Journal of Ethology (2021) 39:47–54
https://doi.org/10.1007/s10164-020-00671-1

ARTICLE

Winner and loser effects of juvenile cricket *Gryllus bimaculatus*

Toshiki Abe[1] · Chihiro Tada[2] · Toshiki Nagayama[2]

Received: 9 January 2020 / Accepted: 12 August 2020 / Published online: 24 August 2020

Abstract

Agonistic encounters of juvenile male crickets were analyzed behaviourally. In a pairing between adult and juvenile male crickets, the juvenile crickets were usually beaten by the adult males of over 3 days after their final moult. Juveniles, by contrast, won significantly more bouts against young adult males 2 days after their final moult. These findings are good indicators to predict which cricket will defeat which opponent. To examine the effect of previous social experience, two juvenile animals were paired first and then juveniles that became subordinate were paired with day 2 adults, while juveniles that became dominant were paired with day 3 adults 5 min after first pairing. Subordinate juveniles were beaten by day 2 adults, while dominant juveniles tended to win against day 3 adults. This is the first time that winner and loser effects have been demonstrated in juvenile crickets. Similar pairings with day 2 or day 3 adult males were performed 2 h after first pairings. Subordinate juveniles were still beaten by day 2 adults, while the winning rate of dominant juveniles against day 3 adults was decreased significantly. These results suggest that the retention time of loser effect lasted more than 2 h while that of the winner effect disappeared within a shorter period.

Keywords Agonistic encounter · Social experience · Aggression · Winner effect · Loser effect

Introduction

Agonistic encounters and establishment of hierarchical orders are one of the essential behavioural acts for conspecific communication (Wilson 1975). Animals that acquire a dominant status increase their opportunity to access good food, mating partners and/or shelters, while animals that became subordinate reduce the risk of severe injury or death by avoiding dominant opponents (Herberholz et al. 2007)..

Physical asymmetries have been shown to be adequate predictions of the outcome of agonistic bouts. Larger and/or heavier animals as well as animals with larger weapon tend to win in both vertebrates and invertebrates (Clutton-Brock et al. 1979; Francis 1983; Abbott et al. 1985; Tokarz 1985; Hack 1997; Schuett 1997; Mathis and Britzke 1999; Sneddon et al. 2000; Kasumovic et al. 2010). In addition to physical asymmetries, previous social experience also affects the outcome of agonistic bouts. A previously winning experience increases the winning probability of the next agonistic encounter, whereas a previous losing experience has the opposite effect. These winner and loser effects have been widely observed in both vertebrates and arthropods (Beacham and Newman 1987; Bakker et al. 1989; Hsu and Wolf 1999) in fishes (Fuxjager et al. 2010) in mice (Moore et al. 1988; Otronen 1990) in insects (Whitehouse 1997) in spiders (Bergman et al. 2003; Momohara et al. 2013) in crayfish: for review (Hsu et al. 2006; Rutte et al. 2006). The retention time of winner and loser effects is, however, variable among animals from the order of tens of minutes to several weeks (Chase et al 1994; Bergman et al. 2003; Lan and Hsu 2011). Furthermore, the duration of winner and loser effects most often differs, with loser effects frequently lasting longer than winner effects (Beacham and Newman 1987; Bakker et al. 1989; Kaczer et al. 2007; Kasumovic et al. 2010; Goubault and Decuigniere 2012) with the exception of crayfish in which the winner effect lasts longer than the loser effect (Momohara et al. 2015).

The intraspecific aggression and the dominance hierarchy formation are observed from very early stage of postembryonic development in both vertebrates and arthropods

✉ Toshiki Nagayama
nagayama@sci.kj.yamagata-u.ac.jp

[1] Division of Biology, Graduate School of Science and Engineering, Yamagata University, Yamagata 990-8560, Japan

[2] Department of Biology, Faculty of Science, Yamagata University, Yamagata 990-8560, Japan

(Goldman and Swanson 1975; McDonald and Topoff 1986). For example, a dominant–subordinate relationship is formed in juvenile crayfish as early as the third stage of development (Sato and Nagayama 2012). Furthermore, dominance hierarchy is present in human children as young as 2 years old (Frankel and Arbel 1980). In the crickets, however, Balsam and Stevenson (2020) suggest that aggressive interactions between male juveniles are far less fierce than for adults in terms of escalation and no winner/loser effects are distinguished. On the other hand, Simmons (1987) and Abe et al. (2018) show that juvenile male crickets exhibit distinguished aggressive behaviours and form discrete dominant–subordinate relationship. However, it is still unclear that winner and loser effects are also formed in juvenile crickets.

