FLIGHT MANOEUVRES USED BY MALE ELATERID BEETLE *CORYMBITES PECTINICORNIS* L. (*COLEOPTERA, ELATERIDAE*) TO LOCATE THE PHEROMONE EMITTING FEMALE IN THE FIELD

Enno MERIVEE

Eesti Põllumajandusülikooli Taimekaitse Instituut (Estonian Agricultural University, Institute of Plant Protection), Riia 12, EE-2400 Tartu, Eesti (Estonia)

Presented by K. Elberg

Abstract. Two different types of flight trajectories of distant pheromone orientation in male elaterid beetle *Corymbites pectinicornis* are described. The first type comprises upwind zigzagging or casting manoeuvres across the wind line, or downwind casting, both of which express an internal counterturning programme. The other flight trajectory type is a series of shorter or longer relatively straight upwind flights. Beetles, having made an intermediate landing before starting a new straight upwind flight, perform orientation movements on the spot. The other type of flight trajectories in the case of *C. pectinicornis* refers to an alternative possibility in distant orientation of insects by odour, without starting an internal counterturning programme. In a number of cases the upwind flight of the males before landing near a female turned into a narrow casting flight across the wind. On losing scent males made wide crosswind or downwind casts with an increasing amplitude, or short straight downwind flights and intermediate landings, and thus located the female pheromone trail again. After landing near a female within a radius of 15—20 cm the males started searching behaviour during which a male walks around rather randomly than directedly, making numerous zigzags and loops before locating the female.

Since there exist, among elaterid beetles, a number of pests dangerous for field crops, their pheromone communication has been intensively studied so that synthetic pheromones might be applied in their control. Hereby, main emphasis has been laid on the morphological description of female pheromone glands (Иващенко, Олещенко, 1974; Иващенко, Адаменко, 1980; Орлов, Исмаилов, 1986), and on the identification and synthesis of sex pheromones (Borg-Karlson et al., 1988; Яцынин et al., 1980; Яцынин, Лебедева, 1984; Олещенко et al., 1986; Яцынин et al., 1988; Яцынин, Рубанова, 1988). At the same time, the little attention paid to the behavioural aspects of pheromone communication in elaterid beetles has not been fully justified. Field experiments carried out with labelled specimens (Орлов, Исмаилов, 1986) showed that the maximum communication distance in the case of specimens of the genera *Ampedus* and *Agriotes* is from a few metres up to 300 m. Males arrive at the pheromone source either flying or walking, depending on the species. However, more detailed data on the pheromone orientation behaviour of the elaterid beetles are still lacking.

The aim of the present work was to study and describe the flight trajectories and orientation manoeuvres of female *Corymbites pectinicornis* in their approaching the pheromone source in field conditions.

MATERIAL AND METHODS

The male and female *C. pectinicornis* beetles used in the work were caught from 20 May to 15 June, 1984, in South Estonia. We used only such females whose scent attracted males in large numbers and who were evidently not yet fertilized, and only such males who responded to the female pheromone by upwind orientation flight. The field experiments were carried out from 10 a. m. to 5 p. m. on the same dates, to coincide with the time of mating behaviour in the field. In order to eliminate the effect of "strange" female beetles on the results, the experiments were performed on an open grassland where this species did not occur naturally. At the time of emitting the pheromone the female beetles were situated in grass, about 30 cm above the ground, and were relatively immobile. Only one signalling female beetle was used at a time. Cylindrical cages of plastic net (length 20 cm, diam. 7 cm) with the males were placed 10 m downwind of the female so that they were exposed to an aerial pheromone trail. The males were released from the cage singly, and they all immediately started on their upwind orientation flight.

The speed of the orientation flight of the males was relatively low, which enabled to watch the low-flying beetle visually, and to follow it while walking, marking its flight trajectory with a stick in a horizontal plane on the ground. After each experiment the obtained trajectories were recorded in a field journal, taking account of their scale, of wind direction and the location of the female. Altogether 115 male orientation trajectories were recorded. In some of the experiments the location of the signalling female was changed at the time when a male approaching it had reached a distance of 2.5—3 m or a few centimetres, respectively.

