Original Article

Cost of an elaborate trait: a trade-off between attracting females and maintaining a clean ornament

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Many sexually selected ornaments and weapons are elaborations of an animal's outer body surface, including long feathers, colorful skin, and rigid outgrowths. The time and energy required to keep these traits clean, attractive, and in good condition for signaling may represent an important but understudied cost of bearing a sexually selected trait. Male fiddler crabs possess an enlarged and brightly colored claw that is used both as a weapon to fight with rival males and also as an ornament to court females. Here, we demonstrate that males benefit from grooming because females prefer males with clean claws over dirty claws but also that the time spent grooming detracts from the amount of time available for courting females. Males, therefore, face a temporal trade-off between attracting the attention of females and maintaining a clean claw. Our study provides rare evidence of the importance of grooming for mediating sexual interactions in an invertebrate, indicating that sexual selection has likely shaped the evolution of self-maintenance behaviors across a broad range of taxa.

Key words: **cost, fiddler crab, grooming, mate choice, sexual selection.**

INTRODUCTION

Sexually selected ornaments and weapons are assumed to be costly to produce and bear (Andersson 1994; Kotiaho 2001; Searcy and Nowicki 2005). For example, antler development in deer results in seasonal osteoporosis (Moen et al. 1999); colorful ornaments in guppies make males more conspicuous to predators (Godin and McDonough 2003); and elaborate tails in swordtails make swimming more energetically demanding (Basolo and Alcaraz 2003). Costs are an essential factor in explaining why choosy females and rival males pay attention to sexually selected traits because traits that are costly to produce and bear are likely to be reliable indicators of a male's quality (Zahavi 1975; Nur and Hasson 1984; Grafen 1990; Kotiaho 2001; Searcy and Nowicki 2005). However, despite the importance of costs to sexual selection theory, our understanding of the costs of most ornaments and weapons remains limited (Kotiaho 2001; McCullough and Emlen 2013; Thavarajah et al. 2016).

Self-maintenance behaviors, such as grooming, preening, and bathing, are major components of an animal's daily repertoire (Spruijt et al. 1992), and mammals (Boccia 1983; Mooring et al. 2004; Kalueff et al. 2016), birds (Cotgreave and Clayton 1994),

insects (Kovac 1993; Basibuyuk and Quicke 2008), and crustaceans (Bauer 1978) all devote a considerable percentage of their daily time budget to maintaining the condition of their outer body surface. Although grooming confers obvious health benefits (Spruijt et al. 1992), primarily due to the removal of harmful ectoparasites (Bauer 1978; Mooring et al. 2004; Waite et al. 2012), it also incurs significant fitness costs by increasing energy requirements (Croll and McLaren 1993; Giorgi et al. 2001) and reducing the time available for other behaviors, such as vigilance, feeding, and resting (Redpath 1988; Maestripieri 1993; Cords 1995; Christe et al. 1996; Hawlena et al. 2007). Because many sexually selected ornaments and weapons are elaborations of the outer body surface (e.g., long feathers, colorful skin and plumage, manes, crests, and rigid outgrowths), they may contribute further to an individual's self-maintenance costs. Specifically, the extra time and energy required to keep these traits clean, attractive, and in good condition for signaling may represent an important but relatively unexplored fitness cost of bearing sexually selected traits (Walther 2003; Walther and Clayton 2004). Here, we investigate the costs of maintaining an elaborate ornament using fiddler crabs as a model system.

Fiddler crabs are visually oriented and brightly colored intertidal crustaceans with complex social systems (Detto et al. 2006; Zeil et al. 2006; Zeil and Hemmi 2006). They are an excellent model for studying sexual selection because males have a greatly enlarged (major) claw that is used both as a weapon in male–male fights over

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ownership of breeding burrows and as an ornament in waving displays to attract mate-searching females (Crane 1975; Hyatt and Salmon 1978; Pope 2000). Males with larger claws are more likely to win fights with other males (Jennions and Backwell 1996; Pratt et al. 2003) and are also more likely to be chosen by females as mates (Backwell and Passmore 1996; Milner et al. 2010).

