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# THE INFLUENCE OF ANDROGENIC GLAND IMPLANTATION
ON THE AGONISTIC BEHAVIOR OF FEMALE CRAYFISH
(CHERAX QUADRICARINATUS) IN INTERACTIONS
WITH MALES

by

ILAN KARPLUS[1,2], AMIR SAGI[3], ISAM KHALAILA[3] and ASSAF BARKI[1,4]

([1] Department of Aquaculture, Institute of Animal Science, Agricultural Research
Organization, P.O. Box 6, Bet Dagan, 50250, Israel; [3] Department of Life Sciences and the
Institute for Applied Biosciences, Ben-Gurion University of the Negev, P.O. Box 653,
Beer-Sheva, 84105, Israel)

## Summary

The effect of the androgenic gland (AG) on female agonistic behavior was studied in the
Australian freshwater crayfish *Cherax quadricarinatus*. Interactions between large males and
smaller individuals of three types — sham-operated females, females implanted with the AG
and intact males — were compared. Half-hour-long pair encounters were staged in large
aquaria and monitored with a video camera. Interactions between crayfish of the same or
opposite gender(s) were of a clearly agonistic character, without any courtship or reproductive
elements. The large males were the winners of all fights. Small males fought more often and
for longer periods of time, and grasped their male opponents for longer periods of time, than
sham operated females. AG-implanted females occupied an intermediate position between
the two genders in their fighting behavior. In addition, AG-implanted females performed
'crawling over' (a tolerance-indicative act which is more pronounced towards the other sex)
over the large males less frequently than the sham operated females did, and were also treated
by these males more like males than females, with regard to this behavior. The behavioral
changes in AG-implanted females followed the general trend of masculinization also evident
in the morphological and physiological changes in their gonads and the appearance of male
secondary sexual characters.

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## Introduction

Animals commonly exhibit aggressive behavior during competition for limited resources. Males fight particularly fiercely when the resource at stake is a mate. Thus, in general, the same hormones that control sexual characteristics are likely also to influence agonistic behavior (Huntingford & Turner, 1987). Numerous studies have shown the role of androgens in the regulation of aggressive behaviors in vertebrates. However, the study of the hormonal regulation of agonistic behavior in crustaceans is still in its infancy (*e.g.* Bolingbroke & Kass-Simon, 2001), in contrast to the fact that this elaborate behavior pattern in crustaceans has been well studied, particularly among Decapoda (Dingle, 1983; Hyatt, 1983).

The source of androgens in male crustaceans is the androgenic gland (AG). This gland was first discovered over half a century ago by Cronin (1947) in the decapod crab *Callinectes sapidus*. Several years later Charniaux-Cotton (1954) and Legrand (1955) suggested for the first time the involvement of this gland in the regulation of the differentiation of primary and secondary male sexual characteristics, and inhibition of female differentiation, in amphipods and isopods. Recently, the AG hormone (AGH) was purified and characterized as a glycosylated protein in the isopod *A. vulgare* (Martin *et al.*, 1999; Okuno *et al.*, 1999).

Since the AGH has not yet been identified in decapod crustaceans most of the research on the AGH in this group still relies on AG implantation into females and removal from males. The AG has been manipulated in various decapod crustaceans (*e.g.* Nagamine *et al.*, 1980; Mohamed & Diwan, 1991) including crayfish (*e.g.* Taketomi & Nishikawa, 1996; Khalaila *et al.*, 2001). Overall, the rate of success of these manipulations was dependent on the age of the subject: the younger the subject the greater the impact (Sagi & Khalaila, 2001). The greatest impact of AG implantation, *i.e.* complete sex reversal and the formation of fertile neo-males, have been obtained in the freshwater prawn, *Macrobrachium rosenbergii* (Nagamine *et al.*, 1980; Malecha *et al.*, 1992). In studies involving crayfish, AG implantation inhibited the ovaries and development of secondary female characteristics and induced secondary male characteristics (Taketomi & Nishikawa, 1996; Fowler & Leonard, 1999), but no fertile males were obtained. The AG of *Cherax quadricarinatus*, the model crayfish of this study, has been identified as a long, thin, cord-like tissue attached to the subterminal (ejaculatory) portion