The winner and loser effects are practical forms of learning in contest behaviour since a previously winning (or losing) experiences increase (or decrease) the winning probability of the next agonistic encounter. To confirm winner and loser effects of juvenile crickets would provide the insight that premature animals also possess learning ability. Thus, we make a hypothesis that winner and loser effects are formed by premature juvenile crickets. To examine the validity of this hypothesis, we must obtain adequate indicators to predict which cricket will defeat which opponent. Agonistic encounters of both crayfish and crickets have been reported from the early 1950s (Bovbjerg 1953; Alexander 1961). For crayfish, only a 3–7% difference of body length is sufficient for larger animals to tend to win (Ueno and Nagayama 2012). However, if small animals win the previous agonistic bouts, they could frequently defeat larger opponents. Furthermore, losing larger animals are usually beaten by physically disadvantaged small opponents (Momohara et al. 2013). The physical advantage of a paired crayfish is a good indicator to predict which crayfish will defeat which opponent and provide a key criterion as to whether a winner or loser effect is formed or not. In contrast to crayfish that increase in size with repeated moulting for their entire life, adult crickets do not undergo any significant increase in size once moulted. Hack (1997) has reported that heavier male crickets defeated their opponents, but the fighting success advantage of heavier animals was observed only for physical asymmetries in mass greater than 10%. Thus, the physical asymmetries of crickets are insufficient to predict the outcomes of agonistic bouts because winner and/or loser effects might be masked by physical advantages of heavier opponents. Since sexually mature males are more aggressive than adult males which have not yet produced a spermatophore (Dixon and Cade 1986), we make a hypothesis that fighting ability of adult crickets must develop gradually with days after final moult and young adults will be beaten by similar-weighted juveniles. We have examined the validity of these hypotheses based on the outcomes of pairings between final juvenile and adult males, and found strong indicator that sexually immature young adult 2 days after final moult was frequently beaten by juvenile. Using this prediction of outcomes of agonistic bouts, we demonstrate that juvenile crickets show winner and loser effects.

Materials and methods

Animals

Male two-spotted crickets, *Gryllus bimaculatus* (de Geer), were used in all experiments. They were purchased from commercial suppliers in Okayama and Hakodate, Japan. Crickets were maintained at 25 °C under a 12:12 h light:dark cycle (lights on at 06:00 h). After juveniles moulted to the final instar stage, individual animals were isolated in opaque plastic cups (37 mm height × 81 mm diameter) to become adults so that the exact age of the adult crickets from their final moult was established. Each cricket was fed an equal number of small food pellets and water every three days before experiments.

Pairings

Final instar juvenile male crickets and adult male crickets that were 2, 3, 5 or over 7 days old were paired in various combinations in an opaque fighting container of 100 mm diameter with 45 mm height. The body mass of each cricket was measured one day before pairing (0.47–0.67 g in juveniles and 0.46–0.69 g in adults). All pairings were performed between animals with a maximum 5% weight difference. To distinguish individuals, each animal was marked with odourless white correction fluid. The fighting container was first divided into two areas with an opaque acrylic partition. Two crickets were placed initially in different areas to prevent immediate contact. After acclimatization for 5 min, the divider was removed. The agonistic bouts were recorded by a video camera (JVC GZ-E265-N, Japan) for 10 min and analyzed using single frame measurement for each second of the encounter. The two crickets made contact with each other and started fighting within 1 min (34.3 ± 5.5 s, mean ± SE). A dominance hierarchy was typically established within 3.5 min (53.7 ± 6.8 s). Dominant and subordinate relationships were determined when loser crickets fled following the approach of the opponents on at least three times consecutive occasions. Dominant adults usually showed body jerking and sang aggressive songs. Dominant juveniles also showed body jerking, similar to singing adult males. If a dominance relationship was not established within 10 min after pairing, the pair's data were excluded from the analyses. The number of fights and total duration of fights were measured from video analysis. The intensity of a fight was scored on a scale of 0 to 6 to denote aggressive escalation according to Stevenson et al. (2000). Individual levels were as follows: Level 0: mutual avoidance without aggression. Level 1: one cricket attacks and the opposite retreats. Level 2: antennal fencing. Level 3: mandible spreading by one cricket. Level 4: mandible spreading by both crickets. Level 5: mandible engagement. Level 6: grappling.

Pairings were as follows: male juveniles were paired with male juveniles (= 10 pairings) and adult males over 7 days old were paired with adult males over 7 days old (day 7 adults) (= 26 pairings). Furthermore, male juveniles were paired with either day 7 adults (= 17 pairings), male adults of 5 days old (day 5 adults) (= 17 pairings), with male adults of 3 days old (day 3 adults) (= 23 pairings) or male adults of 2 days old (day 2 adults) (= 18 pairings). To examine the influence of previous experience of fighting, two juvenile males were paired first and their dominant and subordinate relationship established. The dominant juvenile was then paired with a naive day 3 adult 5 min (= 16 pairings) or 2 h (= 8 pairings) after the winning experience in their first pairing, while the subordinate juvenile was paired with a naive day 2 adult 5 min (= 16 pairings) or 2 h (= 8 pairings) after the losing experience in the first pairing.

Statistical analyses

The winning rate was determined by the number of animals that won the pairings/total number of pairings and analyzed with multiple comparison using Fisher's exact test after Bonferroni's correction to alpha and the significance level set to 0.016 (= 0.05/3) if 3 groups were compared, or to 0.008 (= 0.05/6) if 4 groups were compared in all pairwise comparisons. Aggression levels and total duration of fights were analyzed using a Mann–Whitney rank-sum test after Bonferroni's correction. Statistical analyses were carried out using SigmaPlot v13.