The wind was a variable in both the direction and the strength.

RESULTS

After overwintering in the soil, sexually mature elaterid beetles are in a state of internal readiness (motivated), they may begin behaving in a manner which increases the probability of exposure to a female sex pheromone (releasing stimulus). This has appropriately been called appetitive behaviour. Appetitive behaviour does not reduce the motivation and is likely to continue until the insect comes into contact with the appropriate releasing stimulus. The most common appetitive behaviour is probably an increased locomotion; in the case of a male *C. pectinicornis* this can be noted as waiting behaviour. In favourable weather conditions male beetles crawl up grass blades, bushes etc., they raise their antennae and orient with their heads upwind (Fig. 1). Beetles may remain up to a couple of hours in such a characteristic posture, altering only slightly their body posture or moving their antennae or heads. In this waiting posture beetles responded 100% to a female pheromone at a distance of 10 m and started upwind-directed orientation flight.

Visual observations and the analyses of the recorded flight trajectories showed two different types of trajectories in male *C. pectinicornis* flying along an aerial pheromone trail. In the first case flight consisted of alternating turns, resulting in an upwind zigzag course in a horizontal plane (Fig. 2-*1*). Forward progress in a straight line along the longitudinal

axis of the pheromone trail depended on whether alternating turnings were directed more or less upwind (cf. flight paths in Figs. 2-*1*, 3-*2*). At a distance of 10 m, flight zigzag amplitudes amounted to 3 m; however, the nearer the male reached the female, the smaller the zigzag amplitude became, until they were reduced to some tens of centimetres. In many cases the narrow upwind zigzagging of the males changed to narrow casting flight across the wind near the female. Narrow casting flight across the wind near the pheromone source enabled the male *C. pectinicornis* beetles to locate the signalling female very precisely already while in flight, and to land on it. Mostly, however, males landed in the vicinity of a female within a radius of some tens of centimetres, after which they adopted searching behaviour (random walking). Though the flight speed of the males has not been measured in the experiments, it is essential to note that it was considerably lower during orientation, especially near the signalling female beetle, than during an ordinary flight.

The other type of the male flight trajectory was a series of short relatively straight upwind flights (see certain stretches of flight trajectories in Figs. 2-*3*, 3-*1*, 4-*1*). Before starting a new flight the beetles, having landed on grass blades, orientated with their heads upwind, vibrating their raised antennae and moving their heads from side to side, similar to what they do in waiting behaviour (orientation movements on the spot); however in this case active flight manoeuvres continued. Having ascertained the direction of the scent source (wind), the males performed the next straight flight of a few metres. Sometimes the males flew, without intermediate landings, upwind in a straight line up to a female 10 m away (Fig. 2-*2*). However, in most cases, the males passed over to narrow upwind zigzagging or narrow casting flight across the wind before landing near a female (Figs. 2-*2*, 2-*3*). Visual observations showed that in the experiments where the males passed over to narrow casting flights across the wind before landing on females, they succeeded in locating the females more precisely, and they landed nearer to the signalling females than the other males did.

The pure form of the first or the latter flight trajectory occurred rarely, because at pheromone orientation in field conditions the beetles resorted to the elements of either trajectory type. The flight manoeuvres described above were used by males in the cases of the so-called distant orientation. After a male had landed near a female at a radius of a few tens of centimetres, it would not, in most cases, make an attempt to flush again, but started on energetic searching behaviour (close-range orientation) (Fig. 4). During searching behaviour the male walked around rather randomly instead of directionally, and searched all the area round the signalling female within a radius of 15—20 cm, performing quite a number of zigzags and loops before locating it (Fig. 4-*2*). The location of the female was probably also facilitated by the pheromone adsorbed on the substrate, since the female beetle sometimes moved slowly about plant stalks and leaves while the male followed it along the same trail at some distance (visual contact was evidently still lacking), touching the substrate with his antennae all along.