Given the importance of visual signaling for mediating social interactions in fiddler crabs (Zeil et al. 2006), and in particular the importance of claw color and ultraviolet (UV) reflectance (Detto et al. 2006; Detto 2007; Detto and Backwell 2009), males are likely to benefit from maintaining the appearance of their claws and, therefore, should devote considerable time and energy to grooming. In support of this hypothesis, males in some species (e.g., *Uca chlorophtalmus*) spend more than 10% of their daily time budget on grooming (Weis and Weis 2004), and males generally spend more time grooming than females (Weis and Weis 2004; Tina et al. 2016; Tina et al. 2019). However, no study has tested whether the time spent grooming detracts from other fitness-enhancing activities or whether claw cleanliness affects the outcome of intrasexual or intersexual interactions. In this study, we conducted a series of field experiments in the banana fiddler crab, *Austruca mjoebergi*, to evaluate the importance of grooming in mediating social interactions with both rival males and choosy females. We also test the hypothesis that the elaborate claws of male fiddler crabs are costly to maintain due to a temporal trade-off with courtship activities.

METHODS

We studied a population of *A. mjoebergi* in their natural intertidal habitat at East Point Reserve in Darwin, Australia. Data were collected from October to December to correspond with the species' peak mating period. Males frequently use their feeding claw to clean particles of sediment off their major claw, a behavior hereafter called grooming. Grooming occurs typically in bouts that last a few seconds in between waves (Supplementary Video 1) or sometimes in a single bout lasting several seconds after a male emerges from his burrow (Supplementary Video 2). By contrast, females do not appear to groom their two feeding claws.

We studied the importance of male grooming in four different contexts: time budgets, male–male competition, female choice, and temporal trade-offs. The time-budget samples, female choice trials, and temporal trade-off observations were conducted during the diurnal neap tides when females are most active in searching for mates. The male–male competition trials were conducted during the diurnal spring tides when males are most territorial.

Time budgets

We conducted 10-min focal observations (Altmann 1974) on surface-active individuals ($n = 50$) to estimate the amount of time males spend grooming their claws. Observations were conducted through 8×25 binoculars between 10 AM and 3 PM when crabs are most active. We measured the total amount of time a male spent grooming his major claw during the 10-min sample using a stopwatch. Focal males were haphazardly selected from surface-active individuals on the mudflat, and we alternated between individuals initially identified in the sun and shade to account for potential differences in time budgets between microhabitats (Chou et al. 2019). Because crabs were not individually marked, we sampled individuals from different locations on the mudflat to avoid repeat sampling. Males that were not surface-active for the entire 10-min focal sample (e.g., because they retreated into their burrow) were excluded

from the analyses (<10% of males). At the end of the sample, we captured the focal male and measured his claw length to the nearest 0.1 mm using dial calipers. We used a two-tailed *t*-test to compare the amount of time males spent grooming in the sun and shade. We fitted a general linear model with claw size as the explanatory variable and time spent grooming as the response variable to test whether males with longer claws spend more time grooming.

Male–male competition

To evaluate whether males benefit from having clean claws in the context of male–male fights over burrow ownership, we staged fights between unmanipulated resident males and focal intruder males with either clean ($n = 51$) or dirty claws ($n = 49$). Burrows are used as refugia from predators, high tide, high temperatures, and during mating, so burrow ownership is important for both survival and reproduction. Resident males frequently and aggressively defend their burrows against wandering intruder males that have either lost their burrow in a fight with another male or forfeited their burrow to a female following mating (Jennions and Backwell 1996; Backwell and Jennions 2004; Morrell et al. 2005).

To stage fights, we captured males that were defending their territories and released them back into the colony (Jennions and Backwell 1996; Morrell et al. 2005). Captured males were released several meters from their burrow to avoid encounters with familiar neighbors and observed through binoculars as they wandered across the mudflat. Males were measured for claw length and then their claw was painted either with mud from the mudflat (Figure 1; "dirty" claw) or a clean brush ("clean" claw). In order to get the mud to stay on the claw, our painting treatment inevitably made claws slightly dirtier than typically observed in the field. However, males are sometimes found with large clumps of debris on their claws under natural conditions, and what appears dirty to a human observer may not appear equivalently dirty to a crab or vice versa. To minimize handling disturbance, experimenters wore latex gloves and placed a plastic sheet between the crab's claw and body during the painting treatment.

