Animal Behaviour 123 (2017) 441–450

Contents lists available at ScienceDirect

Animal Behaviour

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

Born to win or bred to lose: aggressive and submissive behavioural profiles in crickets

Jacqueline Rose [a, *], Darron A. Cullen [b], Stephen J. Simpson [c], Paul A. Stevenson [a]

[a] Institute for Biology, University of Leipzig, Leipzig, Germany
[b] Zoological Institute, KU Leuven (University of Leuven), Leuven, Belgium
[c] Charles Perkins Centre and School of Life and Environmental Sciences, University of Sydney, Sydney, NSW, Australia

ARTICLE INFO

Article history:
Received 12 May 2016
Initial acceptance 4 July 2016
Final acceptance 21 October 2016
Available online 22 December 2016
MS. number: 16-00420R

Keywords:
aggression
agonistic behaviour
animal personality
attraction
exploratory behaviour
insects
loser effect
motility
video tracking
winner effect

Aggression between conspecific males is widespread in the animal kingdom, as is the fact that some individuals are far more aggressive than others. Consistent interindividual differences in behavioural profiles are generally regarded as a hallmark for animal 'personality' in both vertebrates and invertebrates, but their proximate causes are poorly understood. While the social experiences of winning and losing are known to lead to heightened and depressed aggressiveness, respectively, and that different fighting experiences can lead to changes in other behaviours, the extent to which interindividual variation in aggression and correlated behaviours are determined alone by fighting experience, environmental factors or inherited predisposition is unclear. In this study, we video tracked individual, virgin adult male crickets, *Gryllus bimaculatus*, to quantify their general motility, exploratory behaviour and attraction to conspecific males after 48 h of social isolation, and compared this with their performances 24 h later, immediately after a fighting tournament that yielded cohorts of aggressive winners and submissive losers. Although all known behavioural effects of previous social experience in crickets last only a few hours at most, we found significant behavioural differences between the 48 h isolated future winners and losers, i.e. before the fight tournament. However, the experiences of winning and losing led to more pronounced and some additional changes in behaviour. We discuss whether these different behavioural profiles associated with the chances of winning and losing ('personalities') could arise from factors other than fighting experience, or possibly from dominance and subjugation experiences gathered under crowded culture conditions before social isolation with cumulative effects that may persist longer than those presently known.

Aggression between conspecifics is a highly plastic behaviour that is expressed by numerous animal species and influenced by a wide variety of experiences, particularly winning or losing previous encounters (Hsu, Ryan, & Wolf, 2006). However, the proximate mechanisms underlying winner and loser effects are barely known. Recent studies in crickets have shown that winning increases aggressiveness via the neuromodulatory action of the biogenic amine octopamine (Rillich & Stevenson, 2011), the invertebrate analogue of noradrenaline (Pflüger & Stevenson, 2005), whereas reduced aggressiveness results from the action of the neuromodulator nitric oxide (Stevenson & Rillich, 2015, 2016). Since these neuromodulators have widespread effects on central circuits controlling the operation of numerous motor circuits (Simpson & Stevenson, 2015; Verlinden et al., 2010), activation of these pathways as a result of agonistic experiences is likely to have multiple and widespread behavioural consequences. Other studies have indeed shown that an 'individual's absolute fighting ability' or 'win chances', i.e. its resource-holding potential (Hurd, 2006; Parker, 1974), often correlates with the expression of unrelated behavioural traits (Briffa, Sneddon, & Wilson, 2015).

Winning, for example, can increase an individual's tendency to move in a novel environment ('boldness'), and these proactive individuals are often more likely to win aggressive contests (Courtene-Jones & Briffa, 2014; Mowles, Cotton, & Briffa, 2012; Verbeek, Boon, & Drent, 1996). Aggressive experience is thus both a potential cause and a consequence of interindividual behavioural variability documented in both vertebrates and numerous

* Correspondence: J. Rose, Institute for Biology, University of Leipzig, Talstraße 33, 04103 Leipzig, Germany.
E-mail address: jaqueline.rose@uni-leipzig.de (J. Rose).

http://dx.doi.org/10.1016/j.anbehav.2016.11.021
0003-3472/

arthropods (e.g. fish: Budaev & Brown, 2011; birds: Verbeek et al., 1996; rodents: Benus, Koolhaas & Van Oortmerssen, 1987; Koolhaas, Boer, Ruiter, Meerlo, Sgoifo, 1997; honeybees: Wray, Mattila, & Seeley, 2011; spiders: Sweeney et al., 2013; hermit crabs: Mowles et al., 2012; crickets: Kortet & Hedrick, 2007). Consistent interindividual differences in behaviour are frequently regarded as a hallmark for a 'behavioural syndrome' (Sih, Bell, & Johnson, 2004), animal 'personality' (Dingemanse, Kazem, Réale, & Wright, 2010; Gosling, 2001, 2008; Réale, Reader, Sol, McDougall, & Dingemanse, 2007) or 'behavioural profile' as a more formal term (Groothuis & Trillmich, 2011). Evidence that different behavioural profiles result from aggressive experience is, however, limited, and the degree to which individuality emerges from environmental or inherited genetic predisposition, rather than social experience, is still unclear.