of the sperm duct (Khalaila *et al.*, 2001). Studies in this species (Khalaila *et al.*, 1999, 2001; Sagi *et al.*, 1999) revealed, as in other crayfish, inhibition of female primary and secondary sex characteristics and induction of male secondary sex characterisitics by the AG. So far, to the best of our knowledge, there have been no studies which directly tested the behavioral effect of the AG in crustaceans by means of either AG removal or implantation, despite the fact that both morphological and physiological effects of this gland have been known for almost half a century (see reviews by Sagi *et al.*, 1997; Sagi & Khalaila, 2001).

Previous studies of the agonistic behavior of *C. quadricarinatus* (Levi, 1997; B.A. Hazlett, pers. comm.) revealed the typical crayfish pattern (*e.g.* Bruski & Dunham, 1987; Tierney *et al.*, 2000) in this species. In accordance with predictions of game theory models (Enquist & Leimar, 1983; Leimar & Enquist, 1984), contests between two crayfish generally progress in a stepwise manner of an escalating sequence of aggressive elements. During the initial approach the two opponents assume an elevated position and face each other with the chelipeds moderately spread frontally. When facing each other, the two opponents may sometimes exchange several rapid strikes of both chelipeds before they come into physical contact. Escalated fighting starts when the opponents perform chelae contact, usually with interlocked chelae. During fighting the opponents engage in pushing against each other, which appears to be a contest of strength. The escalated fighting culminates in grasping each other's anterior body (*e.g.* mouthparts, antenae, walking legs). The contest may be terminated by the loser retreating (either walking or tail flipping) or turning and lowering its body against the substrate, at any stage of the contest. Escalated fighting commonly occurred in encounters between sexually mature females in various stages of their reproductive cycle (*i.e.* non-berried and berried females carring non-hatched or hatched eggs) (Levi, 1997). However, a different pattern, which did not include fighting, was sometimes seen in interactions between males and females (B.A. Hazlett, pers. comm.). In a preliminary account of the reproductive behavior of *C. quadricarinatus* Sammy (1988) suggested that males exhibit some elements of courtship prior to copulation. A detailed investigation of the mating behavior (Barki & Karplus, 1999) revealed that in order to accomplish a successful copulation the male should roll over its back and assume a male-beneath-female position. This action is performed with the aid of the female and requires a high degree of cooporation between the

male and female, which is unlikely under aggressive circumstances. Taken together, these findings imply that each gender might exhibit differing agonistic behavior in intra- and inter-gender interactions. Thus, we hypothesized that if an adrogenic factor from the AG influences male behavior, then interactions between AG-implanted females and males should differ from normal intergender interactions and tend to resemble male intargender interactions in terms of agonistic behavior.

In the present study we examined this hypothesis by comparing the agonistic behavior of AG-implanted females with that of males or females in interactions with dominant males. We demonstrated alterations in AG-implanted females towards male-like agonistic behavior, indicating some masculinization effects of the AG on behavior.

## Materials and methods

### Animals, AG implantations and apparatus

Large males (42.0 ± 15.3 g) originating from a pond population were transferred to the laboratory at the Department of Aquaculture, ARO, Bet Dagan, where they were placed in 50 × 25 × 40-cm aquaria, divided into two by an opaque partition, with a single male occupying each half. The males were maintained at 26-28 °C under a 12L/12D photoperiod for 6-7 months, until testing; they were isolated visually and tactually but not chemically, as all shared the same recirculating water system. They were fed daily on a mixed diet of 35% protein fish pellets and wheat grains provided *ad libitum*.