In natural conditions male beetles, when orientating by scent, may lose the odour trail for various reasons. Experiments showed that missing the pheromone trail caused a number of specific orientation manoeuvres in males, which helped them detect it again. It was found that their further behaviour depended on the fact whether, at the moment of losing the trail, the distance from the signalling female was small (a few centimetres in the experiment) and they had started on searching behaviour (Figs. 4-*1*, 4-*3*), or whether they were at a few metres' distance downwind from the female (Figs. 3 and 5).
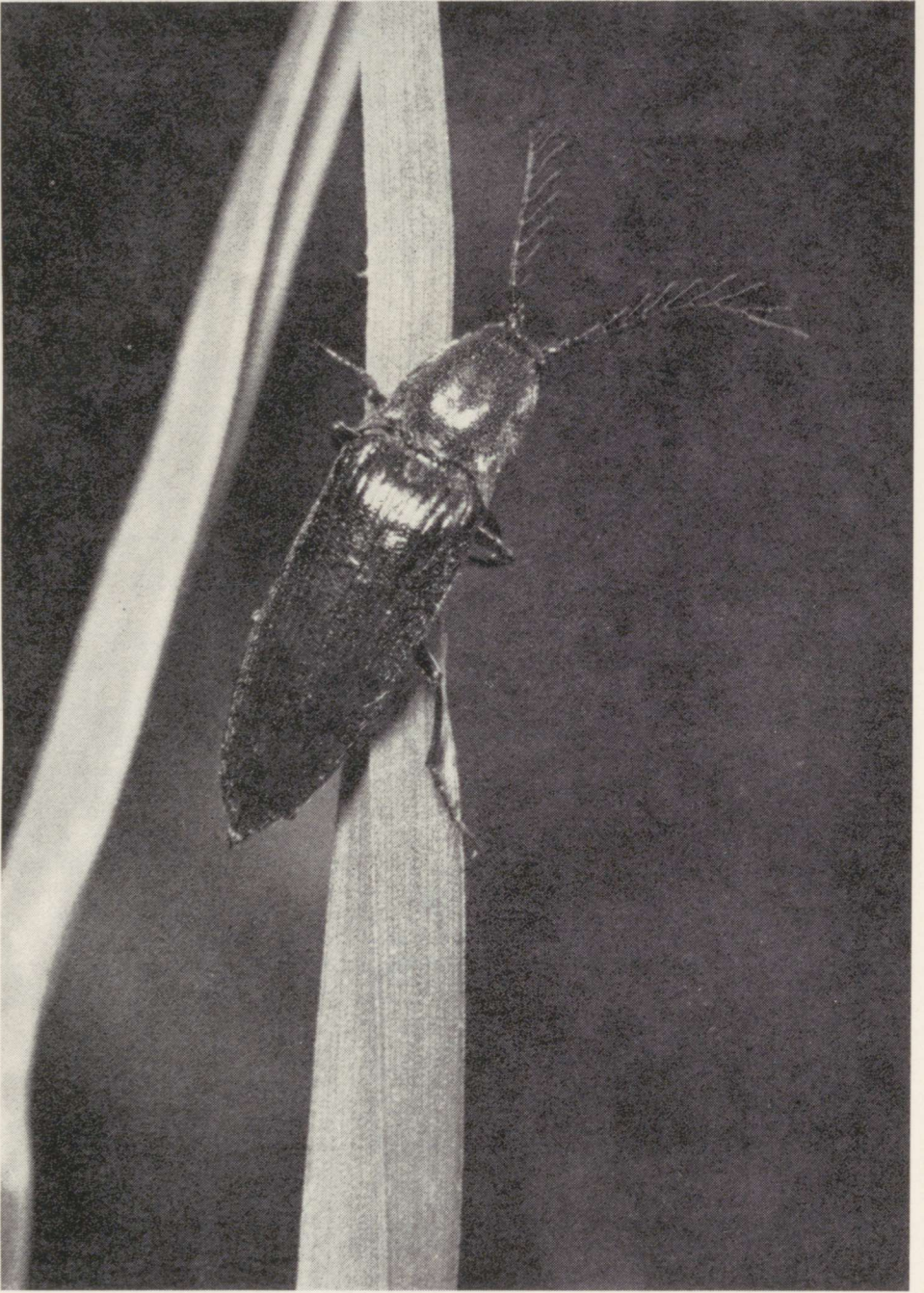
Fig. 1. Waiting posture with raised antennae as an expression of the appetitive behaviour in male elaterid beetle *Corymbites pectinicornis*.
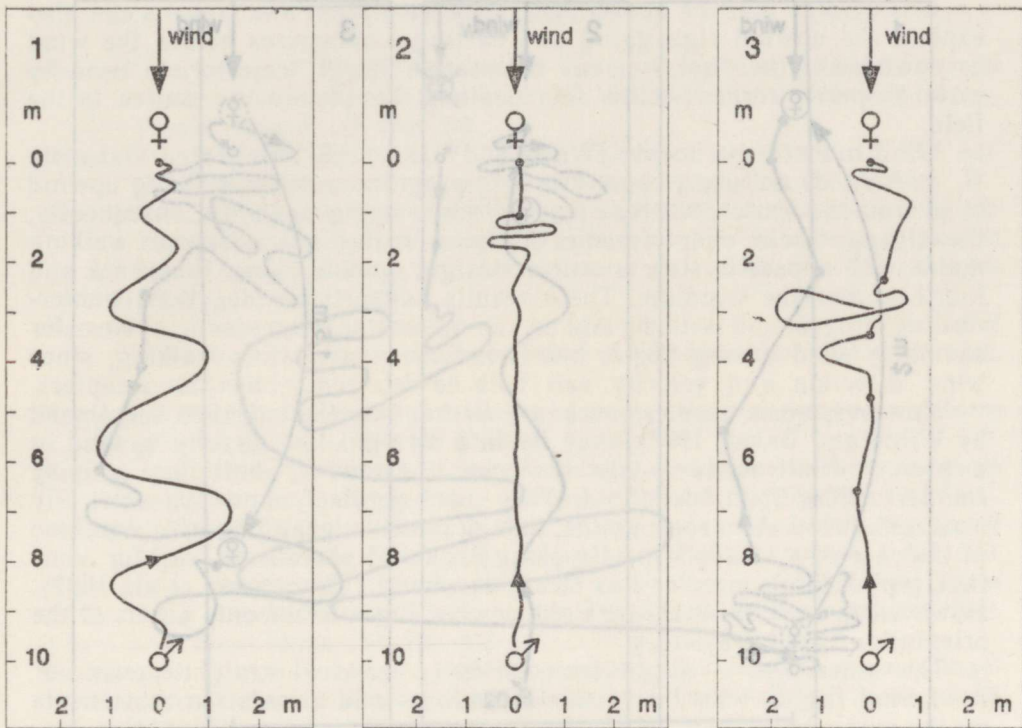
Fig. 2. Flight trajectories of male *C. pectinicornis* along an aerial pheromone trail. Landing sites are denoted with dots. Explanations in the text.
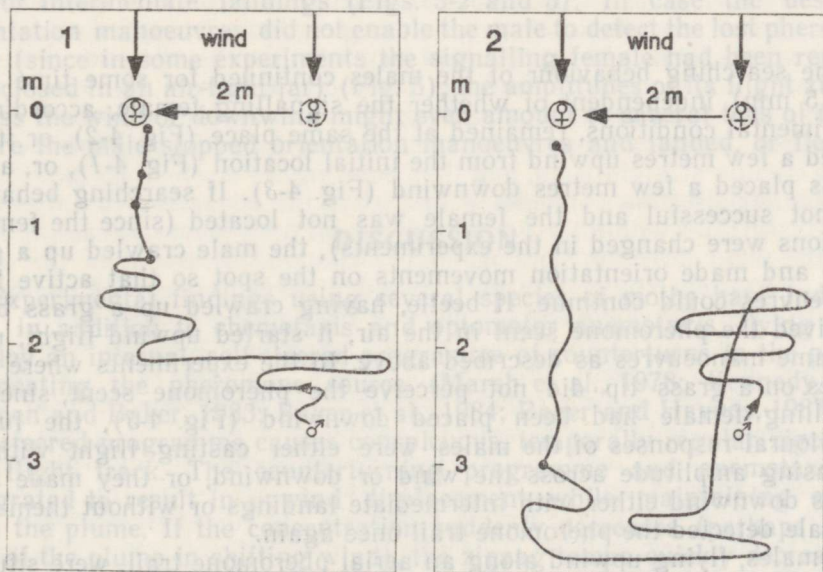