After being released, most males took several seconds before resuming normal activity. We, therefore, measured a male's fighting latency as the time elapsed between becoming active and initiating a fight with another resident male. We also recorded whether a

Figure 1
Example of male using his feeding claw to groom his experimentally dirtied major claw.

male spent any time grooming his claw before initiating a fight (yes/no) and whether the male won or lost the fight. Males were defined as winners if they displaced the resident from his burrow and as losers if they were unable to displace the resident and continued wandering. Previous studies have shown that fights end when a male is displaced from his burrow and that the displacement is permanent (Backwell and Jennions 2004; Morrell et al. 2005). We used Fisher's exact tests to compare the likelihood of grooming for males with clean or dirty claws, the likelihood of winning for males with clean or dirty claws, and the likelihood of winning for males that did or did not groom their claw. We used a two-tailed *t*-test to compare the fighting latency between males that did or did not groom.

Female choice

We conducted female mate choice trials ($n = 40$) to evaluate whether males benefit from having clean claws in the context of attracting mates. We captured mate-searching females wandering on the mudflat and tested their preference for males with clean versus dirty claws using custom-built robotic crabs (Booksmythe et al. 2008; Reaney et al. 2008; Kahn et al. 2013). Each robot consisted of a plaster claw replica (21.0 mm long) molded from a real male claw and painted with yellow enamel paint. Because natural *A. mjoebergi* claws reflect UV light, and females prefer UV-reflecting claws over claws that do not reflect UV light (Detto and Backwell 2009), we also painted the entire surface of the claw replicas with a UV marker (Edding 8280). Each claw was attached to a metal arm that was driven by a small motor to mimic the species' claw waving pattern at a rate of 16.8 waves/min. A pair of identical robots were placed in a 60- × 60-cm-level test arena that was covered with a smooth layer of mudflat sediment and positioned 15 cm away from each other and 25 cm away from the choosing female. Once positioned, the claws were painted either with mud from the mudflat ("dirty" claw) or a clean brush ("clean" claw). We alternated the position of the clean and dirty claw every fifth trial to control for potential side preferences.

At the start of each mate-choice trial, a female was placed under a transparent cup in front of the robotic crabs, allowed to observe the robotic crabs for two complete wave cycles, and then released from the cup using a remote trigger. Females were counted as having chosen a male if they moved directly toward and stopped at the base of one of the robotic crab units. Females that gave a startle response (i.e., dashed on release to the perimeter of the arena) or were motionless for >3 min after release were retested a maximum of three times before being excluded from the data set. At the end of the trials, females were released into the population to continue mate searching. We compared female choices between clean and dirty claws using a binomial test.

Temporal trade-offs

We tested for a potential cost of grooming due to a trade-off in the time spent maintaining a clean claw and courting females. Specifically, we conducted 2-min focal observations on males with either clean or dirty claws to measure the amount of time spent grooming versus waving. For each sample, we captured a resident male from his burrow and placed a plastic fence around the entrance to prevent other individuals from entering. Captured males were measured for claw length, painted either with mud ("dirty" claw, $n = 23$) or a clean brush ("clean" claw, $n = 23$) as described above, and then returned to their territory. We widened the burrow entrance slightly with a stick to minimize the chances of a "dirty"

claw being wiped clean as the male entered or exited his burrow. To encourage the males to emerge from their burrow and engage in courtship activity, we tethered a mate-searching female to a short (~5 cm) piece of cotton thread and anchored the tether near the male's territory. Focal males were recorded with a video camera (Sony Handycam HDR-PJ410 or DCR-SR45) and observed for 2 min following the initiation of his first wave (Supplementary Video 1). Focal observations were limited to 2 min to minimize stress on the tethered females. We measured the amount of time a male spent either grooming his major claw or waving using a stopwatch. We fitted general linear models to compare the relationships between time spent grooming, time spent waving, and claw size, and used one-tailed *t*-tests to compare whether males with dirty claws spend more time grooming and/or less time waving. All statistical analyses were performed in R version 3.6.3.

RESULTS
Time budget

During the 10-min focal samples, males groomed for 13.2 ± 2.6 s (mean ± standard error [SE]; $n = 50$), indicating that approximately 2.2% of a male's time budget is devoted to grooming. These results are comparable to scan sampling data from the same population (see Chou et al. 2019 for details) that estimated that 1.4% of a male's time budget is devoted to grooming (PRY Backwell, unpublished data). For comparison, *A. mjoebergi* males spend 14.7% of their time waving and 34.8% of their time feeding (PRY Backwell, unpublished data). Males spent as much time grooming in the sun and shade ($t = -1.76$, $P = 0.09$), and there was no relationship between time spent grooming and claw size ($F_{1,48} = 2.44$, $P = 0.12$).

