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Mechanisms of decision making during contests in green anole lizards: prior experience and assessment

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Prior contest experiences can predictably alter an individual's contest performance and probability of contest success. Although winner and loser effects have been well studied across many animal taxa, the mechanisms underlying these effects and their adaptive value currently are topics of intense interest. Two predominant hypotheses posit that contest experiences alter either an individual's perceived fighting ability or its actual fighting ability. We addressed these hypotheses, and potential physiological and behavioural mechanisms driving experience effects in the green anole lizard, *Anolis carolinensis*. Prior losers went on to lose a significant proportion of future contests while prior winners were equally likely to win or lose against size-matched opponents. Further analysis revealed that the loser effect arose as a result of individuals updating their perceived fighting ability following a loss. Both prior losing and winning experiences influenced future contest performance with prior losers decreasing and prior winners increasing their aggressiveness in subsequent contests. Status-dependent changes in metabolic physiology were not associated with the presence of the observed loser effect. However, contest status and contest performance interacted to influence metabolic physiology. Plasma glucose concentrations decreased as a function of the frequency of high-risk, escalated behaviours performed by eventual losers, and muscle lactate concentrations increased as a function of the frequency of low-risk threat displays performed by eventual winners. Our results support the notion that prior contest experiences influence an individual's perceived, not actual, fighting ability and that status-dependent changes in metabolic physiology are not a likely mechanism underlying the presence/magnitude of experience effects.

Prior contest experiences predictably alter an animal's decisions during competitive interactions; prior wins increase while prior losses decrease an individual's aggressiveness in subsequent contests (reviewed in: Hsu, Earley, & Wolf, 2006; Rutte, Taborsky, & Brinkhof, 2006). Such behavioural changes can manifest as winner and loser effects, defined as any change in contest performance and probability of contest success following a win or loss (Chase, Bartolomeo, & Dugatkin, 1994; Goubault & Decuigniere, 2012; Hsu et al., 2006; Huang, Yang, & Hsu, 2010; Kasumovic, Elias, Sivalinghem, Mason, & Andrade, 2010; Schuett, 1997). Experience effects often are short-lived, persisting from hours (e.g. pumpkinseed sunfish, *Lepomis gibbosus*: Chase et al., 1994) to days (e.g. copperhead snakes, *Agkistrodon contortrix*: Schuett, 1997), and sometimes up to 1 month (Lan & Hsu, 2011). Furthermore, the effects of prior contest dynamics (e.g. escalated versus nonescalated) on future contest behaviour and success often can supersede the effects of prior status alone (Beaugrand & Goulet, 2000; Garcia et al., 2012; Huang et al., 2010).

Despite the breadth of information on winner and loser effects, the proximate and ultimate mechanisms underlying these experience-induced behavioural changes have yet to be elucidated. Some theorize that winner and loser effects play a pivotal part in the formation of social hierarchies (Dugatkin, 1997; Dugatkin & Earley, 2003; Hock & Huber, 2009). Hock and Huber (2009) demonstrated that the presence of strong loser effects and weak winner effects could reduce the frequency of costly aggressive interactions between group members and lead to the formation of stable hierarchies. Others theorize that prior contest experiences provide animals with information regarding their resource-holding potential; the culmination of factors (e.g. size, motivation, residency, etc.) that aid an individual in obtaining or retaining fitness-related resources (Fawcett & Johnstone, 2010; Hsu et al., 2006; Mesterton-Gibbons, 1999; VanDoorn, Hengeveld, & Weissing, 2003a, 2003b). These models predict that selection should favour individuals that utilize prior contest experiences to reassess their fighting ability under conditions where asymmetries in resource-holding potential dictate contest outcome, where information of

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one's own resource-holding potential may be imperfect (VanDoorn et al., 2003a, 2003b), and when overestimating resource-holding potential carries significant costs (Mesterton-Gibbons, 1999). Prior contest experiences should thus influence an animal's perceived fighting ability but not its actual fighting ability (Hsu et al., 2006; Hsu, Lee, & Lu, 2009; Hsu & Wolf, 2001; but see Kasumovic et al., 2010). These modifications should affect contest performance and success only in nonescalated contests, during which an animal's threshold fighting ability is not revealed and does not influence contest outcome (Hsu et al., 2006, 2009).

A change in perceived fighting ability has often been cited as the mechanism underlying winner and loser effects, but alternative mechanisms have been proposed (Hsu, Earley, & Wolf, 2011; Rutte et al., 2006). Among those alternatives is the by-product hypothesis, which states that an animal's actual fighting ability can change following a win or loss. Animals that win gain fitness-related resources (e.g. food), which increase their resource-holding potential while losers incur energetic costs or injury, which decrease their resource-holding potential. Winner and loser effects would then arise as a by-product of those changes in actual fighting ability (Hsu et al., 2011; Rutte et al., 2006). Rutte et al. (2006) indicated that the adaptive value of by-product experience effects remains unclear, especially for the loser, and noted that winner and loser effects have been revealed in the absence of resource gain or loss (e.g. Bergman et al., 2003; Chase et al., 1994; Schuett, 1997). However, in jumping spiders, *Phidippus clarus*, prior contest experience affects performance in both nonescalated and escalated contests, perhaps by altering both perceived and actual fighting ability (Kasumovic et al., 2010). This study, however, did not address the mechanism(s) underlying potential changes in actual fighting ability and, to the best of our knowledge, no study has investigated the potential link between changes in actual fighting ability following a contest and its effects on future contest performance and success.

