The Role of Visual Organs in the Locomotor Behavior of Bactrocera minax (Diptera: Tephritidae)

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The role of visual organs in the locomotor behavior of *Bactrocera minax* (Diptera: Tephritidae)

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Abstract

Chinese citrus fly, *Bactrocera minax* (Enderlein; Diptera: Tephritidae), which attacks citrus fruits in China is one of the most important international quarantine pests. Understanding the function of visual organs is the basis of trapping and prevention for management of pests such as *B. minax*. In this study, take-off ability and crawling experiments were conducted using 5 groups of *B. minax* all with different visual blinding treatments (blind ocelli, blind left compound eye, blind right compound eye, blind compound eyes, blind ocelli and compound eyes) and a corresponding control that was not blinded. We found that both the left and right compound eyes played a critical role in the vertical and horizontal crawling behavior of *B. minax*, while the ocelli did not. However, the perception of ambient light by ocelli or either compound eye had a significant influence on take-off of *B. minax*. Elucidating the monocular and compound eye functions of *B. minax* will help us to develop better visual traps for this important pest of citrus.

Key Words: take-off ability; crawling experiments; ocelli; compound eyes; visual masking; visual blinding

Resumen

La mosca china de los cítricos, *Bactrocera minax* (Enderlein; Diptera: Tephritidae), que ataca las frutas de cítricos en China es una de las plagas cuarentenarias internacionales más importantes. El comprender la función de los órganos visuales es la base del trampeo y la prevención para el manejo de plagas como *B. minax*. En este estudio, se realizaron pruebas de capacidad de despegue y experimentos de rastreo utilizando 5 grupos de *B. minax*, todos con diferentes tratamientos de cegamiento visual (ocelli ciego, ojo compuesto izquierdo ciego, ojo compuesto derecho ciego, ojos compuestos ciegos, ocelli ciego y ojos compuestos) y un control correspondiente que no fue cegado. Descubrimos que tanto el ojo compuesto izquierdo como el derecho desempeñaron un papel fundamental en el comportamiento de rastreo vertical y horizontal de *B. minax*, mientras que el ocelli no lo hizo. Sin embargo, la percepción de la luz ambiental por parte del ocelli o del ojo compuesto tuvo una influencia significativa en el despegue de *B. minax*. El esclarecer las funciones oculares monoculares y compuestas de *B. minax* nos ayudará a desarrollar mejores trampas visuales para esta importante plaga de los cítricos.

Palabras Clave: capacidad de despegue; experimentos de rastreo; ocelos; ojos compuestos; enmascaramiento visual; cegamiento visual

Insects perceive external light signals through their visual organs, which they use to search for food, avoid enemies, pursue mates, and even escape from predators (Vogt & Desplan 2007; Yang & Yeo 2019). The visual organs of insects mainly include compound eyes, dorsal monocular eyes, and lateral monocular eyes (Gillott 2005; González-Martín-Moro et al. 2017). In the case of complete absence of chemical odor, some insects can identify and locate their hosts by relying on vision (Stenberg & Ericson 2007; Reeves & Lorch 2009; Muijres et al. 2014). Many herbivorous insects express a color preference that helps them find optimal oviposition substrates (Prokopy & Owens 1983; Scherer & Kolb 1987; Ogawa et al. 2013). It is striking that the function of the visual system in many groups has not been investigated at all, and for many families only 1 species has been studied to date (n = 46 families, 55%) (Casper et al. 2021). Many groups of insects are understudied, including numerous early-diverging taxa, e.g., Hemiptera, Thysanoptera, and most fly families (Heath et al. 2020; An et al. 2018; Hannah et al. 2019).