Immature *C. quadricarinatus* females and males of the same age (carapace length 20.8 ± 3.0 mm) were collected from large nursery containers at the Ben-Gurion University of the Negev. Eight mature males, carapace length 51.8±3.9 mm, that had been bilaterally destalked 2 weeks previously, were anesthetized in ice-cold water and dissected, and their hypertrophied AGs were collected in physiological saline and used for implantation into females. Sixteen females were each implanted with one hypertrophied AG as detailed in Khalaila *et al.* (2001), 16 females were sham-operated and 16 males were left intact. Crayfish maintenance was as detailed in Khalaila *et al.* (2001). Seven months after the AG implantation, 91.6% of the implanted females had developed a soft red-patch on their claw — a conspicuous male secondary sexual trait (Sagi *et al.*, 1996). The females that developed a red patch, along with all the surviving sham-operated females, and males, were transferred to the laboratory at the Department of Aquaculture at least 2 weeks prior to testing, and each was maintained in a separate 50 × 20 × 40-cm aquarium, similarly to the pond-raised males.

Encounters were conducted in large aquaria (120 × 50 × 50 cm), surrounded by black screens with a small peep-hole to enable filming. Each aquarium was divided into two equal sections by an opaque perspex partition, which could be lifted by a pulley system. Two short 18-W neon tubes were installed above each test aquarium, to provide it with uniform illumination (500 lux, measured at the water surface). Water temperature at testing was 25.9 ± 0.8 °C. Aquaria were drained after each test to eliminate any influence of residual water-borne chemical cues on the following match.

*Procedure*

The effect of the androgenic gland on female agonistic behavior was tested by contrasting the interactions between large pond-raised males and smaller laboratory-raised individuals of three types: sham-operated females ($N = 13$), AG-implanted females ($N = 10$), and intact males ($N = 9$). The size asymmetry between the adversaries in this study ensured the winning of all contests by the large pond-raised males. Thus all three types of laboratory-raised crayfish were losers, alleviating the need to split the relatively small number of replicates within each type by contest outcome.

Tested crayfish were healthy and free of apparent injuries, and were all in molt state C (Intermolt). All crayfish were only tested once. Crayfish weight, carapace length, and left and right propodus lengths, and molt state were measured and determined one day prior to testing. Contestants were selected so that the propodus of the pond-raised male was larger by 10% than that of its opponent, since in several species of decapod crustaceans claw size has been found to be the most important morphological parameter in determining the winner and loser of a contest (Stein, 1976; Snedden, 1990; Barki *et al.*, 1992, 1997). There were no statistically significant differences in weight, and carapace and propodus lengths among the three tested types of laboratory-raised crayfish ($p > 0.2$), or in their size difference indexes (Glass & Huntingford, 1988) relative to their opponents, the large pond-raised males ($p > 0.18$).

The two contestants were simultaneously transferred to a test aquarium and left for a 10-min adjustment period before the partition was lifted. Video recording started shortly before the first contact between the crayfish and was continued for 30 min from that event. Behavioral acts of the two contestants were transcribed from the videotaped encounters.

*Behavior recorded*

The frequencies of occurrence of 13 acts presented in Table 1 were analyzed. Description of the agonistic acts was mostly based on partial ethograms of *C. quadricarinatus* females (Levi, 1997) and of the related *C. destructor* (Coombe, 1976). Behavioral acts were exchanged between crayfish in bouts, each of which began with the approach of one or both animals to within one body length. All behavioral acts were tallied within this distance. A bout terminates with the increase in the distance between the two crayfish to more than one body length. In each contest, the total duration of three common acts, which occupy a relatively long period of time (*i.e.* 'Grasp', 'Embrace' and 'Crawling-over'), was computed as well. The frequency and duration of escalated fighting ('ESF') was analyzed. 'ESF' starts when the two opponents face one another, in close body contact, with their carapace elevated obliquely and antenna pointing upwards, and their uropods often flared. In this position the opponents perform 'chela contact' (Tierney *et al.*, 2000) usually with 'interlocked' chelae (Bruski & Dunham, 1987) and engage in pushing against each other and grasping the antennae, pereiopods and other anterior body parts. 'ESF' terminates by the loser retreating (either walking or tail flipping) or 'tilting' while lowering its body against the substrate.