Fig. 3. Flight trajectories of male *C. pectinicornis* on their losing the pheromone trail. Dots show the landing sites. The female's sign denotes the location of the female before (dotted circle) and after (solid circle) the beginning of the experiment. Explanations in the text.
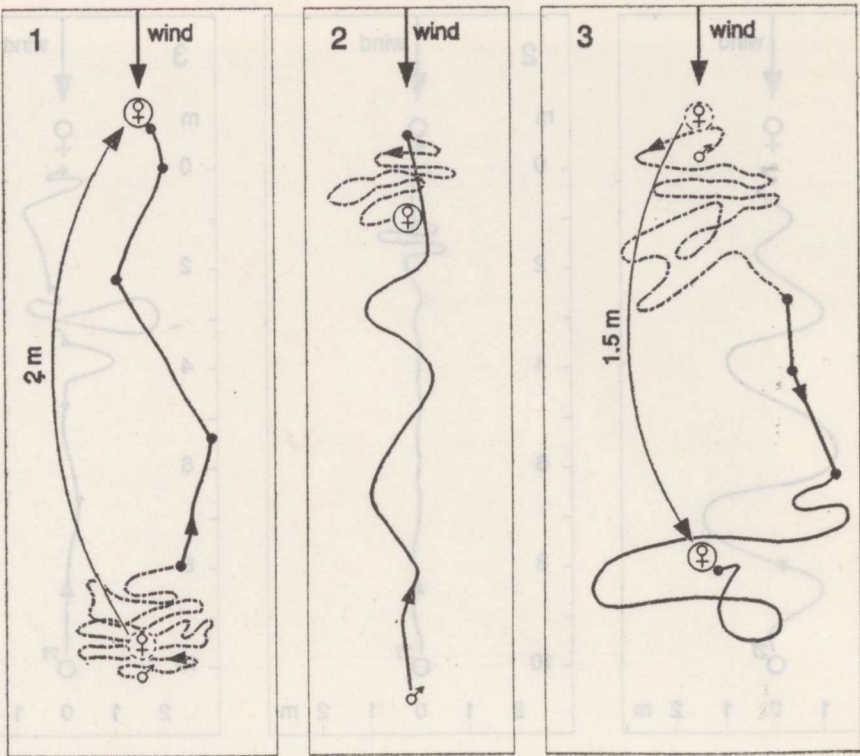
Fig. 4. Orientation trajectories of male *C. pectinicornis*. The location of the signalling female was changed after the male had started with searching behaviour. Dotted line denotes the area of searching behaviour (close-range orientation). Dots show the landing sites. The female's sign denotes the location of the female before (dotted circle) and after (solid circle) the beginning of the experiment. Explanations in the text.