Compound eyes are the most important visual organs of insects and exist mainly in the vast majority of adults and semi-metamorphosis nymphs, they are located on both sides of the head, are mostly oval or oblong, and are usually composed of a series of closely arranged ommatidia (Chapman 2013; Nityananda et al. 2016). The unique compound eye structure of insects enables them to collect panoramic images in 360° azimuth around their eyes and use the image motion generated by their own motion to measure distance, avoid obstacles, and to control speed, altitude, cruising, and landing, etc. (Srinivasan et al. 2000; Woong & Heung 2018). Large flies such as *Calliphora* spp. and *Musca* spp., and more recently the fruit fly *Drosophila*, have been used as remarkable model systems with which to study the principles of motion detection (Riehle & Franceschini 1984; Wehrhahn 1985; Franceschini et al. 1989; Borst & Haag 2002; Borst et al. 2010; Borst & Euler 2011; Borst 2014; Borst & Helmstaedter 2015). Principles of motion detection can be categorized by vision type: for example, spatial, color, and polarization vision (Borst 2014). In the fruit fly, spatial vision is conveyed by R1 to R6 (rhabdomeres 1 through 6; Hardie & Raghu 2001) and color vision is enabled by R7 and R8 (Wernet et al. 2012). Polarization vision is mediated by specialized R7 and R8 photorecep-

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tors in the dorsal rim of the compound eye and by a combination of photoreceptors R1 to R6 as well as R7 and R8 in the central area of the eye (Wernet et al. 2012). As with color vision, polarization of light seems to be analyzed by the fly visual system globally and is used for long-range orientation of the animals with respect to the sun (Weir & Dickinson 2012).

Ocelli are the auxiliary organ of the adult insect compound eye, they are sensitive to weak light but their spatial resolution is low (Kleef et al. 2008; Ribi & Zeil 2018). Ocelli is generally used to refer to the dorsal monocular eye. The ocelli of some insects can focus light on the retina, typically to facilitate horizon detection (Stange et al. 2002) or for flight stability by detecting rapid changes in the pitch and yaw orientation (Taylor 1981; Parsons et al. 2006; van Kleef et al. 2008; Krapp 2009). Ocelli also can be used in navigation, for detecting the evector direction of polarized light (Mote & Wehner 1980; Fent & Wehner 1985; Ribi et al. 2011; Taylor et al. 2016) or can be involved in information processing for motor behavior (Wehrhahn 1984; Mizunami 1995; Honkanen et al. 2018). The lateral monocular eye is the only photoreceptor in the larval stage of complete metamorphosis insects, it has a visual function, and its structure is basically the same as ommatidia in the compound eye (Gilbert 1994; Munz 2005). The visual organs of insects are working as a whole unit, and the acquisition and analysis of optical signals require the functional coordination of compound eyes and monocular eyes (Vogt & Desplan, 2010; Zhou et al. 2017).

Fruit flies (Diptera: Muscidae) are known as the world's most destructive agricultural pests (White & Elson-Harris 1992; Bhattacharya et al. 2013). They damage fruits and vegetables by laying eggs in them, the larvae that hatch then cause the fruits to rot and drop early, thus causing significant losses to production (Hollingsworth et al. 1997; Bhattacharya et al. 2013). *Bactrocera minax* (Enderlein) (*Tetradacus minax*) (Diptera: Tephritidae) is one of the most important international quarantine pests that attacks citrus fruits (EPPO/CABI 1997; van Schoubroeck 1999; Wang et al. 2014; Carroll et al. 2019). Citrus is one of the most important fruit crops in Florida and throughout the world (Zhang 2014) and controlling *B. minax* is essential for citrus fruit production. Mass trapping using various food-based traps and visual cue lures such as colored sticky spheres with insecticides are the primary pest management options (Xia et al. 2018). Understanding the function of visual organs is the basis of trapping and prevention to control pests. However, the role of *B. minax* vision in motor behavior is still unclear.

Chinese citrus fly adult individuals have 1 pair of compound eyes and 1 ocellus, so far there is nearly no behavioral evidence to support their role in vision. To elucidate the role of compound eyes and ocelli in *B. minax* locomotive behavior, these 2 visual organs were respectively suppressed (i.e., blinded) to determine their role in vision function.