*Statistical analysis*

Morphometric data of crayfish (*i.e.* weight, carapace and propodus lengths) were analyzed with a parametric one-way ANOVA. Size difference indexes were compared following arcsine transformation. The proportions of crayfish of each type engaged in escalated fighting

TABLE 1. *Description of the agonistic acts of Cherax quadricarinatus, analyzed in this study*

| Behavior | Brief description |
|---|---|
| ***Aggressive acts*** | |
| Push | One crayfish pushes the body of another crayfish by extending the claw, usually with the exterior side of the propodus. |
| Lunge | A short and rapid movement of one crayfish towards another, usually with contact. The claws are parallel and horizontal and are often simultaneously extended while hitting the other crayfish. |
| Squeeze | A vigorous snapping together of the chelipeds as if to squeeze its opponent. |
| Embrace | One crayfish embraces the other with its claws from behind or the side, usually while the embracing crayfish is higher than the other. |
| Grasp | One crayfish closes its claw's dactylus on body parts of another. |
| Extend | Extending of the claw of one crayfish towards another without contact. |
| ***Submissive acts*** | |
| Tilt | The submissive crayfish turns its side towards the dominant crayfish accompanied by the lowering of its body and rotating its axis so that the dorsal mid-line faces its opponent. |
| ***Locomotory acts*** | |
| Approach | One crayfish moves towards another crayfish within one body length of the other animal. This movement has to be performed over a distance of at least half of a crayfish body length. |
| Turn toward | A crayfish rotates around its own axis changing its position relative to the other crayfish so that its front is directed towards the other crayfish. |
| Retreat | A crayfish moves away from another crayfish when they are within one body length of each other. A distance of at least half a body length has to be covered. |
| Turn away | A crayfish rotates around its own axis changing its position relative to the other crayfish so that its front is directed away from the other. |
| Tail flip | A rapid contraction of the abdomen which propels a crayfish backwards or upwards, often into midwater. |
| ***Other acts*** | |
| Crawling-over | One crayfish crawls over the other. |

were compared by means of the chi-square test. Because of lack of normality (according to Shapiro-Wilk's test for normality: $p < 0.001$) of the behavioral data, the non-parametric Kruskall-Wallis tests were applied to evaluate differences in the frequencies and durations of behavioral acts among the three tested crayfish types. For behaviors differing statistically overall, the Mann-Whitney $U$ tests were applied to compare all possible types of pairs. Because multiple tests were performed (three crayfish types resulted in three pairwise comparisons for each behavioral category), the critical significance level was set at $p < 0.016$ for

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TABLE 2. *Means (̄*
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| Crayfish type | | |
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| | | |
| Male | | |
| Sham-operated female | | |
| AG-implanted female | | |

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## Results

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TABLE 2. *Means (± standard deviations) of several parameters of half-hour-long encounters between large C. quadricarinatus males and three types of smaller crayfish: males, sham operated females and AG-implanted females*

| Crayfish type | Time lapse to first contact (sec) | No. of acts | No. of bouts | Interaction time (sec) |
|---|---|---|---|---|
| Male | $66.5 \pm 51.6$ | $118.1 \pm 33.0$ | $20.3 \pm 6.7$ | $1164.8 \pm 229.5$ |
| Sham-operated female | $65.8 \pm 42.7$ | $109.9 \pm 57.6$ | $20.7 \pm 4.0$ | $1156.9 \pm 195.2$ |
| AG-implanted female | $83.6 \pm 60.6$ | $103.9 \pm 22.1$ | $21.0 \pm 5.3$ | $1061.6 \pm 301.0$ |

all Mann-Whitney $U$ tests, following the Dunn (1964) procedure in which the critical significance level ($p < 0.05$) is divided by the number of all possible pairwise comparisons (3).