Although aggression in crickets is well studied (Alexander, 1961; Dixon & Cade, 1986; Khazraie & Campan, 1999; Stevenson & Rillich, 2016), the relationship between fighting experience and general behavioural profiles is unclear. In the house cricket, *Acheta domesticus*, general activity and exploratory behaviour did not correlate with aggression as measured by the durations of agonistic actions (Wilson et al., 2010), while individual *Gryllus integer* with a shorter latency to become active in a novel environment were more likely to win a subsequent fight (Kortet & Hedrick, 2007). Unfortunately, neither of these studies tested whether aggression itself subsequently influenced motility or exploratory behaviour and hence provided no insight into whether interindividual behavioural variability apparent before the contest could have arisen from earlier social experience.

In our study, we video tracked adult male Mediterranean field crickets, *Gryllus bimaculatus*, that had been socially isolated for 48 h to evaluate general motility, exploratory behaviour and attraction to conspecific males 24 h before and the same crickets immediately after a fight tournament which generated cohorts of highly aggressive winners and submissive losers. Since all known behavioural effects of previous aggressive encounters last little more than 3 h (Rillich & Stevenson, 2014; Stevenson & Rillich, 2013), this experimental procedure should provide insights into the causes of interindividual behavioural differences associated with aggression. In particular, if the propensity to win or lose an aggressive encounter depends solely on earlier fighting experience, then we would expect to find no consistent differences in the behavioural profiles of socially isolated crickets before the fight tournament, but clear differences after the tournament due to the social experiences of winning or losing. Conversely, consistent differences between future winners and future losers before the tournament would indicate the involvement of other factors.

METHODS

Experimental Animals

Virgin, mature adult male *G. bimaculatus* were taken from a crowded breeding stock at the University of Leipzig. All experiments were performed at room temperature (22–25 °C) during daylight hours, in the months of April–June, excluding times when aggression tends to be depressed (1500–1700 hours and on generally rainy and overcast days, see Dixon & Cade, 1986; Stevenson, Hofmann, Schoch, & Schildberger, 2000).

Ethical Note

Animals were bred and maintained at the animal housing facility of the University of Leipzig, where they were kept in groups of 20–25 male crickets in transparent plastic boxes (35 × 19 cm and 30 cm high). The bottom of each box was covered with sand and egg cartons provided shelter opportunities. The boxes were kept at 22–25 °C room temperature, 60% humidity and a dark:night cycle of 12:12 h. Crickets were fed daily with fresh carrot and apple. Our analysis is based on observations of 110 crickets, in which none were used more than once for an experiment. No harmful or invasive tests were performed and all animals were returned to the breeding stock after the experiment.

Experimental Procedure

All crickets were socially isolated for 48 h prior to experimentation in individual glass jars (inner diameter 7 cm, height 9 cm) with ample food (fresh carrot, apple) and water. Data were accumulated over 3 months, whereby each experimental trial took 2 consecutive days to complete. On day 1, a subset of four weight-matched crickets (<5% difference, Fig. 1a) was selected and the general exploratory behaviour of each evaluated pairwise in two adjacent observation arenas (Fig. 1d and e) by video tracking as described below. On day 2 (24 h after the first behavioural assay and 72 h after initial isolation), fighting tournaments were staged between the same four animals and immediately after this each was video tracked once more.

Fight Tournaments

From each weight-matched cohort, two randomly selected pairs of crickets were matched simultaneously in separate fighting arenas. The latter were fashioned from clear Perspex (16 × 9 cm and 7 cm high) and had a sand-covered floor and an opaque dividing door in the middle. Each animal was placed at opposite ends of their arena. After removing the door, the crickets interacted aggressively within seconds. These encounters are characterized by an escalating sequence of stereotyped motor performances, which we scored on a scale of 0–6 (Hofmann & Stevenson, 2000; Stevenson, Dyakonova, Rillich, & Schildberger, 2005; Stevenson et al., 2000): level 0: mutual avoidance; level 1: one cricket attacks, the other retreats; level 2: antennal fencing, whereby the contestants lash each other's antennae; level 3: one contestant spreads its mandibles in a threat display; level 4: mandible spreading by both crickets; level 5: mandible engagement, whereby the two opponents interlock their mandibles; level 6: grappling with repeated mandible engagements with pushing, biting and body flipping. Fights last only a few seconds and are concluded the moment the loser retreats, leaving the winner, which then typically generated the aggressive rival song (Rillich & Stevenson, 2011). To check that a contest was indeed settled, we rematched the same opponents 3 min after the conclusion of the first fight, as described above (Fig. 1a). This generated a set of four crickets with different fighting experiences: one that won two successive fights (WWs), one that lost two successive fights (LLs), along with intermediates that were not considered further (one that first won then lost, and one that first lost and then won).

Video Tracking of Exploratory Behaviour

Before and after the fight tournament, exploratory behaviour of individual crickets was recorded for 5 min in an observation arena (Fig. 1d and e) using a video camera (Panasonic WV-CP 500, 65203 Wiesbaden, 25 frames/s) connected to a PC via a frame-grabber card (Euresys, Picolo Dilligent U4 H.264). For each observation trial, two crickets were placed simultaneously into