Materials and Methods

INSECTS

Larvae of Chinese citrus flies were collected from citrus orchards at Songzi, Hubei, China (30.3000000 °N, 112.2833333 °E) in Oct 2020, and kept in plastic pots (diameter 17 cm, height 11 cm) in a laboratory at Yangtze University, Hubei Province, China. The larvae were covered with river sand (4 to 5 cm in height) and left to pupate. The river sand had been disinfected for 2 h at 80 °C). Through the winter, pupae were kept in a growth chamber at 25 °C during the day and 20 °C during the night, at approx. 65% relative humidity (R.H.), and a 14:10 h L:D photoperiod. In May, the plastic pots containing the pupae were taken from the laboratory to the test location 10 d before use in experiments, and the pots were housed in cages (35 × 35 × 35 cm) covered with white nylon gauze (2 mm mesh size) and kept moist with a gentle water spray 3 to 4 times each day. Five-day-old adults were used as the test insects (Huang et al. 2012; He et al. 2013).

VISUAL BLINDING METHOD

Healthy, lively 5-day-old male and female *B. minax* adults were selected as test insects, and nail polish (Love Tribe, Panan County People Cosmetics Co., Ltd., China) was applied evenly to cover the compound eye or ocelli with soft brushes under a stereoscopic microscope (ST60N; Shunyu Optics, China). The treatment groups were blind ocelli, blind left compound eye, blind right compound eye, blind compound eyes, and blind ocelli and compound eyes (Fig. 1). The insects were examined for the presence of defects, such as bubbles, insects with defects were not used in the experiment.

The experiments were carried out in the Laboratory of Insect Ecology, Yangtze University, Hubei Province, China (temperature 25 ±2 °C, relative humidity 65%, natural light). All tests were conducted from 9 AM to 4 PM.

FLIGHT ABILITY

According to the behavioral characteristics of *B. minax* (Huang et al. 2012), the take-off platform (Fig. 2-A) was designed, and the adults were put into the take-off platform under natural light conditions. The take-off platform was a cylindrical platform (height 80 cm, diameter 5 cm) inside a transparent plexiglass box (length × width × height, 50 × 50 × 160 cm). The box had 1 side that was removable for placing equipment and insects for the experiments. For each replicate, a single adult was selected randomly and released on the take-off platform, and the test duration was 3 mins. If the landing point of the adult was higher than the height of the platform, it was determined that the adult could take off. If the adult took off within 3 mins, but the landing point was below the height of the platform, it was determined that the take-off was unsuccessful. If the adult could not take off within 3 mins, it was determined that it could not take off. The experimental setup included males and females and 6 visual blinding treatments. A total of 12 treatments were conducted and each treatment was replicated 30 times. The test insects were only used 1 time. Take-off (%) = number of take-off insects / (number of take-off insects + number of non-take-off insects) × 100.

HORIZONTAL CRAWLING BEHAVIOR

Observation system of horizontal crawling behavior was consisted of a Petri dish (12 cm in diameter, 2.5 cm in height, new for each replicate) in a Plexiglass box (length × width × height, 50 × 50 × 160 cm), which was observed from 30 cm above using a video camera (PXW-FS7, SONY) (Fig. 2-B). First, a randomly selected adult was placed on the central point of the Petri dish, then the Petri dish was placed in the box, then the horizontal crawling behavior was recorded using the video camera. The locomotion of adults was recorded continuously for 30 s after the beginning of the experiment. The experimental setup included males and females and 6 visual blinding treatments. There were a total of 12 treatments, each treatment was replicated 30 times, and the test insects were not reused. The video was analyzed by Adobe Premiere Pro CC software (Adobe), and the crawling distance was obtained. The image file was exported to a frame by Adobe Premiere software (Adobe), the picture format of JPEG was adopted, and the length and other parameters were measured by Image J software (National Institutes of Health; Schneider et al. 2012).