Results

Agonistic bouts between two juvenile or adult crickets

To confirm the influence of weight difference of two male crickets, agonistic bouts either between a pair of two juveniles or between a pair of two adult crickets with a maximum 5% weight difference (0.5331 ± 0.014 g vs 0.5325 ± 0.013 g in adults and 0.5398 ± 0.014 vs 0.5332 ± 0.015 g in juveniles) were performed (Fig. 1a). In juveniles, heavier animals won in 5 pairings and lighter animals also won in 5 pairings. In adult crickets, the winning rate of heavier males was 57.7% (15 out of 26 pairs), but there was no statistically significant difference from the winning rate of smaller animals ($P = 0.557$; binomial test). The lack of physical advantage of heavier animals was confirmed in this study with a weight difference of 5%. The aggressiveness of fights between a pair of two adult animals was higher than that of agonistic bouts between a pair of two juveniles (Fig. 1b). Intensity level of adult pairs [median level 5, IQR (interquartile range): 4–5] was statistically significantly higher ($U = 151.5$; $P = 0.031$; Mann–Whitney rank-sum test) than that of juvenile pairs (median level 4, IQR: 3–5). The total duration of fights between a pair of two adults (median duration 3.3 s, IQR: 2.4–4.8 s) was slightly longer than that between a pair of two juveniles (median duration 2.2 s, IQR: 1.2–4.3 s), but no statistically significant difference was observed between adults and juveniles ($U = 173.0$; $P = 0.149$; Mann–Whitney rank-sum test).

Agonistic bouts between a pair of adult and juvenile animals

Figure 2a showed the winning rate of adult crickets 2, 3, 5 or 7 days after their final moult in the pairing with juvenile

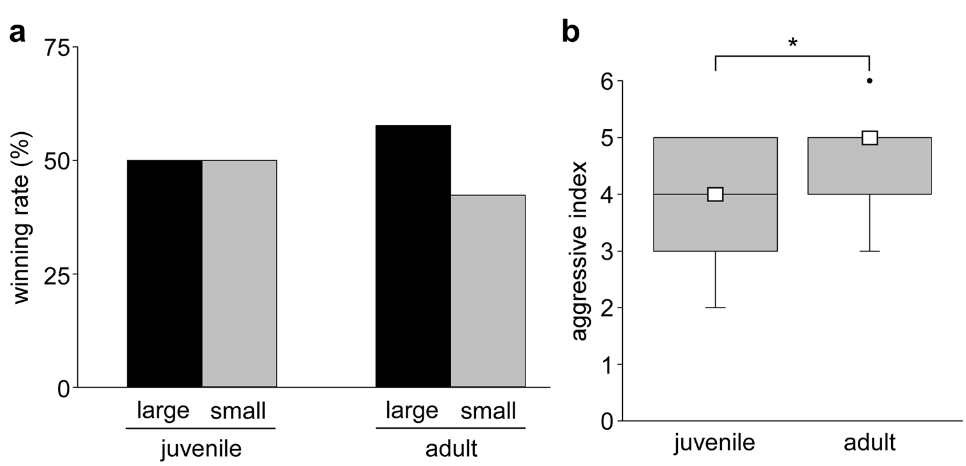

Fig. 1 Agonistic bout between juveniles and between adult crickets. **a** Winning rates between large and small crickets. **b** Intensity level of pairings. Solid black line with open square in the box shows median, box length indicates interquartile range (the 25th and 75th percentiles) and line bars show the 10th and 90th percentiles. Asterisk indicates significant difference of aggression between juvenile and adult animals (*$p < 0.05$)

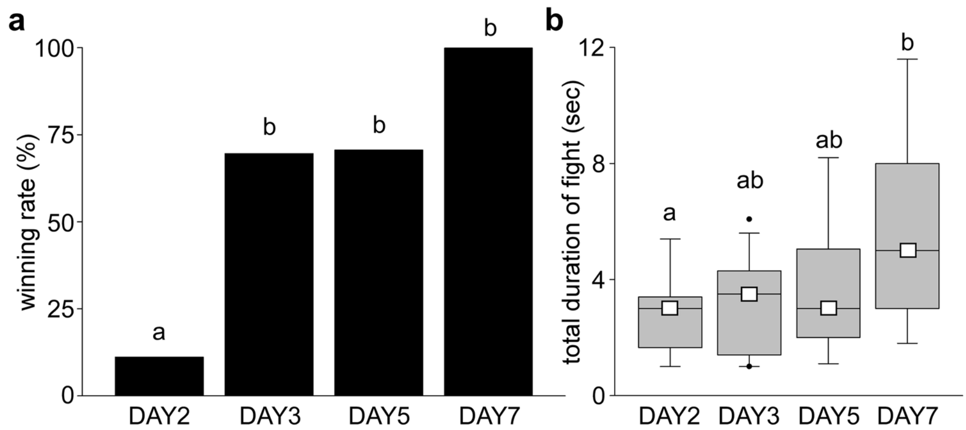

Fig. 2 Agonistic bouts of pairings between juvenile and adult crickets. **a** Winning rates of adult crickets of different ages from final moult against juveniles. **b** Total duration of agonistic bouts. Letters above each plot show statistical differences

