Naturwissenschaften 66, S. 370 (1979)

Quantitative Analysis of the Spatial Relationships between Male and Female Grasshoppers during Courtship

K. Riede and F. Huber
Abt. Huber, Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen

D. Varjú
Lehrstuhl für Biokybernetik der Universität, D-7400 Tübingen

Before a male of the grasshopper species *Gomphocerus rufus* L. (Acridinae) begins courtship behavior, he adopts a characteristic position relative to the female, from which he proceeds to give the courtship song. This orientation behavior has been described qualitatively [1–3]. In this paper a quantitative analysis is presented, along with some of its implications.

The courtship behavior of sexually mature males and sexually mature virgin females was recorded by closed-circuit television; the animals were in an arena 50 cm in diameter, uniformly illuminated from above (3000 lux). The spatial coordinates of head and abdomen were measured in each successive frame, and the associated behavior was noted.

Previous observations had suggested that the male, in order to court successfully, must position himself such that the long axis of his body is at a particular angle to that of the female [1, 2]. However, histograms of the angles adopted by males in the presence of virgin females (Fig. 1A, upper diagram) show that the parameter "angle" is highly variable. Moreover, the position of the male is not uniquely described by this angle alone; therefore two further parameters were measured, "distance" (that separating the animals' heads) and "target point" (the point of intersection between the long axes of the two animals). The histograms of these parameters (Fig. 1A, middle and lower diagrams) show that both exhibit less variance than the angle parameter.

Measurement of the fields of view of the eyes of males and females (M. Land, personal communication) revealed that if the target point is at the anterior end of the female, and if an inter-head distance of 1 cm is maintained, then the "head-thorax region of the female" is brought into the binocular field of the male. This situation may be a prerequisite for the performance of the approach jump, by which the male seizes the thorax of the female in order to assume the copulation posture.

If the male is blinded by covering the compound eyes and ocelli with lacquer, he exhibits courtship behavior only after touching the female. Under these conditions males orient by means of the foreleg tarsi and the antennae. The most frequently occurring "distance", 1 cm for seeing animals, is reduced to 0.5 cm for blinded grasshoppers. Females courted in this way frequently run away because of the tactile stimulus. It follows that visual orientation is necessary for successful courtship even though the males are capable of tactile orientation. Moreover, blind males are usually unsuccessful in performing the "approach jump".

From the female's point of view, the effect of the orientation described is that a particularly large part of the anterior aspect of the male is within her visual field (Fig. 1B). Thus the female can well perceive the visual elements of the courtship display – the

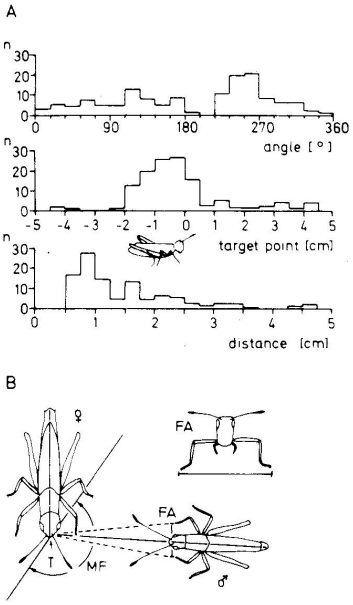

Fig. 1. (A) Parameter histograms of courtship-display positions; each diagram shows the number *n* of courtship displays in each class of one position parameter. *Top*: angle between the long axes of male and female, mathematically defined as positive. *Middle*: target point, the point of intersection of the male and female long axes. If the target point coincides with the frontal edge of the female's head it is given the value 0; in front of the head it is positive, and behind the head negative. *Bottom*: distance between the two heads. (B) Courtship position of the male within the female's visual field, seen from above. This is a typical position with the target point $T=0$. With this orientation, the front aspect *FA* of the male is within the monocular field of view (*MF*) of the female. The inset shows the male as seen by the female when in this position

movements of the antennae and palps (Fig. 1B, inset *FA*). With any other target point more of the lateral aspect of the male would be visible, and thus less of the head appendages.

To understand the significance of such a complicated courtship sequence, the behavior of the female must be considered. Before the male has taken up his final courting position with respect to the female, he walks with a sideways gait back and forth in front of the female, vibrating his palps [1]. If the female moves away during this preliminary phase, the male catches up and reaches her anterior end, where he again presents his own front view. As a rule, the female then stops and remains quietly in place during the courtship display. The significance of the courtship behavior could thus lie in "immobilization" of the female. The strong, periodically repeated visual and mechanical stimuli during the courtship could bring the female into a "hypnosis-like" state [4]. It is known that nerve cells which could participate in control of the flight reflex – for example, the LGMD neuron – habituate very rapidly [5, 6]. Periodic stimulation would make them less effective in eliciting flight.

Finally, pilot experiments indicate that both morphological aspects and movement can be used by the male to identify the anterior end of the female; these observations are now being quantified.

Received April 4, 1979

1. Jacobs, W.: Z. Tierpsychol. *7*, 169 (1950)
2. Vaupel, S.: Nachr. Bl. bay. Ent. *5*, 125 (1956)
3. Loher, W., Huber, F.: J. Insect Physiol. *10*, 13 (1964)
4. Weyrauch, K.: Z. Morph. Ökol. Tiere *15*, 109 (1929)
5. Rowell, C.H.F., O'Shea, M., Williams, J.L.D.: J. Exp. Biol. *68* (1977)
6. O'Shea, M., Rowell, C.H.F.: Nature *254*, 53 (1975)