## Results

Interactions between crayfish of the same or opposite gender in this study were of a clearly agonistic character, with no courtship or reproductive elements. There were similarities in several general parameters of the half-hour encounters among the tested crayfish (Table 2), such as time elapsed between lifting of partition and first body contact ($p > 0.7$), number of acts exchanged ($p > 0.3$), number of bouts ($p > 0.98$) and total interaction time ($p > 0.6$). There were two types of bouts, equally often initiated by large and small crayfish: bouts in which the dominance of the large individual was clearly evident, and those in which the dominance was contested and which included escalated fighting. Differences among crayfish types were particularly evident in these bouts.

Intact males and implanted females engaged in 'ESF' during all encounters whereas sham-operated females did so in only 61.5% of the encounters ($p < 0.001$). The duration of 'ESF' per encounter also differed significantly among crayfish types ($p < 0.031$): intact males engaged in 'ESF' for significantly longer times ($p < 0.012$) than sham operated females, and the implanted females occupied an intermediate position, not differing significantly ($p > 0.1$) from either sex (Fig. 1-A). The same pattern of difference was evident, though only near-significant, with regard to the number of 'ESF' events per contest ($p = 0.051$), and non significant with regard to the latency from the start of interaction to the occurrence of 'ESF' ($p = 0.091$). Reanalysis
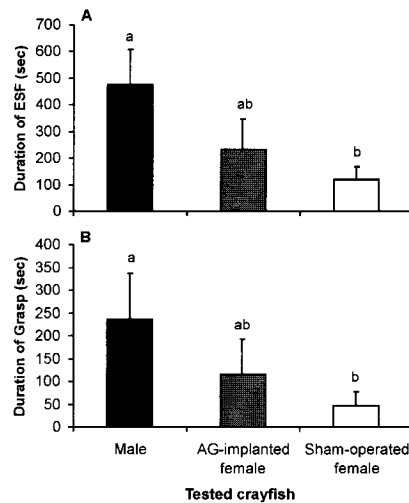
Fig. 1. Aggression measures per half-hour pair encounters between large males and smaller test crayfish, *C. quadricarinatus*, of 3 types: males, androgenic gland (AG)-implanted females and sham-operated females. (A) Total duration of escalated fighting (ESF). (B) Total duration of 'Grasps' performed by the test crayfish. Columns not sharing letters are significantly different (Mann-Witney $U$ test, $p < 0.016$). Bars designate standard errors.

of the data, with the encounters in which sham operated females did not engage in 'ESF' excluded, revealed a similar pattern, *i.e.* intact males engaged in 'ESF' for twice as long as sham operated females, and implanted females' engagements were intermediate, but these differences were non-significant.

Aggressive acts performed with the claws (*i.e.* 'Extend', 'Grasp', 'Lunge', 'Push', 'Squeeze' and 'Embrace') were exhibited frequently mainly by the large males, without differences in frequency or duration (in the case of 'Embrace' and 'Grasp') among their encounters with small males, sham-operated or implanted females ($p > 0.15$). 'Grasp' was the only aggressive act performed at a relatively high rate by the small crayfish, and it was mostly performed during 'ESF'. The three tested crayfish types differed in the accumulated duration of 'Grasp' per encounter ($p < 0.04$): intact males performed 'Grasp' for almost five times longer than sham operated females (237 *vs* 48 s; $p < 0.012$), with the implanted females occupying an intermediate position, not differing significantly ($p > 0.13$) from either intact males or sham operated females (Fig. 1-B). The same pattern of differences was also evident in the number of 'Grasps' per encounter, with significant differences
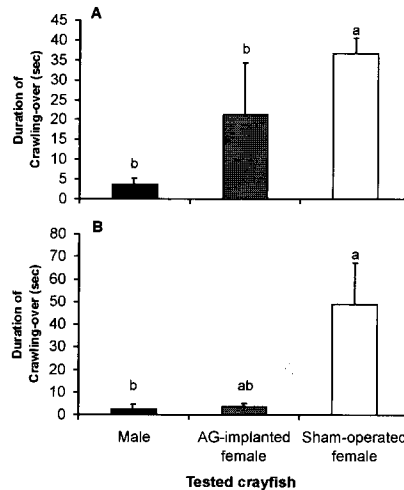
Fig. 2. Tolerance measures per half-hour pair encounters between large males and smaller test crayfish, *C. quadricarinatus*, of 3 types: males, androgenic gland (AG)-implanted females and sham-operated females. (A) Total duration of Crawling-over performed by the large male over the test crayfish. (B) Total duration of Crawling-over performed by the test crayfish over the large males. Columns not sharing letters are significantly different (Mann-Witney $U$ test, $p < 0.016$). Bars designate standard errors.