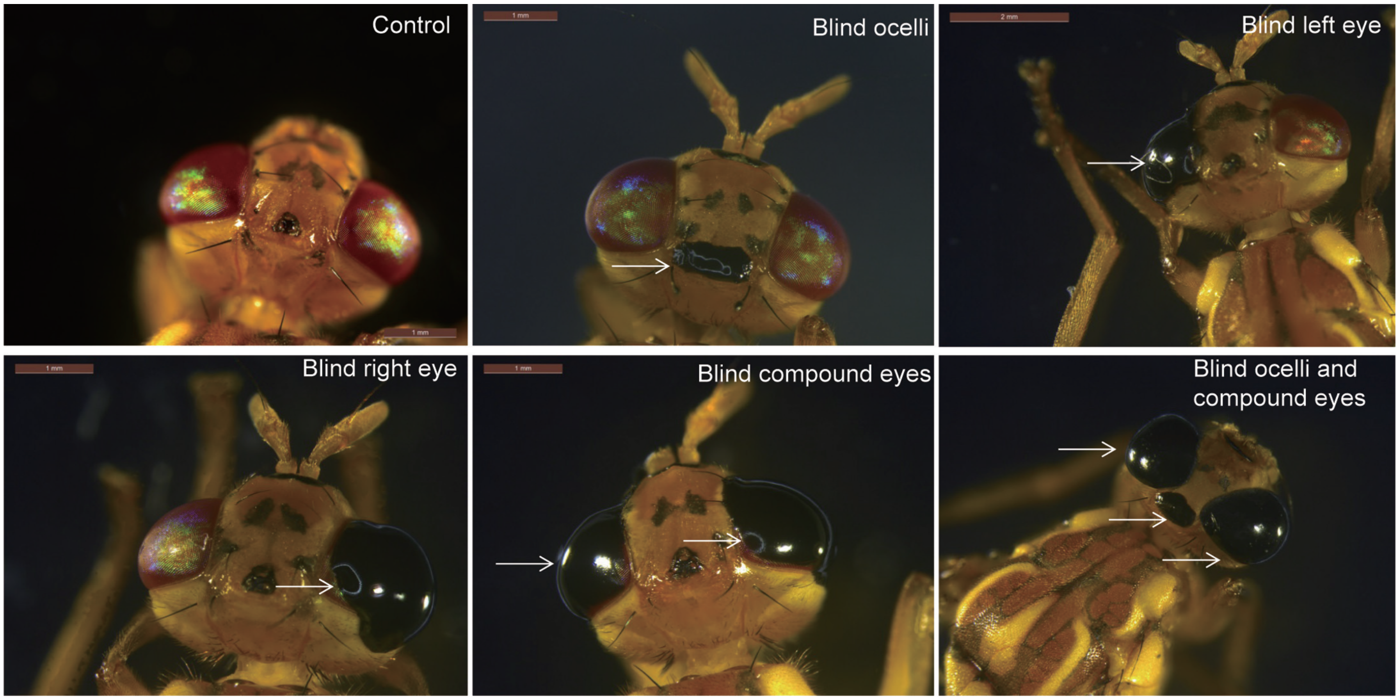

Fig. 1. Schematic diagram of visual blinding treatments on adult Chinese citrus flies, *Bactrocera minax.* The white arrow indicates the blinded visual organ.

VERTICAL CRAWLING BEHAVIOR

The vertical crawling behavior observation system consisted of a crawling column made of hollow PVC pipe (90 cm in height, 4 cm in diameter and 0.5 mm in thickness) and a ruler (Fig. 2-C). In each experiment, 1 adult was randomly selected and placed at the bottom on the inside of the hollow crawling column. The crawling distance within 30 s was recorded once the test insect began to crawl. The experimental setup included males and females and 6 visual blinding treatments. A total of 12 treatments were conducted, and each treatment was replicated 30 times. The test insects were not reused. After each experiment, the crawling column was cleaned with alcohol and dried to reduce the risk of deposition of chemical cues on the column, which could influence the results of the subsequent tests.