The searching behaviour of the males continued for some time (max 10—15 min) independent of whether the signalling female, according to experimental conditions, remained at the same place (Fig. 4-*2*), or it was shifted a few metres upwind from the initial location (Fig. 4-*1*), or, again, it was placed a few metres downwind (Fig. 4-*3*). If searching behaviour was not successful and the female was not located (since the females' locations were changed in the experiments), the male crawled up a grass blade and made orientation movements on the spot so that active flight manoeuvres could continue. If beetle, having crawled up a grass blade, perceived the pheromone scent in the air, it started upwind flight, using the same manoeuvres as described above. In the experiments where male beetles on a grass tip did not perceive the pheromone scent, since the signalling female had been placed downwind (Fig. 4-*3*), the further behavioural responses of the males were either casting flight with the increasing amplitude across the wind or downwind, or they made short flights downwind either with intermediate landings or without them until the male detected the pheromone trail once again.

If males, flying upwind along an aerial pheromone trail, were situated 2.5—3 m downwind of the female at the moment of losing the odour trail, the character of their flight changed abruptly. Upwind flight breaks off and passes over the casting flight with the increasing amplitude across the wind or even downwind until the odour trail was found (Fig. 3). In some cases the males performed also short straight downwind flights
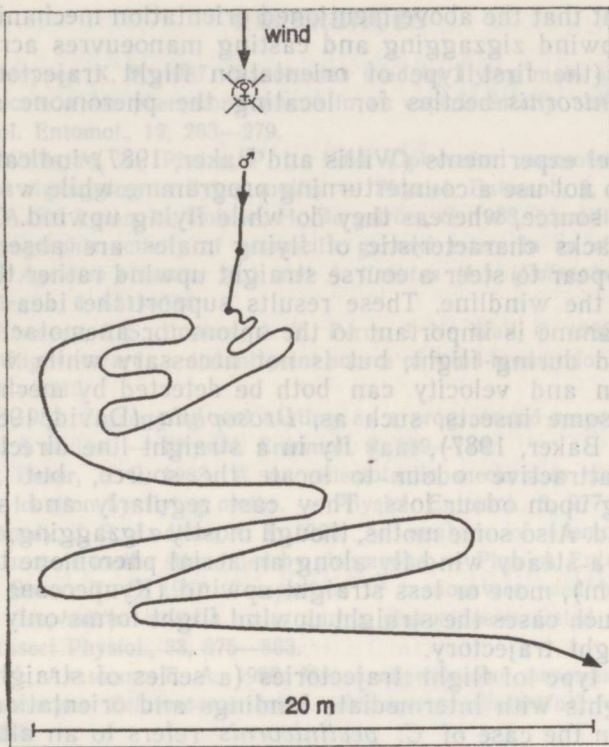
Fig. 5. Flight trajectory of a male *C. pectinicornis* on losing the pheromone trail. Dots show the landing sites. The female's sign (within dotted circle) denotes the location of the female before its removal. Explanations in the text.

and/or intermediate landings (Figs. 3-*2* and 5). In case the described orientation manoeuvres did not enable the male to detect the lost pheromone trail (since in some experiments the signalling female had been removed and closed in an air-tight jar) (Fig. 5), the amplitudes of its flight zigzags across the wind or downwind might even amount to several tens of metres before the male stopped orientation manoeuvres and landed, or flew off.

DISCUSSION

Experimental findings using several species of moths have indicated that, in addition to chemotaxis and optomotor anemotaxis, flying males employ an internal, self-steered programme of counterturns in the process of locating the pheromone source (Marsh et al., 1978; Kennedy, 1983; Kuenen and Baker, 1983; Baker et al., 1984; Baker and Haynes, 1987). The self-steered programme causes conspicuous, temporally regular zigzags in the flight track. The counterturning programme and anemotaxis are integrated to result in upwind displacement while maintaining contact with the plume. If the concentration suddenly decreases (perhaps due to loss of the plume in shifting wind), the zigzag tempo quickly decreases in conjunction with a change in anemotactic steering to result in casting flight across the windline. The primary functions of counterturning of all amplitudes in both zigzagging and casting, appear to be the maintaining of contact with an elusive odour plume and detecting shifts in the wind direction more accurately (Kennedy, 1983; Willis and Baker, 1987).

It is evident that the above mentioned orientation mechanisms can also explain the upwind zigzagging and casting manoeuvres across the wind or downwind (the first type of orientation flight trajectories) used by male *C. pectinicornis* beetles for locating the pheromone source in the field.

Wind tunnel experiments (Willis and Baker, 1987) indicated that male *G. molesta* do not use a counterturning programme while walking upwind to pheromone source, whereas they do while flying upwind. Consequently, the zigzag tracks characteristic of flying males are absent in walking males, who appear to steer a course straight upwind rather than back and fourth across the windline. These results support the idea that counterturning programme is important to the optomotor anemotactic system for sampling wind during flight, but is not necessary while walking, since wind direction and velocity can both be detected by mechanoreceptors.