among crayfish types ($p < 0.05$), and the implanted females not differing from either sham operated females and intact males ($p > 0.16$).

The submissive act, 'Tilt' was carried out equally often by the three small crayfish types ($p > 0.8$), but the dominant large pond-raised males did not perform it even once. The frequency of the locomotory acts performed by the large males or the small crayfish did not differ among the different types of encounters ($p > 0.13$).

The performance (frequency and total duration) of 'Crawling-over' by the large males differed significantly ($p < 0.002$) among their encounters with different types of small crayfish. Large males performed six times more acts of 'Crawling-over' and their total duration was seven times longer, in encounters with sham operated females than in those with males ($p < 0.001$), and their 'Crawling-overs' with implanted females were of intermediate duration (Fig. 2-A) and frequency. Frequency of 'Crawling over' and their total duration were significantly different between implanted and sham operated females ($p < 0.013$) but not between implanted females and males ($p > 0.2$).

Different types of small crayfish performed the 'Crawling-over' act towards large males at significantly different rates ($p < 0.02$): sham operated females crawled over most frequently, intact males least, and the implanted females came in between ($4.3 \pm 4.2$, $0.2 \pm 0.4$ and $0.7 \pm 0.7$ 'Crawling-over' acts per encounter, respectively). Differences in 'Crawling over' frequency were significant between males and sham operated females ($p < 0.009$), however, implanted females did not differ significantly from either males or sham operated females ($p > 0.04$). The total duration of 'Crawling-over' by small crayfish followed the same pattern as frequency: it was significantly longer by sham-operated females than by males, and implanted females again came in between (Fig. 2-B).

## Discussion

The major finding of this study is that implantation of the AG into young *C. quadricarinatus* females induces alterations in the agonistic behavior in the adult, namely, increased aggression and decreased tolerance towards males. The same females used for this study were subsequently examined for morpho-anatomical and physiological changes that followed AG implantation (Khalaila *et al.*, 2001). Alterations were evident in inhibition of female primary sex characteristics (*e.g.* low gonado-somatic index, small oocyte diameter, inhibition of secondary vitelogenesis) and secondary characteristics (*e.g.* inhibition of morphological traits related to egg brooding), and induction of male secondary sexual characteristics (*e.g.* large claw with a soft red patch). Thus, the behavioral alterations followed the general trend of masculinization in the AG-implanted females. Overall, these females occupied an intermediate position between sham-operated females and males.

The AG has previously been suggested to be involved in reproductive behavior by regulating the periodicity of receptivity of *Callinectes sapidus* males to a pheromone present in the urine of pubertal females (Gleeson *et al.*, 1987). However, these suggestions were mostly based on correlative data of the co-occurrence of AG hypertrophy and the spontaneous performance of the male courtship display following eyestalk ligation. In a parallel study (Barki *et al.*, 2003) we investigated the effects of AG implantations into females in the context of female-female interactions. We compared interaction between and within pairs of AG-implanted and intact females. We provided

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direct evidence for the involvement of the AG in male reproductive behavior, in addition to agonistic behavior. Despite lacking testes and male genital openings, the AG-implanted females performed male courtship and copulation when paired with normal females. In addition, aggression in interactions between AG-implanted and intact females was lower than in AG-implanted or intact pairs of females, similarly to the reduced aggression exhibited in heterosexual interactions in the present study. Taken together, our findings strongly indicate the involvement of the AG in the modulation of agonistic and reproductive behavior in crustaceans.