males. Day 7 adults won in all 17 pairings against juveniles. Ten of day 7 adults were heavier and 7 were lighter than juvenile opponents. The winning rates of day 5 and day 3 adults were about 70% (12 won out of 17 pairings in day 5 adults and 16 won out of 23 pairings in day 3 adults). In contrast with these older adult animals, day 2 adults were more likely to lose against juveniles ($P = 0.0013$; binomial test). Only two day 2 adults won while the opponent juveniles won in the remaining 16 pairings. Two winners were heavier than juvenile opponents, while 8 heavier day 2 adults were beaten by lighter juveniles. Thus, no effects of body weight were observed. The winning rate of day 2 adult was 11.1%, which was statistically significantly lower than that of adults of other ages ($P < 0.001$; Fisher's exact test). The averaged aggression levels in each paired group were 3.4–4.5 and were not statistically significantly different ($P = 0.329$ between day 7 and day 5 adults, $P = 0.314$ between day 7 and day 3 adults, $P = 0.202$ between day 7 and day 2 adults, $P = 0.096$ between day 5 and day 3 adults, $P = 0.075$ between day 5 and day 2 adults, and $P = 0.912$ between day 3 and day 2 adults; Mann–Whitney rank-sum test). The median of the total duration of fights between a pair of a day 7 adult and a juvenile was 5.0 s and IRQ was 3.0–8.0 s, 3.0 s (IRQ; 2.0–5.1 s) between a pair of a day 5 adult and a juvenile, 3.5 s (IRQ; 1.4–4.3 s) between a pair of a day 3 adult and a juvenile, and 3.0 s (IRQ; 1.7–3.4 s) between a pair of a day 2 adult and a juvenile (Fig. 2b). day 7 adults tended to catch juveniles for a long period that was statistically significantly longer than the fight duration between a pair of a day 2 adult and a juvenile ($U = 68.0$; $P = 0.005$; Mann–Whitney rank-sum test). Spearman rank-order correlation also detected statistically significant positive relationship between DAYs and fight duration ($r_s = 0.330$, $N = 75$; $P = 0.004$).

Loser and winner effects of juvenile crickets

As shown in Fig. 2a, naive juveniles were more likely to win during agonistic bouts against day 2 adults ($P = 0.0013$; binomial test), while they were usually beaten by day 3 adults ($P = 0.09$: binomial test). If juvenile animals acquire a winner or loser effect through previous fighting experience, the outcome of agonistic bouts may likely change. To confirm the validity of this hypothesis, two juveniles were paired first to establish a dominant and subordinate social order, and then, the losing juvenile was paired with a naive day 2 adult, while the winning juvenile was paired with a naive day 3 adult with different intervals of 5 min and 2 h from the first pairing (Fig. 3, inset).

When losing juveniles were paired with day 2 adults, the win rate of juveniles 5 min after a losing experience was 20% (4 wins out of 16 pairs) while the opponent day 2 adults won in the remaining 12 pairs. The win rate of subordinate juveniles was 25% (2 wins out of 8 pairs) following a 2 h interval from their initial losing experience (Fig. 3a). The winning rate of both subordinate juveniles was statistically significantly lower than that of the naive juveniles as a pairing with day 2 adults ($P < 0.001$ in juveniles after a 5 min interval and $P = 0.003$ in juveniles after a 2 h interval; Fisher's exact test), while there was no statistical difference of winning rates between them ($P = 1$: Fisher's exact test). Thus, when juveniles became losers in the previous agonistic bouts, they could not overcome day 2 adults who were beaten by juveniles under usual circumstances. These results strongly suggest that the previous losing experience of an agonistic bout affected subsequent fighting and this loser effect lasted for at least 2 h. The intensity level between naive juveniles and day 2 adults was 3 (median) and an IRQ of 2–5 (Fig. 3b). The aggressive index between a pair of day 2 adults and subordinate juveniles 5 min after losing experience was 2 (median) and an IRQ of 2, while the intensity level between a pairing of day 2 adults with subordinate juveniles after 2 h intervals had a median of 2.5 and an IRQ of 2–3.75 (Fig. 3b). The aggression levels between a pair of day 2 adults and subordinate juveniles 5 min after the losing experience were statistically significantly lower than the aggression level between a pair of naive juveniles and day 2

