



UNIVERSITÀ
DEGLI STUDI
FIRENZE

FLORE

Repository istituzionale dell'Università degli Studi di Firenze

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

Questa è la Versione finale referata (Post print/Accepted manuscript) della seguente pubblicazione:

Original Citation:

Crayfish females eavesdrop on fighting males before choosing the dominant mate / L. AQUILONI; M. BUŘIČ; F. GHERARDI. - In: CURRENT BIOLOGY. - ISSN 0960-9822. - STAMPA. - 18:(2008), pp. 462-463. [10.1016/j.cub.2008.04.006]

Availability:

This version is available at: 2158/252694 since:

Published version:

DOI: 10.1016/j.cub.2008.04.006

Terms of use:

Open Access

La pubblicazione è resa disponibile sotto le norme e i termini della licenza di deposito, secondo quanto stabilito dalla Policy per l'accesso aperto dell'Università degli Studi di Firenze (<https://www.sba.unifi.it/upload/policy-oa-2016-1.pdf>)

Publisher copyright claim:

(Article begins on next page)

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>

Acknowledgments

We thank Sarah Maguire, Melissa Bowlin, Stephanie Bohlman, and Jeremy Lichstein for field assistance and Elizabeth Tourville for scoring feather color. Suggestions were provided by Jeanne Altmann, Sam Flaxman, Mark Hauber, Daniel Rubenstein, Dustin Rubenstein, Martin Wikelski and Rachael Winfree and three anonymous referees. Funds were provided to R.J.S. from Princeton University's Council on Science and Technology, to K.J.M. by the School of Life Sciences and the College of Liberal Arts and Sciences at Arizona State University, and to M.H. by the National Science Foundation (Integrated Research Challenge Grant no. 0212587).

References

1. Zahavi, A. (1975). Mate selection: selection for a handicap. *J. Theor. Biol.* 53, 205-214.
2. Folstad, I., and Karter, A.J. (1992). Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* 139, 603-622.
3. Wingfield, J.C., and Wada, M. (1989). Changes in plasma levels of testosterone during male-male interactions in the song sparrow, *Melospiza melodia*: Time course and specificity of response. *J. Comp. Phys. A.* 166, 189-194.
4. Oliveira, R.F. (2004). Social modulation of androgens in vertebrates: Mechanisms and function. *Adv. Stud. Behav.* 34, 165-239.
5. Hau, M. (2007). Regulation of male traits by testosterone: implications for the evolution of vertebrate life histories. *Bioessays* 29, 133-144.
6. Adkins-Regan, E. (2005). *Hormones and Social Behavior* (Princeton: Princeton University Press).
7. Blas, J., Perez-Rodriguez, L., Bortolotti, G.R., Vinuela, J., and Marchant, T.A. (2006). Testosterone increases bioavailability of carotenoids: Insights into the honesty of sexual signaling. *Proc. Natl. Acad. Sci. USA* 103, 18633-18637.
8. Ketterson, E.D., Nolan, V., Wolf, L., Ziegenfuss, C., Dufty, A.M., Ball, G.F., and Johnsen, T.S. (1991). Testosterone and avian life histories: the effect of experimentally elevated testosterone on corticosterone and body-mass in dark-eyed juncos. *Horm. & Behav.* 25, 489-503.
9. Safran, R.J., Neuman, C.R., McGraw, K.J., and Lovette, I.J. (2005). Dynamic paternity allocation as a function of male plumage color in barn swallows. *Science* 309, 2210-2212.
10. Perez-Rodriguez, L., Blas, J., Vinuela, J., Marchant, T.A., and Bortolotti, G.R. (2006). Condition and androgen levels: are condition-dependent and testosterone-mediated traits two sides of the same coin? *Anim. Behav.* 72, 97-103.

¹Department of Ecology and Evolutionary Biology 106A Guyot Hall Princeton University Princeton, New Jersey 08544, USA.

²Department of Ecology and Evolutionary Biology University of Colorado Boulder, Colorado 80309, USA. ³School of Life Sciences, Arizona State University, USA.

*E-mail: Rebecca.Safran@Colorado.EDU

Crayfish females eavesdrop on fighting males before choosing the dominant mate

Laura Aquiloni¹, Miloš Buřić² and Francesca Gherardi¹

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,

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 (\pm 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.

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].

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>

References

- McGregor, P.K. (2005). *Animal Communication Networks* (Cambridge: Cambridge University Press).
- Grosenick, L., Clement, T.S., and Fernald, R.D. (2007). Fish can infer social rank by observation alone. *Nature* 445, 429–432.
- Crockford, C., Witting, R.M., Seyfarth, R.M., and Cheney, D.L. (2007). Baboons eavesdrop to deduce mating opportunities. *Anim. Behav.* 73, 885–890.
- Dugatkin, L.A. (1992). Sexual selection and imitation: females copy the mate choice of others. *Am. Nat.* 139, 1384–1389.
- Zulandt, T., Zulandt-Schneider, R.A., and Moore, P.A. (2008). Observing agonistic interactions alters subsequent fighting dynamics in the crayfish, *Orconectes rusticus*. *Anim. Behav.* 75, 13–20.
- Zucker, N. (1983). The role of hood-building in defining territories and limiting combat in fiddler crabs. *Anim. Behav.* 29, 387–395.
- Aquiloni, L., and Gherardi, F. (2008). Mutual mate choice in crayfish: large body size is selected by both sexes, virginity by males only. *J. Zool.* 274, 171–179.
- Simon, J.L., and Moore, P.A. (2007). Male-female communication in the crayfish *Orconectes rusticus*: the use of urinary signals in reproductive and non-reproductive pairings. *Ethology* 113, 740–754.
- Zulandt-Schneider, R.A., Schneider, R.W.S., and Moore, P.A. (1999). Recognition of dominance status by chemoreception in the red swamp crayfish, *Procambarus clarkii*. *J. Chem. Ecol.* 25, 781–794.
- Chan, J.P.Y., Lau, P.R., Tham, A.J., and Li, D. (2008). The effects of male-male contests and female eavesdropping on female mate choice and male mating success in the jumping spider, *Thiania bhanoensis* (Araneae: Salticidae). *Behav. Ecol. Sociobiol.* 62, 639–646.

¹Department of Evolutionary Biology, University of Florence, Via Romana 17, 50125 Florence, Italy. ²Institute of Fish Culture and Hydrobiology, University of South Bohemia, Zatisi 728/II, 38925 Vodnany, Czech Republic. E-mail: laura.aquiloni@unifi.it