However, some insects, such as, *Drosophila* (David, 1986, mentioned by Willis and Baker, 1987), may fly in a straight line directly upwind in a plume of attractive odour to locate the source, but they employ counterturning upon odour loss. They cast regularly and symmetrically across the wind. Also some moths, though mostly zigzagging, may continue in the case of a steady wind fly along an aerial pheromone trail for some time (up to 50 m), more or less straight upwind (Купрессова et al., 1981). However, in such cases the straight upwind flight forms only a part of the orientation flight trajectory.

The other type of flight trajectories (a series of straight upwind or downwind flights with intermediate landings and orientation movements on the spot) in the case of *C. pectinicornis* refers to an alternative possibility in the distant orientation of insects by odour, without starting an internal counterturning programme.

In the field, the wind direction is never constant, but it swings about, causing an odour plume to meander and "snake". At any instant much of such a plume lies more or less across the wind. It has been established by atmospheric physicists (reviewed and illustrated in: David et al., 1982), that over short grass in open country each single "parcel" of smoke (or other material e. g. pheromone) composing a plume is carried away from its source in a relatively straight line for a considerable distance, while the plume as a whole may be snaking to and fro across the mean wind direction. The snake is not the path of the wind: the plume snakes simply because the wind does so. At any point of such an odour plume the wind will be coming straight from, and thus pointing to, the source. Consequently, the wind direction coincides with that of the odour source only as far as the insect flies within the aerial odour trail. As it leaves the aerial odour trail, the wind direction does no longer coincide with that of the odour source. Persistent flying straight upwind, therefore, does not enable the insect to locate the pheromone source in the shifting wind.

As one can see, these facts are in good agreement with the second type of pheromone orientation behaviour of male *C. pectinicornis*. On landing sites they set, and during flight they maintain, an upwind course when the air stream contains pheromone. On emerging from the aerial pheromone trail the males land quickly. In case the beetles perceive pheromone again, with their antennae, in shifting wind, they perform their next straight upwind flight etc., approaching thus the signalizing female, with every straight upwind flight. However, one should not forget that males can resort to the elements of both types of orientation flight alternately.

REFERENCES

Baker, T. C., Haynes, K. F. 1987. Manoeuvres used by flying male oriental fruit moths to relocate a sex pheromone plume in an experimentally shifted wind-field. — Physiol. Entomol., 12, 263—279.

Baker, T. C., Willis, M. A., Phelan, P. L. 1984. Optomotor anemotaxis polarizes self-steered zigzagging in flying moths. — Physiol. Entomol., 9, 365—376.

Borg-Karlson, A.-K., Agren, L., Dobson, H., Bergström, G. 1988. Identification and electroantennographic activity of sexspecific geranyl esters in an abdominal gland of female Agriotes obscurus (L.) and A. lineatus (L.) (Coleoptera, Elateridae). — Experientia, 6, 531—534.

David, C. T., Kennedy, J. S., Ludlow, A. R., Perry, J. N., Wall, C. 1982. A reappraisal of insect flight towards a distant point source of wind-borne odor. — J. Chem. Ecol., 8, 1207—1215.

Kennedy, J. S. 1983. Zigzagging and casting as a programmed response to wind-borne odour: A review. — Physiol. Entomol., 8, 109—120.

Kuenen, L. P., Baker, T. C. 1983. A non-anemotactic mechanism used in pheromone source location by flying moths. — Physiol. Entomol., 8, 277—289.

Marsh, D., Kennedy, J. S., Ludlow, A. R. 1978. An analysis of anemotactic zigzagging flight in male moths stimulated by pheromone. — Physiol. Entomol., 3, 221—240.

Willis, M. A., Baker, T. C. 1987. Comparison of manoeuvres used by walking versus flying Grapholitha molesta males during pheromone-mediated upwind movement. — J. Insect Physiol., 33, 875—883.

Иващенко И. И., Адаменко Е. А. 1980. Место образования феромона у самок широкого щелкуна Selatosomus latus (Coleoptera, Elateridae). — Зоол. ж., 59, 225—228.

Иващенко И. И., Олещенко И. Н. 1974. Половой аттрактант степного щелкуна (Agriotes gurgistanus). — Зоол. ж., 53, 1030—1035.

