and not RRV induces behavioural plasticity. Therefore, it remains unclear which state variable: RRV, ageing, or indeed both, are responsible for changes in risk-taking behaviour.

Here, we examined the state-dependent plasticity of risky mate-searching behaviour in relation to RRV and age, using female Australian field crickets, *Teleogryllus oceanicus*. Importantly, we aimed to differentiate the effects of age and RRV on risky mate searching by quantifying RRV based on the lifetime number of eggs laid by a female and observing the effects of both age and RRV on behaviour in a cross-sectional experiment. The asset protection principle predicts that risk-taking behaviour will increase with decreasing RRV. Thus, we expected to find that females with higher RRV would conduct less risk-taking behaviour than those with lower RRV over and above any effects of age.

METHODS

Animals

Crickets were drawn from an outbred laboratory stock population that originated from Carnarvon, Western Australia. Penultimate instar nymphs were placed into individual plastic containers (7×7 cm and 5 cm high), supplied with cat chow and water ad libitum, and monitored daily until the adult moult. Seven days after the adult moult, a single adult male was placed into each female's container and the pair were left to mate for 8 h. Females spent the remainder of their life alone in their individual container.

Residual Reproductive Value

After females had mated they were provided with a dish of damp sand in which to oviposit. Dishes were replaced weekly. The eggs laid by each female were collected and counted on a weekly basis, starting 7 days after mating and then every 7 days until death (approximately 2 months later). An estimate of RRV was then calculated by determining the residual fecundity of each female at the point at which her behaviour was assessed, that is, the total number of eggs produced in a female's lifetime minus the number she had produced prior to her behavioural trial. Among-individual variation in egg laying was then controlled for by centring residual fecundity within subjects (see van de Pol & Wright, 2009). Within-subject centring involves subtracting an individual's mean value from its observation value. Therefore, RRV at the time of the behavioural assay was calculated by first determining the residual fecundity at every week of a female's life, then subtracting the average of these values from her residual fecundity at the time of the behavioural trial.

Behavioural Trials

A total of 105 female crickets were randomly assigned to one of three groups representing different age classes: 'early', 'mid' and 'late' (35 females per group). Each female completed only one behavioural trial in her lifetime. The behaviour of the females assigned to the 'early' group was assayed 14 days after the adult moult, the females from the 'mid' group at 28 days and the 'late' females at 42 days. Nine of the 105 females died before their assay day; therefore, the final numbers of crickets per group were 33 in the 'early' group, 32 in the 'mid' group and 31 in the 'late' group. The average life span of these 105 individuals was 60.13 ± 16.78 days.

The experimental set-up for the behavioural trials was derived from Rudin et al. (2017). The experimental arena (Fig. 1) consisted of a 31 cm deep plastic trough (32×46 cm at base) with a thin layer (ca. 2 cm) of fine sand covering the base, within which there was a single shelter made from PVC pipe (height: 8.5 cm; diameter: 8 cm) located in one corner. The shelter was fitted with a moveable door which enabled it to be opened from the outside by pulling an attached piece of string.

To record the movement of the crickets, a video camera (Panasonic WV-CL930) connected to a nearby PC was installed above the arena and the movement of the crickets was subsequently analysed from video recordings using EthoVision v8.5 (Noldus Information Technology Inc., Wageningen, The Netherlands). Using EthoVision, the arena was segmented into three separate areas, each representing different levels of mobility: 'near' was defined as the area within a 16 cm radius of the corner in which the shelter was placed; 'far' was defined as the area within a 16 cm radius of the opposite