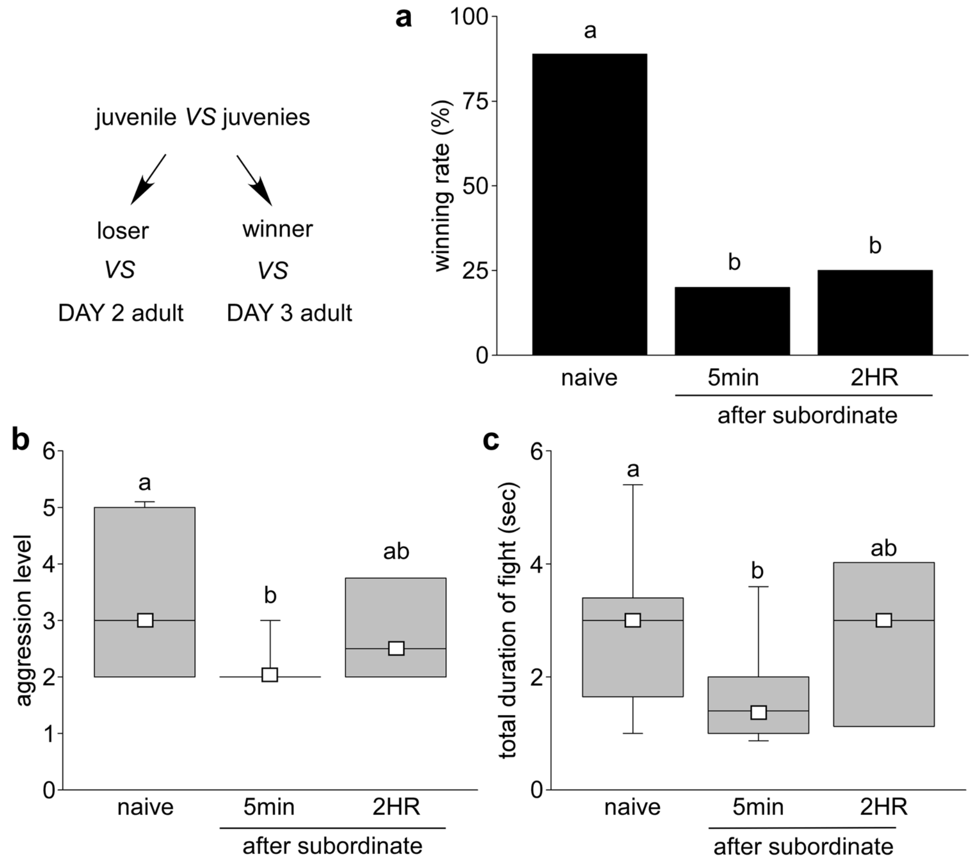

Fig. 3 Loser effect of juvenile crickets. **a** Winning rate of juvenile crickets against day 2 adult crickets. **b** Degree of aggression in pairings between juvenile and day 2 adult crickets. **c** Total duration of agonistic bouts. In **b** and **c**, solid black lines with open squares in the box shows median, box length indicates interquartile range (the 25th and 75th percentiles) and line bars show the 10th and 90th percentiles. Letters above each plot show statistical differences

adults ($U=66.0$; $P=0.003$; Mann–Whitney rank-sum test). Many subordinate juveniles were immediately retreated after antennal contact with day 2 adults (13 out of 16 animals) that suggested a reduction of aggressive motivation of subordinate juveniles as they became losers. Aggression levels of subordinate juveniles were increased as time passed after the losing experience, and no statistically significant differences were found between subordinate juveniles 2 h after the losing experience and naive juveniles ($U=56.5$; $P=0.380$; Mann–Whitney rank-sum test). The total duration of a fight in each pairing group was shown in Fig. 3c. Subordinate juveniles 5 min after first pairing showed the shortest fight duration with a median of 1.4 s and an IRQ of 1.0–2.0 s while naive juveniles and subordinate juveniles 2 h after first pairing had a median of 3.0 s. Statistically significant difference was found between naive and subordinate juveniles 5 min interval after first pairing ($P=0.013$; Mann–Whitney rank-sum test), but no statistically significant difference was observed between other combinations of pairings ($P=1.0$ between naive and subordinate 2 h interval, and $P=0.0.123$ between subordinate 5 min and 2 h intervals; Mann–Whitney rank-sum test).

As shown in Fig. 2a, only 30% of naive juveniles won against day 3 adults (7 wins out of 23 pairs). The juveniles that won in a previous pairings tended to win against naive day 3 adults (Fig. 4a). The win rate of dominant juveniles 5 min after the winning experience was 75% (12 won out of 16 pairings), and was statistically significantly higher than that of naive juveniles ($P=0.009$; Fisher's exact test). After a 2 h interval from the winning experience of the dominant juveniles, the win rate was reduced to 50%, but no statistical difference was found against the win rate of dominant juveniles 5 min after the winning experience ($P=0.363$; Mann–Whitney rank-sum test). The win rate of them was still higher than that of naive juveniles, but no statistically significant difference was found between them ($P=0.405$; Fisher's exact test). Thus, juveniles also showed winner effect but this effect lasted for a shorter period in comparison with the loser effect. The aggression levels of agonistic bouts between day 3 adults and juveniles were not statistically significantly different among the 3 combinations of pairings ($P=0.833$ between naive and dominant juveniles 5 min interval from the winning experience, $P=0.962$ between naive and dominant juveniles 2 h interval, and $P=0.820$ between dominant juveniles 5 min and 2 h intervals; Mann–Whitney rank-sum test). The aggression level was 4 (median) with an IRQ of 2–5 between a pair of naive juveniles and day 3 adults and 3.5 (median) with an IRQ of 2–5 between a pair of day 3 adults and dominant juveniles after 5 min and 2 h intervals (Fig. 4b). Furthermore, the total

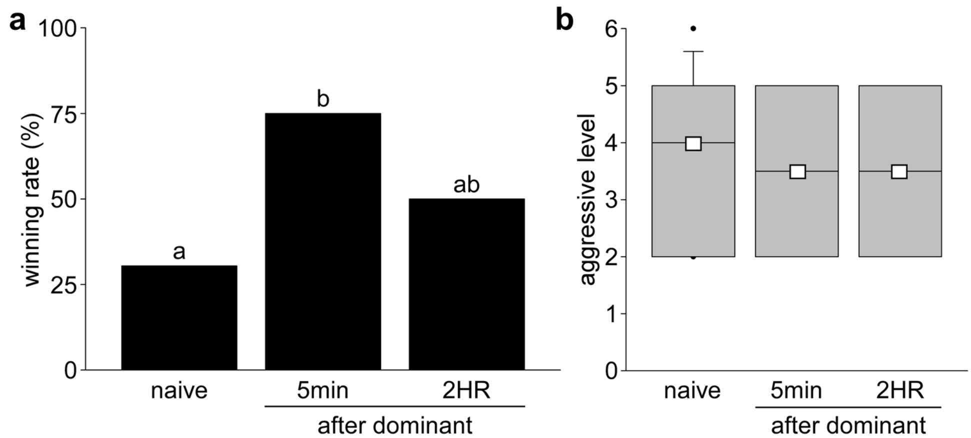

Fig. 4 Winner effect of juvenile crickets. **a** Winning rate of juveniles against day 3 adult crickets. Letter above each plot shows statistical differences. **b** Aggression level of agonistic bouts between juvenile and day 3 adult crickets. Solid black line with open square in the box shows median and, box length indicates interquartile range (the 25th and 75th percentiles). Line bars show the 10th and 90th percentiles and each dot shows each outlier. Letters above each plot show statistical differences