In various crayfish species, males are often dominant over females (Bovbjerg, 1953, 1956; Capelli, 1975; Lindqvist & Lahti, 1983; Ranta & Lindstrom, 1993; Gherardi et al., 1999, 2000). However, the effect of sex on the outcome of contests may be confounded with inter-sexual differences in size and claw dimensions. In the present study, since the differential advantages in propodus length and in weight of the large male was the same relative to males and females, the two genders were faced with similarly asymmetric opponents. According to predictions of game theory, animals like crayfish, with potentially damaging weapons, acquire information about their opponent's strength and fighting abilities in a stepwise fashion, with escalating intensity of fighting during encounters. The timing of the decision to withdraw thus becomes the key factor in determining the duration and development of the contest. During this process, contesting individuals acquire increasingly detailed information concerning the opponent's strength, at minimized risk, since they give up the fight as soon as the advantage of the opponent is recognized (Parker & Rubenstein, 1981; Enquist & Leimar, 1983; Leimar & Enquist, 1984). In the present study male and female C. quadricarinatus differed in the evaluation of their own fighting ability relative to that of their opponent: about 40% of the sham operated females decided to give up prior to the development of escalated fighting, and females which moved one step further into escalated fighting, gave up the fight much sooner than males. Following AG implantation the females' aggressiveness was increased, and they escalated the fight in all encounters, and persisted in fighting longer than sham-operated females, thus delaying their decision to give up the fight. A similar result, namely a change in fight structure caused by a delay in the decision to withdraw, was obtained with Astacus astacus following injection of the biogenic amine serotonin into their pericardial sinus, compared with individuals injected with saline (Huber et al., 1997; Huber & Delago, 1998).

Crawling over another individual in *C. quadricarinatus* is an act, which is neither agonistic nor reproductive in nature. This tolerance-indicative action was performed more often and for longer periods of time during heterosexual than same-sex interactions. AG-implanted females occupied an intermediate position between the two genders as reflected in the levels of tolerance, both displayed and received, when they interacted with large males. Increased tolerance (*i.e.* duration of Crawling-over periods), as in the case of male-female interactions, was also evident in interactions between AG-implanted and intact females compared with interactions between females of the same type (Barki *et al.*, 2003). Several cues may incite large males not to tolerate implanted females, as reflected in their refraining from climbing over them. Conspicuous male secondary sexual characteristics, such as the soft red patch and the larger more robust claw, may convey visual information that their bearer, an implanted female is actually a male (Karplus *et al.*, 2003). AG implantation may also have changed urine-borne cues used in sex recognition (*e.g.* in crayfish, Ameyaw-Akumfi & Hazlett, 1975; Dunham & Oh, 1996). The avoidance of large males by implanted females by not climbing over them may be due to possible changes in the way these females perceive the large male as a same-sex competitor and not as a potential sexual partner.

Extensive research has been carried out on decapod crustaceans' social behavior, especially agonistic behavior; it has covered a wide range of aspects, such as communication, factors affecting the outcome of aggressive contests, intra- and interspecific competition, territoriality, and dominance hierarchies (see reviews by Dingle, 1983; Hyatt, 1983 and Gherhardi, 2002). However, very little has been published on the control of agonistic behavior in decapod crustaceans, by identified hormones. Studies in this area have shown in the American lobster, *Homarus americanus* a correlation between aggression and the molt cycle (Tamm & Cobb, 1978) and revealed increased levels of aggression following injection of 20-hydroxyecdysone, the active form of the molting hormone ecdysone (Bolingbroke & Kass-Simone, 2001). This study and Barki *et al.* (2003) in *C. quadricarinatus* provide for the first time in crustaceans evidences for the role of the AG in aggressive and reproductive behavior, possibly by a modulatory effect of a yet non identified adrogenic hormone on neural circuits underlying these social behavior patterns.

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