Male–male competition

Males with dirty claws were more likely to groom their claw before initiating a fight than males with clean claws (odds ratio = 5.92, $P < 0.001$), and males that groomed their claws initiated fighting significantly later than males that did not groom ($t = -3.01$, $P < 0.01$). However, there was no difference in the likelihood of winning a fight for males with clean versus dirty claws (odds ratio = 1.97, $P = 0.17$) or for males that did versus did not groom (odds ratio = 1.25, $P = 0.63$). These results suggest that grooming, and thereby maintaining a clean claw, is not important in the context of male–male competition.

Female choice

Twenty-nine of 40 females (or 73%) preferred the clean claw over the dirty claw in our mate-choice trials, indicating that females have a strong preference for males with clean claws (Figure 2; binomial test: $P < 0.01$). These results suggest that grooming, and thereby maintaining a clean claw, is important in the context of female mate choice.
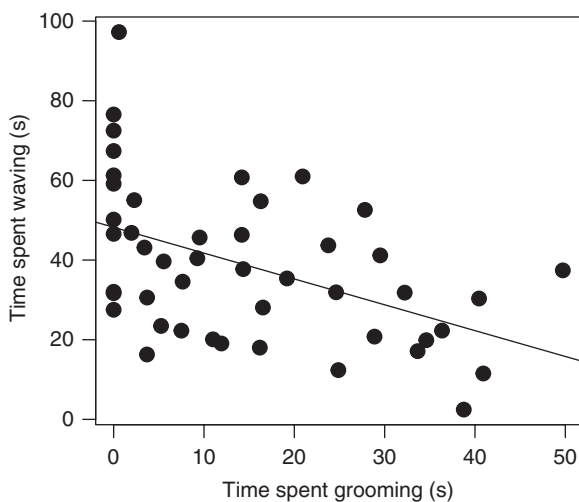
Temporal trade-offs

There was a negative relationship between time spent grooming and time spent waving in our 2-min, temporal trade-off observations (Figure 3; $R^2 = 0.23$, $F_{1,44} = 12.87$, $P < 0.001$), which suggests that males face a trade-off between maintaining a clean claw and courting females. Additionally, males with dirty claws spent more time grooming ($t = 3.60$, $P < 0.001$) and less time waving ($t = -1.71$, $P < 0.05$) than males with clean claws. There was a positive relationship between claw size and time spent grooming
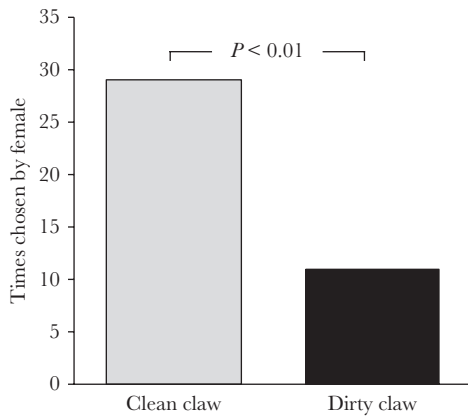
Figure 2
Female preferences for robotic male crabs with either clean or dirty claws. Twenty-nine females chose the clean claw, whereas only 11 females chose the dirty claw (binomial test: $P < 0.01$).

Figure 3
Relationship between time spent grooming versus waving during the temporal trade-off focal observations. Males that spent more time grooming spent less time waving to mate-searching females ($R^2 = 0.23$, $F_{1,44} = 12.87$, $P < 0.001$).

($F_{1,44} = 4.65$, $P < 0.05$), indicating that males with larger claws spend more time grooming than males with smaller claws. There was also a trend that males with larger claws spent less time waving ($\beta = -1.89$, SE = 1.27), but the relationship between claw size and time spent waving was not statistically significant ($F_{1,44} = 2.22$, $P = 0.14$).

DISCUSSION

The major claw of male fiddler crabs is a classic example of the extremes in trait exaggeration that can result from sexual selection, with claws comprising nearly half a male's total body mass in some species (Crane 1975). Previous studies have shown that the exaggerated claws incur significant physiological costs due to increased metabolic demands and reduced locomotor performance (Allen and Levinton 2007; Gerald and Thiesen 2014; Tullis and Straube 2017). Here, we provide evidence for an additional cost: the time required to maintain a clean claw. We

demonstrate that *A. mjoebergi* males devote a nontrivial amount of their daily time budget to claw grooming and that they benefit from doing so because females prefer mates with clean claws over dirty claws. However, because the time spent maintaining a clean claw cannot be devoted to other fitness-enhancing activities, males face a trade-off between the time they can spend grooming and courting females. Our study indicates that the time constraints of grooming are an important but understudied cost of sexually selected ornaments (Walther and Clayton 2004).