duration of a fight in each pairing group was 3.5 s (median) with an IRQ of 1.4–4.3 s, 2.4 s (median) and an IRQ of 1.6–3.8 s, and 2.1 s (median) with an IRQ of 1.4–3.4 s, respectively. There was also no statistical difference between them ($P=0.258$ between naive and dominant juveniles 5 min interval, $P=0.455$ between naive and dominant juveniles 2 h interval, and $P=0.830$ between dominant juveniles 5 min and 2 h intervals; Mann–Whitney rank-sum test).

Discussion

Agonistic bouts between a pair of adult and juvenile animals

We confirmed in this study that a weight difference of about 5% between a pair of two crickets was not sufficient to allow heavier crickets to win for agonistic bouts. This result is consistent with Hach's argument (1997) that physical asymmetries in mass greater than 10% were necessary for heavier crickets to defeat opponents. On the other hand, we confirmed that day 2 adults cannot beat juveniles, but day 3 and older aged adults can win. Thus, our hypotheses were validated and the pairings between adult and juvenile crickets appear to be good indicator to predict which cricket will defeat an opponent. Sexually mature males are more aggressive than adult males which have not yet produced a spermatophore (Dixon and Cade 1986). Males are considered to be sexually mature if they were 7 or more days past their final moult. Indeed, day 7 adult crickets defeated juveniles in all pairings in this study. Since fat body fresh mass, lipids, protein and glycogen begin to increase from day 3 after adult emergence (Anand and Lorenz 2008), accumulation of them might be related to outcome of agonistic bouts for adult crickets after final moult, since evicted defenders of hermit crabs show low glucose levels (Briffa and Elwood 2004). Furthermore, biogenic amine level in hemolymph mediates cricket aggression (Adamo et al. 1995) and ecdysteroid titres appear to be critical in establishment of dominance hierarchies in the paper wasp (Röseler et al. 1984, 1985). Some neurohormonal factors also might affect agonistic encounters. Further investigations are needed to clarify this point.

Winner and loser effects of juvenile animals

After a defeat against a conspecific adult male cricket, subordinate males show decreased aggressiveness (Adamo and Hoy 1995; Hofmann and Stevenson 2000; Iwasaki et al. 2006). On the other hand, adult winners exhibit hyper-aggressiveness after victory and tend to win their next agonistic bouts (Khazraire and Campan 1999; Rose et al. 2017). Here, we have shown for the first time that juvenile crickets also show winner and loser effects according to the outcome of agonistic bouts between adult and juvenile animals. The winners of sexually immature animals would have benefit that the motivation to fight must be based on competition over other resources than mates and on the prospect to secure future access to an emerging resource (Herberholz et al. 2007).

Naive juveniles were frequently beaten by day 3 adult males, but their winning probability was significantly increased if juveniles were winners in their previous bout. Furthermore, when juveniles became subordinate, they were beaten by day 2 adults. Many subordinate juveniles showed no physical contact or avoided their opponents after initial antennal contact. This depression period in loser juveniles continued for at least 2 h while the hyper-aggressiveness of winner juveniles lasted for no longer than 2 h after victory. More quantitative analyses are needed to determine the exact period of winner and loser effects. These retention times of winner and loser effects of juveniles are, however, consistent to those of adult males. Winners exhibited hyper-aggressiveness for no longer than 20 min, while submissive losers regain their aggressiveness 0.5–3 h after defeat (Adamo and

Hoy 1995; Iwasaki et al.2006; Rillich and Stevenson 2014; Rose et al. 2017).

Crayfish as well as fishes have also been analyzed in detail regarding winner and loser effects during agonistic encounters (Rutte et al. 2006). Size differences of 3% of body length are sufficient for larger crayfish to win (Ueno and Nagayama 2012). In steelhead trout, relative size with a weight advantage of 5% being sufficient to assume dominant status for the larger fish (Abbott et al. 1985). However, winning small animals frequently defeat larger opponents, while losing large animals are beaten by small opponents. In fishes, a loser effect often appears to be more pronounced and to last longer than a winner effect (Bakker et al. 1989; Chase et al 1994; Hsu and Wolf 1999). In the crayfish, by contrast, the winner effects last more than 2 weeks and the loser effect last about 10 days (Momohara et al. 2016). These long-lasting effects involve the action of serotonin, octopamine and tyramine by means of regulating a cAMP-PKA signalling pathway (Momohara et al. 2013, 2016, 2018). Thus, winner and loser effects of the crayfish demonstrate clear practical learning in arthropods and long-term memory formation, since previous agonistic experiences modulate aggressive state of crayfish. By contrast, the retention times of winner and loser effects in crickets are rather short and only last for several hours. This might mean that no second messenger systems are involved in the formation of winner and loser effects in the crickets despite the presence of various biogenic amines that can affect the aggressiveness levels of the crickets. Subordinate males show prolonged depression periods of aggressive motivation for 24 h when repeated defeats are experienced (Rose et al. 2017). Dopamine is necessary for recovery of aggression after social defeat (Rillich and Stevenson, 2014). Dopaminergic receptors activate the cAMP signalling pathway in crayfish (Shiratori et al. 2017). In addition, nitric oxide (NO) is reported to establish the submissive status (Rillich and Stevenson, 2017). Since NO is known to activate cGMP levels and to affect cAMP signalling cascade in both crayfish and crickets (Matsumoto et al. 2009; Mita et al. 2014), an increase in cAMP level might underpin the long-term memory of loser effects in crickets. Further pharmacological behavioural analyses are indispensable to clarify this point.