Our study explored whether changes in metabolic physiology (by-product hypothesis) or perceived fighting ability (perceived ability hypothesis) following a prior win or loss are associated with changes in an animal's performance in subsequent contests. Although we draw a distinction between the two hypotheses, they need not be mutually exclusive (Kasumovic et al., 2010). We chose metabolic physiology because it has been shown to be a significant component of an individual's resource-holding potential in many taxonomic groups (reviewed in Briffa & Sneddon, 2007; see also Brandt, 2003; Copeland, Levay, Sivaraman, Beebe-Fugloni, & Earley, 2010; Milligan, 1996; Ros, Becker, & Oliveira, 2006). The rate at which energy is spent and lactic acid is accumulated influences whether an individual persists in or retreats from a contest (Briffa & Elwood, 2001; Briffa & Sneddon, 2007; Wilson & Gatten, 1989). Changes in metabolic physiology commonly are observed after agonistic contests in both winners and losers (Briffa & Sneddon, 2007; Copeland et al., 2010), but these status-dependent changes have yet to be linked to changes in future contest success.

We hypothesized that the outcome and dynamics of prior contests, but not status-dependent changes in metabolic physiology, would predict the probability of future contest success. We predicted that experience effects (winner and/or loser) would persist longer than any status-related changes in metabolic physiology. Although we hypothesized that status-dependent changes in metabolic physiology would not affect future contest success, we expected that acute changes in metabolic physiology would occur in response to an initial contest (e.g. Wilson & Gatten, 1989). We also expected that any observed metabolic changes would be a function of both prior contest status (winner versus loser) and prior contest dynamics (escalated versus nonescalated). As such, we hypothesized that focal individuals would show significant changes in metabolic physiology (e.g. decreased plasma glucose or increased muscle lactate) following the initial contest and that the magnitude of these changes would depend upon both prior contest status and dynamics.

We used the green anole lizard, *Anolis carolinensis*, as a model organism. For male green anoles, reproductive opportunities depend critically on their ability to successfully establish and defend a high-quality territory (Forster, Watt, Korzan, Renner, & Summers, 2005; Jenssen, Decourcy, & Congdon, 2005; Korzan, Øverli, & Summers, 2006; Lovern & Jenssen, 2003). In the wild, neighbouring males often compete in dyadic interactions at their respective territory boundaries (Jenssen, Greenberg, & Hovde, 1995). Competitive interactions follow a phasic pattern (Jenssen et al., 2005) starting with highly ritualized display tactics (e.g. headbobs, dewlap extensions, colour changes, eyespot formation), which may escalate to high-risk behaviours (e.g. charging, mouth locking, wrestling) until one of the contestants retreats (Henningsen & Irschick, 2012; Lailvaux, Herrel, VanHooydonck, Meyers, & Irschick, 2004; Lailvaux & Irschick, 2007; McMann, 1993). Interactions between green anoles can elicit significant changes in metabolic physiology (e.g. lactate accumulation and oxygen consumption; Wilson & Gatten, 1989; but see Wilson, Gatten, & Greenberg, 1990) and neuroendocrine profiles (e.g. serotonin and cortisol: Korzan et al., 2006; Ling, Summers, Renner, & Watt, 2010). Success in dominance interactions also is linked to individual performance capacity (e.g. bite force or jumping ability: Henningsen & Irschick, 2012; Lailvaux et al., 2004; Lailvaux & Irschick, 2007), and several studies have revealed that the decisions green anoles make during contests depends on prior contest experiences. Forster et al. (2005) showed that individuals confronted with an opponent to whom they had previously lost perform fewer aggressive acts and retreat faster (see also Larson & Summers, 2001; Ling et al., 2010). Garcia et al. (2012) showed that the interaction between prior contest performance and status can significantly influence an individual's competitive success when faced with a novel opponent.

Our choice of model organism and experimental set-up has given us the added advantage of re-evaluating previous findings on assessment strategies in green anole lizards. Previous work suggests that green anoles use different assessment strategies, either self-assessment or mutual assessment, depending on the intensity of a contest (Garcia et al., 2012; but see Henningsen & Irschick, 2012). In low-intensity, nonescalated contests, individuals use a mutual assessment strategy, but in high-intensity, escalated contests, individuals use a self-assessment strategy (Garcia et al., 2012). When using mutual assessment, individuals gather information and gauge asymmetries in resource-holding potential through behavioural exchanges; contests escalate to high-risk behaviours when asymmetries in resource-holding potential cannot be determined through low-risk displays alone (e.g. Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990). Conversely, when using self-assessment, individuals base their competitive decisions solely on assessment of their own resource-holding potential, often irrespective of their opponents' actions (pure self-assessment: Arnott & Elwood, 2008; Briffa, 2008; Briffa & Elwood, 2010; Mesterton-Gibbons, Marden, & Dugatkin, 1996; Payne & Pagel, 1996), but not always (i.e. cumulative assessment: Payne, 1998). We thus hypothesized that individuals would use different assessment strategies (e.g. mutual versus self-assessment) depending on the intensity of the contest in which they engaged.

METHODS

Animal Housing and Care

All procedures were approved by the University of Alabama Institutional Animal Care and Use Committee (IACUC number 08-