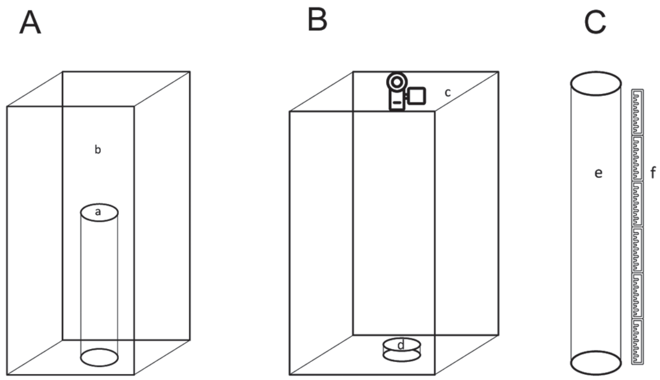

Fig. 2. Schematic diagrams of experimental chambers. A. Take-off platform; B. Horizontal crawling device; C. Vertical crawling device; a. take-off platform; b. Plexiglass box; c. video camera; d. Petri dish; e. crawling column; f. ruler.

DATA PROCESSING

All the data in the experiment were analyzed by SPSS (SPSS for windows 17.00, Inc., Chicago, USA) data processing system. Data are presented as means ± standard error (SE). Statistical significance was determined with one-way ANOVA. In each figure presented, means with different lowercase letters are significantly different ($p < 0.05$).

Results

EFFECT OF VISUAL BLINDING ON THE FLIGHT ABILITY OF ADULT CHINESE CITRUS FLY

The flight ability of *B. minax* was affected both by blind ocelli and compound eye treatments ($F_{5,24} = 34.327$, $P < 0.05$; Fig. 3), and there was no difference between the response of females and males ($F_{1,24} = 1.405$, $P = 0.2892$). The average flight ability of adults was more affected by blind compound eyes (just 31.7% take-off) than blind ocelli (75.0%). Only 26.7% of the adults could take off successfully after both ocelli and compound eyes were blinded.

EFFECT OF VISUAL BLINDING ON HORIZONTAL LOCOMOTION OF CHINESE CITRUS FLY

The horizontal crawling distance of *B. minax* was decreased by all blinding treatments except for blind ocelli ($F_{5,54} = 14.379$, $P < 0.05$), and there was no difference between the response of females and males ($F_{1,108} = 0.437$, $P = 0.5378$) (Fig. 4). The horizontal crawling distance of *B. minax* adults was more affected by blind compound eyes (average just 17.0 cm) than by only blind ocelli (39.9 cm). The function of each compound eye is equally important, and both are needed, and there was no significant difference between blind left eye (17.3 cm), blind right compound eye (18.3 cm) and blind both compound eyes (17.0 cm).

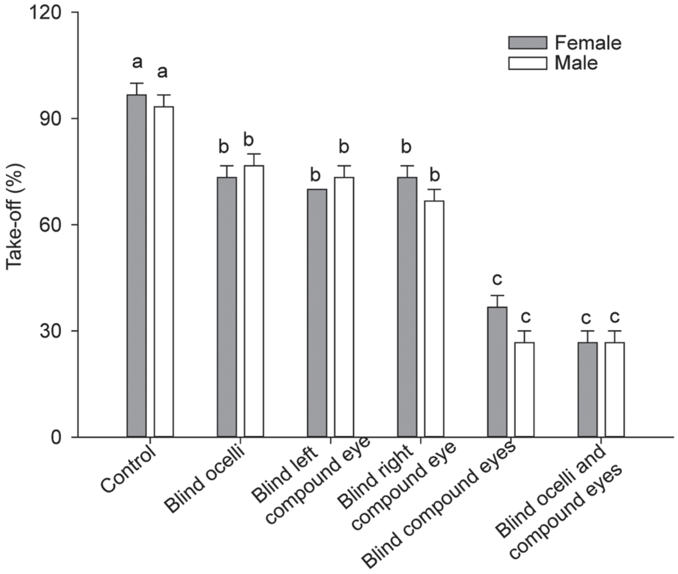

Fig. 3. Take-off (%) by adult Chinese citrus flies, *Bactrocera minax*, males and females tested separately with 6 visual blinding treatments. Values are mean ± standard error. Histograms with different lowercase letters indicate significant difference among treatments ($P < 0.05$).