Females showed a strong preference for males with clean claws compared to males with dirty claws, but we do not know the specific cue(s) that females used as the basis for their mate choice. For example, given that *A. mjoebergi* females use color vision during mate discrimination (Detto 2007) and also prefer claws that reflect UV light over claws that do not reflect UV (Detto and Backwell 2009), females may have found dirty claws less attractive than clean claws due to differences in chroma and/or a reduction in UV reflectance (Zampiga et al. 2004; Griggio et al. 2010). Conversely, dirty claws may have had little effect on the outcome of male–male fights because UV cues are not used in aggressive interactions (Detto and Backwell 2009). We hypothesize that the sediment on dirty claws masks chromatic and/or UV cues that are used by females in mate discrimination, as demonstrated for unpreened feathers in budgerigars (Griggio et al. 2010), but it is also possible that females dislike dirty claws due to cues from the sediment itself.

We found a positive relationship between claw length and time spent grooming in our temporal trade-off observations, which indicates that males with larger claws devote more time to claw maintenance than males with smaller claws. It is currently unclear if males with larger claws also incur a greater cost of claw maintenance than males with smaller claws. Although there was a trend for males with larger claws to spend less time waving, this relationship was not statistically significant, perhaps due to a relatively small sample size. Our findings are consistent with observations in another fiddler crab species, *Tubuca rosea*, in which larger males spent more time grooming than smaller males (Tina et al. 2019), but contrast with observations in *Uca annulipes* (Tina et al. 2016) and our own time budget estimates in which there was no relationship between male size and time spent grooming. We note that the males used in our time budget experiment were not presented with a mate-searching female, so they probably were not engaged in maximum levels of courtship (Pope 2000). Future studies are needed to determine whether male fiddler crabs increase their rates of grooming in the presence of receptive females and if/how males balance their efforts grooming versus waving in order to maximize their attractiveness towards females.

Future comparative studies are also needed to explore how male investment in grooming differs among species depending on the intensity of sexual selection and the relative importance of fighting versus signaling (McCullough et al. 2016). We hypothesize that males spend more time grooming in burrow-mating species, in which males wave vigorously to attract mate-searching females to their burrows, and less time grooming in surface-mating species, in which males search for receptive females and engage in little or no courtship waving before mating (deRivera and Vehrencamp 2001; Zeil et al. 2006; Zeil and Hemmi 2006). Thus, species that spend more time signaling are expected to also spend more time grooming in order to keep their claws (signals) as bright and attractive as possible (McCullough et al. 2016; Tina et al. 2016). Similar patterns have been demonstrated in birds: species with ornamental plumage (i.e., feathers that are not used explicitly for flight or

insulation) devote more time to preening than sister species that lack ornamental plumage, which suggests that intense sexual and/or social selection increases the importance of self-maintenance (Walther and Clayton 2004).

More broadly, this study expands our understanding of the importance of grooming for sexual selection in invertebrates. Previous studies in birds and mammals have shown that self-maintenance behaviors have an important function in sexual contexts. For example, preening in budgerigars improves the UV reflectance of feathers and thereby makes males more attractive to females (Zampiga et al. 2004; Griggio et al. 2010), and self-grooming in prairie voles transmits chemical signals about the groomer that affect interactions with opposite-sex conspecifics (Ferkin et al. 1996, 2001). By contrast, studies in invertebrates have focused primarily on the naturally selected benefits of grooming, such as preventing the buildup of settling organisms (Bauer 1975, 1978) and microbial contamination (Kovac 1993). Grooming in insects has even been described as an essentially individual activity that has little influence on the behavior of conspecifics (Matthews and Matthews 2010). Our findings clearly contradict this interpretation: the fact that female fiddler crabs discriminate between males based on the cleanliness of their claws indicates that grooming can indeed influence the outcome of social interactions in invertebrates. Thus, sexual selection has likely shaped the evolution of self-maintenance behaviors across a broad range of taxa.

SUPPLEMENTAL MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

Supplemental video 1. Representative video of a two-minute, temporal tradeoff focal observation showing typical waving and grooming behavior. The focal male has a "clean" claw. The entrance of his burrow is designated by the wooden pointer. The tethered female appears at the end of the video at the bottom of the frame.

Supplemental video 2. Example of a long grooming bout.

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