The neurochemical bases for the formation of the winner and loser effects in the crickets are quite different from those of the crayfish. Octopamine is known to increase aggressiveness of crickets (Stevenson et al. 2005), while octopamine in the crayfish is involved in the loser effect formation in the crayfish (Momohara et al. 2013, 2018). Serotonin is essential for winner effect formation in crayfish (Momohara et al. 2013, 2015), while serotonin is thought to maintain depressed aggressiveness after defeat of crickets (Rillich and Stevenson 2018). Thus, further characterization of the role of biogenic amines and comparison between crickets and crayfish are necessary to clarify the process of evolution to acquire different neurochemical mechanism for winner and loser effects in arthropods.

Acknowledgements We are grateful to Prof. PL Newland for his critical reading of the manuscript. This work was supported by Grants- in-Aid from the Ministry of Education, Science, Sport, and Culture to TN (16K07432). All experiments were carried out in accordance with the Guide for the Care and Use of Laboratory Animals of Yamagata University (Japan).

References

Abbott JC, Dunbrack RL, Orr CD (1985) The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). Behaviour 92:241–253

Abe T, Fujiyama N, Tomimatsu H, Nagayama T (2018) Age-dependent and social status-dependent behavioural plasticity of the cricket *Gryllus bimaculatus*. Anim Behav 14:1–7

Adamo SA, Hoy RR (1995) Agonistic behaviour in male and female field crickets, *Gryllus bimacufatus*, and how behavioural context influences its expression. Anim Behav 49:1491–1501

Adamo SA, Linn CE, Hoy RR (1995) The role of neurohormonal octopamine during 'fight or flight' behaviour in the field cricket *Gryllus bimaculatus*. J Exp Biol 198:1691–1700

Alexander RD (1961) Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour 17:130–223

Anand AN, Lorenz MW (2008) Age-dependent changes of fat body stores and the regulation of fat body lipid synthesis and mobilisation by adipokinetic hormone in the last larval instar of the cricket, Gryllus bimaculatus. J Insect Physiol 54:1404–1412

Bakker ThCM, Bruijn E, Sevenster P (1989) Asymmetrical effects of prior winning and losing on dominance in sticklebacks (*Gasterosteus aculeatus*). Ethology 82:224–229

Balsam JS, Stevenson PA (2020) Pre-adult aggression and its long-term behavioural consequences in crickets. PLoS ONE 15:e0230743

Beacham JL, Newman JA (1987) Social experience and the formation of dominance relationships in the Pumpkinseed sunfish, *Lepomis gibbosus*. Anim Behav 35:1560–1563

Bergman DA, Kozlowski CP, Meintyre JC, Huber R, Daws A, Moore PA (2003) Temporal dynamics and communication of winner-effects in the crayfish, *Orconectes restucus*. Behaviour 140:805–825

Briffa M, Elwood RW (2004) Use of energy reserves in fighting hermit crabs. Proc R Soc Lond B Biol Sci 271:373–379

Bovbjerg RV (1953) Dominance order in the crayfish, *Orconectes virilis* (Hagan). Physiol Zool 26:173–178

Chase ID, Bartolomeo C, Dugatkin LA (1994) Aggressive interactions and inter-contest interval: how long do winners keep winning? Anim Behav 48:394–400

Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). Anim Behav 27:211–225

Dixon KA, Cade WH (1986) Some factors influencing male-male aggression in the field cricket Gryllus integer (time of day, age, weight and sexual maturity). Anim Behav 34:340–346

Francis RC (1983) Experiential effects on agonistic behavior in the paradise fish, *Macropodus opercularis*. Behaviour 85:292–313

Frankel DG, Arbel T (1980) Group formation by two-year olds. Int J Behav Dev 3:287–298

Fuxjager MJ, Forbes-Lorman RM, Coss DJ, Auger CJ, Auger AP, Marler CA (2010) Winning territorial disputes selectively enhances androgen sensitivity in neural pathways related to motivation and social aggression. Proc Natl Acad Sci USA 107:12393–12398

Goldman L, Swanson H (1975) Population control in confined colonies of golden hamsters (*Mesocricetus auratus* Waterhouse). Z Tierpsychol 37:225–236

Goubault M, Decuigniere M (2012) Previous experience and contest outcome: winner effects persist in absence of evident loser effects in a parasitoid wasp. Am Nat 180:364–371

Hack MA (1997) Assessment strategies in the contests of male crickets, *Acheta domesticus* (L.). Anim Behav 53:733–747

Herberholz J, McCurdy C, Edwards DH (2007) Direct benefits of social dominance in juvenile crayfish. Biol Bull 213:21–27

Hofmann HA, Stevenson PA (2000) Flight restores fight in crickets. Nature 403:613

Hsu Y, Wolf LL (1999) The winner and loser effect: integrating multiple experiences. Anim Behav 57:903–910

Hsu Y, Earley RL, Wolf LL (2006) Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biol Rev 81:33–74

