Crayfish females eavesdrop on fighting males before choosing the dominant mate.

previous experimental evidence of a link between these two traits in birds [10] and our finding in pre-manipulated males that heavier individuals had lower concentrations of androgens. The implication of these results is that androgen concentrations change as a function of an individual's signal expression within a social and reproductive context. Furthermore, such a response might be costly, as darkened males lost mass at a time in the reproductive cycle where individuals typically gain weight after having completed their migration to breeding grounds. The hormonal feedback between signal and physiological traits is a likely mechanism for linking signals appropriately to the expression of sexual or aggressive behavior as both signals and the social environment change.

The existing unidirectional view of how physiology and signals are mechanistically related is not sufficient to explain the bidirectional relationship we uncovered between ventral coloration, androgen concentrations and body mass in male barn swallows. The interactions between the expression of signals, their production processes, and the dynamic qualities (e.g., aspects of health and condition) add important complexity to our understanding of sexual signals. For example, if an animal's androgens change due to social stimuli induced by its own signal, that individual will be more or less likely to perform androgen-associated behaviors, such as mating or aggression. Because physiological parameters in addition to the ones we studied here are temporally variable, we expect our results to apply generally to other animal signals. Signals that are flexible and dynamic themselves (i.e. courtship behavior, vocalizations) may even more strongly affect and respond to an individual's current physiological state. The aim in future studies of the signal–physiology nexus should be to determine the suite of social responses to these flexible signals, including traits that advertise resource defense and parental investment, and their effects on specific physiological processes, such as immune function and stress.

Supplemental data

Supplemental data including experimental procedures are available at http://www.current-biology.com/cgi/content/full/18/11/R461/DC1

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Crayfish females eavesdrop on fighting males before choosing the dominant mate

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Identifying the traits that influence mate choice is a major challenge in behavioral ecology and evolutionary biology. Male dominance often conditions mating decisions by females, but how the hierarchical status of potential mates is assessed remains poorly understood. In crustacean decapods, chemical signals convey information about male sexual responsiveness and quality. At least in the red swamp crayfish *Procambarus clarkii*, however, females appeared unable to recognize dominant mates using smell only. Here, we report the first evidence that a form of social eavesdropping may occur in an invertebrate species.

Since its first formulation in the 1990s [1], social eavesdropping has attracted increasing attention by researchers interested in animal behavior and communication networks. The ability of animals to extract information from signaling interactions between conspecifics [1] and the benefits gained from attending to the behavior of others — instead of gathering the same information on one's own — have stimulated a plethora of studies focused on fish [2], birds [1], and primates [3]. By witnessing interactions between two or more individuals (for example, male–male fights or male–female courtships), bystanders assess the relative or absolute quality of the interactants; such information can be later used in an adaptive fashion when the same individuals are encountered in a social context (for example, territorial aggression or mate choice). The costs of mate choice, for example, may be reduced in female guppies by copying the mating decision of other females [4].

Because of the apparent complexity of the neural machinery involved, social eavesdropping has been assumed until now to be a prerogative of vertebrates. As recently reported [5], the behavior

of a crayfish can be affected by observing social interactions between conspecifics. Conversely, the literature gives only hints on the occurrence of social eavesdropping in invertebrates. Females of the crab *Uca deichmanni*, for example, were described as soliciting male fights before selecting the dominant as a mate [6]; however, these observations were not supported by dedicated experiments.

Males of the crayfish *P. clarkii* also often engage in intra-sexual fights during the reproductive season in the presence of females. The winners are expected to be favored by female crayfish, because they are more likely successful at accessing or defending limited resources, such as shelters. Surprisingly, when tested in the laboratory with the simultaneous sight and smell of two seemingly identical males that had previously battled to form a hierarchy, females appeared unable to choose dominants over subordinates [7]. This result falsified our original idea that a putative dominance odor, possibly combined with visual signals, might be used by *P. clarkii* females to select the winner; it also apparently contradicts evidence that, along with conveying information about sex, reproductive condition [8], and size [7], chemicals are involved in recognizing the dominance status of a conspecific [9]. We thus hypothesized that, before making a decision between two apparently identical males, females should be allowed to witness their agonistic interactions.

To test this hypothesis, we compared the responses of bystander (n = 15) and naïve females (n = 15) towards a dyad of males (dominant/subordinate). The experiment was composed of two phases: in the first phase ('fight phase') the females were either allowed (bystander) or impeded (naïve) to watch and smell two similarly-sized males fighting; in the second phase ('choice phase'), both types of female were free to choose between the dominant and the subordinate male (see the Supplemental data available on-line for detailed experimental procedures). Our results are clear in showing that eavesdropping on agonistic interactions improves the female's ability to recognize the dominant male over the subordinate. In fact, bystander females visited the dominant male more often, remained in his proximity for longer, and engaged him in more numerous pre-copulatory contacts (Table 1). Conversely, naïve females showed no preference for any male. This result is not due to visual signals of dominance released by males during the choice phase: the time spent by them raising the claws, as an index of dominance, did not significantly vary either between dominant/subordinate males ($F_{1,60} = 1.685$, $P = 0.200$) or between treatments ($F_{1,60} = 1.868$, P = 0.177). We thus may conclude that the females cannot recognize dominant males from their posture or from some chemical badges but are instead able to extract information from watching male–male fights without being directly involved in those interactions [1].

Table 1. Results from the choice phase of the experiment, in which female crayfish, either naïve or bystander, were free to select between a dominant and a subordinate male.

Data	Naïve		Bystander	
	Dominant	Subordinate	Dominant	Subordinate
First male visited	7	8	11	4
Total duration of visits (sec)	254.4 (32.3)	247.6 (31.7)	379.0 (44.28)	180.6 (36.9)
Mean duration of visits (sec)	20.65 (2.18)	20.39 (2.7)	32.8 (3.8)	16.8 (2.1)
Number of contacts	10.1 (1.2)	10.5 (0.9)	14.6 (2.4)	8.4 (1.7)
Statistical results	**Naïve**		**Bystander**	
	G/t/Z	P	*G/t/Z*	P
First target visited	0.065	0.500	3.287	0.059
Total duration of visits (sec)	–0.048	0.963	3.895	**0.002**
Mean duration of visits (sec)	0.151	0.882	4.643	**0**
Number of contacts	–0.22	0.826	2.205	**0.027**

First male visited by females, means (±SE) of the total and mean duration of visits, and numbers of contacts (top). Types of male have been compared using G tests (*G*; df = 1) for the first male visited, Student's *t*-tests (*t*; df = 14) for the total and mean duration of visits, and Wilcoxon tests (*Z*; n = 15) for the contacts (bottom). Sample sizes are 15 for both naïve and bystander females. Significant values in bold.

By eavesdropping on fighting males, *P. clarkii* females seem to make low-cost, direct comparisons between the two potential mates, obtain information about the quality of the signalers (for example, their hierarchical status), and can then use this information to guide their future decisions. A similar experiment on jumping spiders [10] provided a less clear result, showing that bystander females are unable to choose the winner over the loser, whereas naïve females prefer the loser. Our study offers a first unequivocal proof that social eavesdropping enables invertebrate females to gather information on the dominance status of potential mates. This finding has the potential to open avenues for the future research on the still understudied field of mating systems in invertebrates.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/11/R462/DC1

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