EFFECT OF VISUAL BLINDING ON VERTICAL LOCOMOTION OF CHINESE CITRUS FLY

The vertical crawling distance of *B. minax* was decreased by all blinding treatments except for blind ocelli ($F_{5,108} = 39.853$, $P < 0.05$), and there was no significant difference between the response of females and males ($F_{1,108} = 3.53$, $P = 0.1191$) (Fig. 5). The vertical crawling distance of *B. minax* adults was more affected by blind compound eyes (just 10.8 cm) than blind ocelli (50.7 cm). The function of each compound eye is equally important, and there is no significant difference between blind left compound eye (13.2 cm), right compound eye (17.5 cm) and blind both compound eyes (10.8 cm).

Discussion

Higher animals are able to perceive their environment through various senses, and vision is possibly the most crucial sense, the same is true in insects. The visual system of insects includes compound eyes and ocelli. The compound eyes play a more important role, with the ocelli typically only playing an auxiliary role (Grarrey 1918; Gilles et al. 2005; Kleef et al. 2008; Chapman 2013). Based on the take-off and crawling ability analysis after blinding treatments for *B. minax* in this study, we found compound eyes played a critical role in the movement behavior of *B. minax*.

The movement behavior of *B. minax* is mediated by the compound eyes and cannot be elicited with stimulation via the ocelli alone. There was no significant difference in the motor behavior of *B. minax* with blind compound eyes compared with *B. minax* with blind compound eyes and ocelli. The common spatial perception ability of the compound eyes was dominant in the crawling behavior. In vertical crawling or horizontal crawling, there was no difference in the results of masking any compound eye or masking all compound eyes, and the crawling behavior was significantly lower than that of control. When one of the compound eyes was obscured, *B. minax* lost the ability of spatial stereoscopic perception and could not crawl properly. Stereopsis could enable an organism to judge the distance to objects in its environment (Nityananda & Read 2017). In both toads and praying mantises, stereopsis has been implicated in judging distance for prey capture (Collett 1977; Rossel 1983; Nityananda et al. 2016). Bees and flies compare optic flow signals between their eyes (Srinivasan & Gregory 1992; Hennig et al. 2011). If the right eye of robber fly (*Proctacanthus*) is blackened, its body and head rotate and tilt to the left (Grarrey 1918). Generally, distance measurement or 'range finding' is important in navigation, prey capture, and predator avoidance (Nityananda & Read 2017). It is interesting to note that the take-off behavior of *B. minax* was not affected by the loss of stereovision. The difference between stereovision in crawling behavior and take-off behavior deserves further study.

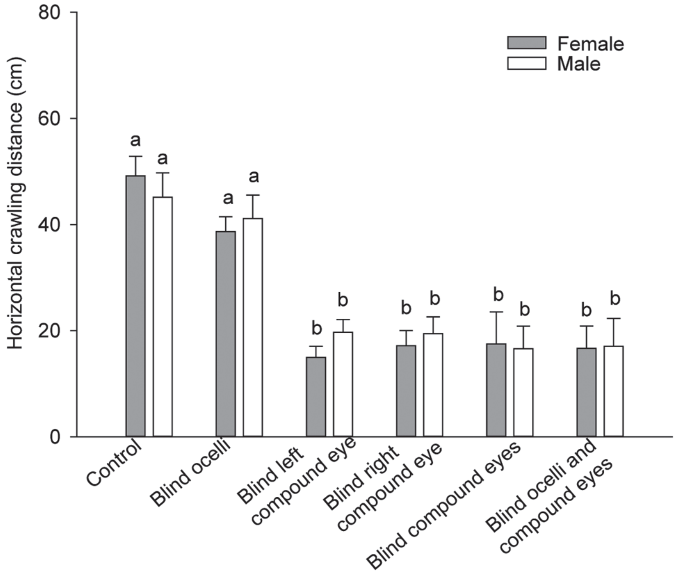

Fig. 4. Horizontal crawling distance (cm in 30 s) of adult Chinese citrus flies, *Bactrocera minax*, males and females tested separately with 6 visual blinding treatments. Values are mean ± standard error. Histograms with different lowercase letters indicate significant difference among treatments ($P < 0.05$).