Iwasaki M, Delago A, Nishino H, Aonuma H (2006) Effects of previous experience on the agonistic behaviour of male crickets, *Gryllus bimaculatus*. Zool Sci 23:863–872

Kaczer L, Pedetta S, Maldonado H (2007) Aggressiveness and memory: Subordinate crabs present higher memory ability than dominants after an agonistic experience. Neurobiol Learn Mem 87:140–148

Kasumovic MM, Elias DO, Sivalinghem S, Mason AC, Andrade MCB (2010) Examination of prior contest experience and the retention of winner and loser effects. Behav Ecol 21:404–409

Khazraie K, Campan M (1999) The role of prior agonistic experience in dominance relationships in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). Behav Process 44:341–348

Lan YT, Hsu Y (2011) Prior contest experience exerts a long-term influence on subsequent winner and loser effects. Front Zool 8:28–10

Mathis A, Britzke E (1999) The roles of body size and experience in agonistic displays of the Ozark zigzag salamander, *Plethodon angusticlavius*. Herpetologica 55:344–352

Matsumoto Y, Hatano A, Unoki S, Mizunami M (2009) Stimulation of the cAMP system by the nitric oxide-cGMP system underlying the formation of long-term memory in an insect. Neurosci Lett 467:81–85

McDonald P, Topoff H (1986) The development of defensive behavior against predation by army ants. Dev Psychobiol 19:351–367

Mita A, Yoshida M, Nagayama T (2014) Nitric oxide modulates a swimmeret beating rhythm in the crayfish. J Exp Biol 217:4423–4431

Momohara Y, Kanai A, Nagayama T (2013) Aminergic control of social status in crayfish agonistic encounters. PLoS ONE 8:e74489

Momohara Y, Yoshida M, Nagayama T (2015) Serotonergic modulation of social status-dependent behavioural plasticity of the crayfish avoidance reaction. J Comp Physiol A 201:1063–1074

Momohara Y, Minami H, Kanai A, Nagayama T (2016) Role of cAMP signalling in winner and loser effects in crayfish agonistic encounters. Eur J Neurosci 44:1886–1895

Momohara Y, Aonuma H, Nagayama T (2018) Tyraminergic modulation of agonistic outcomes in crayfish. J Comp Physiol A 204:465–473

Moore AJ, Clccone WJ, Breed MD (1988) The influence of social experience on the behavior of male cockroaches, *Nauphoeta cinerea*. J Insect Behav 1:157–168

Otronen M (1990) The effect of prior experience on the outcome of fights in the burying beetle, *Nicrophorus humatio*. Anim Behav 40:980–1004

Rillich J, Stevenson PA (2014) A fighter's comeback: dopamine is necessary for recovery of aggression after social defeat in crickets. Horm Behav 66:696–704

Rillich J, Stevenson PA (2017) Losing without fighting—simple aversive stimulation induces submissiveness typical for social defeat via the action of nitric oxide, but only when preceded by an aggression priming stimulus. Front Behav Neurosci 11:1–15

Rillich J, Stevenson PA (2018) Serotonin mediates depression of aggression after acute and chronic social defeat stress in a model insect. Front Behav Neurosci 12:233

Rose J, Rillich J, Stevenson PA (2017) Chronic social defeat induces long-term behavioral depression of aggressive motivation in an invertebrate model system. PLoS ONE 12:e0184121

Röseler P-F, Röseler I, Strambi A, Augier R (1984) Influence of insect hormones on the establishment of dominance hierarcxhies among foundresses of the paper wasp, *Polistes gallicus*. Behav Ecol Sociobiol 15:133–142

Röseler P-F, Röseler I, Strambi A (1985) Role of ovaries and ecdysteroids in dominance hierarchy establishment among foundresses of the primitively social wasp, *Polistes gallicus*. Behav Ecol Sociobiol 18:9–13

Rutte C, Taborsky M, Brinkhof MWG (2006) What sets the odds of winning and losing? Trends Ecol 21:16–21

Sato D, Nagayama T (2012) Development of agonistic encounters in dominance hierarchy formation in juvenile crayfish. J Exp Biol 215:1210–1217

Schuett GW (1997) Body size and agonistic experience affect dominance and mating success in male copperheads. Anim Behav 54:213–224

Shiratori C, Suzuki N, Momohara Y, Shiraishi K, Aonuma H, Nagayama T (2017) Cyclic AMP-regulated opposing and parallel effects of serotonin and dopamine on phototaxis in the Marmorkrebs (marbled crayfish). Eur J Neurosci 46:1863–1874

Sneddon LU, Huntingford FA, Taylor AC, Orr JF (2000) Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). J Zool 250:397–403

Stevenson PA, Hofmann HA, Schoch K, Schildberger K (2000) The fight and flight responses of crickets depleted of biogenic amines. J Neurobiol 43:107–120

Stevenson PA, Dyakonova V, Rillich J, Schildberger K (2005) Octopamine and experience-dependent modulation of aggression in crickets. J Neurosci 25:1431–1441

Tokarz RR (1985) Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Anim Behav 33:746–753

Ueno R, Nagayama T (2012) Interlocking of chelae is a key factor for dominance hierarchy formation in crayfish. J Exp Biol 215:2841–2848

Whitehouse MA (1997) Experience influences male-male contests in the spider *Argyrodes antipodiana* (Theridiidae: Araneae). Anim Behav 53:913–923

Wilson EO (1975) Sociobiology. Harvard University Press, New York