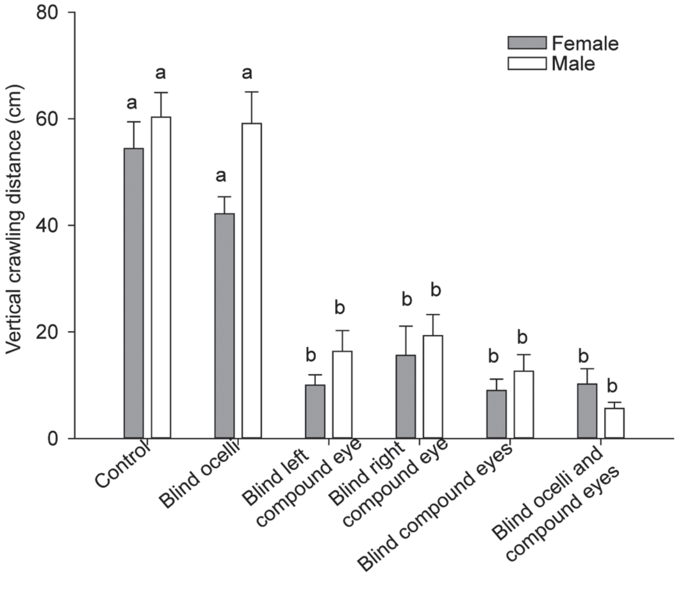

Fig. 5. Vertical crawling distance (cm in 30 s) of adult Chinese citrus flies, *Bactrocera minax*, males and females tested separately with 6 visual blinding treatments. Values are mean ± standard error. Histograms with different lowercase letters indicate significant difference among treatments ($P < 0.05$).

Ocelli were more important in flight behavior than in crawling behavior. Although there was no significant difference in the locomotor behavior of *B. minax* when the compound eye was blinded compared with when the compound and ocelli were blinded, takeoff of *B. minax* was significantly lower compared with the control after only the ocelli was blinded. Behavioral experiments with occluded ocelli or compound eyes, and studies where the ocelli are stimulated, have revealed some possible functions of the ocelli in flight control (Taylor 1981; Parsons et al. 2006; van Kleef et al. 2008). For example, the ocelli are crucial to flight stabilization in dragonflies (Stange & Howard 1979; Stange 1981) and locusts (Taylor 1981). Ocellar contributions to gaze stabilization also have been shown in *Calliphora erythrocephala* (Macquart; Diptera: Calliphoridae) (Schuppe & Hengstenberg 1993). By using only their ocelli, flies orient towards edges and relatively small bright objects situated in the frontal equatorial part of the visual field (Wehrhahn 1984). Ocelli may be able to detect subtle changes of ambient light intensity or contribute to flight stability by detecting rapid changes in the pitch and yaw orientation (Krapp 2009).

In considering the function of ocelli, a related question is: what kind of selective pressures lead to the evolution of ocelli? A unique survival strategy of *B. minax* is that the primary adults (i.e., recently emerged adults) migrate to the nearby woods to feed by flying and crawling after eclosion. After feeding the adults fly directly back to the orange orchard to lay eggs after sexual maturity (Xia et al. 2018). It is worth studying whether the function of *B. minax* ocelli is related to this unique survival strategy. Understanding the eye function of *B. minax* will help to develop targeted trapping devices, reduce the harm caused by *B. minax*, and protect the citrus industry in China, the United States, and the world.

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