Купрессова В. Б., Орлов В. М., Никульшина М. П., Гуров А. В. 1981. Поведение самцов дубового шелкопряда (Antheraea pernyi Guer.) при поиске самок. — Хеморецепция насекомых, Вильнюс, 6, 90—98.

Олещенко И. Н., Исмаилов Б. Я., Кузовникова И. А., Орлов В. Н., Масютин Н. Н., Лээтс К. В., Эрм А. Ю., Сийрде К. Э., Кудрявцев И. Б. 1986. Сложные эфиры гераниола, обладающие аттрактивной активностью, и аттрактант для жука-щелкуна. — SU 1072412, A 01 N 37/02, C 07 C 69/24 (/007), приоритет 19. 02. 82, опубл. в Б. И., 1986, 48.

Орлов В. Н., Исмаилов В. Я. 1986. Строение феромонных желез щелкунов подсемейства Elaterinae (Coleoptera, Elateridae). — Химическая коммуникация животных. Наука, Москва, 14—19.

Яцынин В. Г., Лебедева К. В. 1984. Идентификация многокомпонентных феромонов щелкунов полосатого (Agriotes lineatus L.) и западного (Agriotes ustulatus S.). — Хеморецепция насекомых, Вильнюс, 8, 52—57.

Яцынин В. Г., Олещенко И. Н., Рубанова Е. В., Исмаилов В. Я. 1980. Идентификация активных компонентов половых феромонов щелкунов кубанского, степного и полосатого. — Химия в сельском хозяйстве, 18, 33—35.

Яцынин В. Г., Орлов В. Н., Рубанова Е. В. 1988. Идентификация феромона и исследование его диалектов у самок Agriotes obscurus L. (Coleoptera, Elateridae). — Рефераты IV Всесоюзного симпозиума по хеморецепции насекомых, 22—23 сентября 1988 г. Вильнюс, 42.

Яцынин В. Г., Рубанова Е. В. 1988. Феромон самок жука-щелкуна плавневого Agriotes ponticus Step. (Coleoptera, Elateridae). Идентификация, синтез. — Рефераты IV Всесоюзного симпозиума по хеморецепции насекомых, 22—23 сентября 1988 г. Вильнюс, 42.

SARVIKNAKSURI *CORYMBITES PECTINICORNIS* L. (*COLEOPTERA, ELATERIDAE*) ISASMARDIKATE LENNUTRAJEKTOORID FEROMOONORIENTEERUMISEL VÄLITINGIMUSTES

Enno MERIVEE

Sarviknaksuri isasmardikate lennutrajektoorid feromoonorienteerumisel võivad olla kahte tüüpi. Esimese tüübi puhul on tegemist vastutuult suunatud siksak-lennuga või ristituult suunatud pendeldava lennuga, mis mõlemad väljendavad kesknärvisüsteemis kodeeritud vastupidiste suunamuutuste programmi. Teine trajektooritüüp on lühemate või pikemate vastutuult (või mõnedel juhtudel pärituult) suunatud otselendude jada. Vahemaandunud mardikad teevad enne uue lennu alustamist koha peal orienteerumisliigutusi. Sarviknaksuri orienteerumislennu trajektooride teine tüüp viitab alternatiivsele võimalusele putukate kaugorienteerumiseks lõhna järgi, ilma sisemist vastupidiste suunamuutuste programmi käivitamata.

ТРАЕКТОРИИ ПОЛЕТА САМЦОВ ЩЕЛКУНА ГРЕБНЕУСОГО *CORYMBITES PECTINICORNIS* L. (*COLEOPTERA, ELATERIDAE*) ПРИ ФЕРОМОННОЙ ОРИЕНТАЦИИ В ПОЛЕВЫХ УСЛОВИЯХ

Энно МЕРИВЕЭ

При феромонной ориентации самцов щелкуна гребнеусого наблюдаются два типа траекторий полета. Первый тип — зигзагообразный полет против ветра или маятниковый полет перпендикулярно ветру. Этот тип полета является выражением внутренней программы изменений направления. Второй тип — серия коротких прямых полетов против ветра или при потере феромонного облака — в направлении ветра. В случае промежуточных посадок перед началом следующего прямого полета самцы делают ориентационные движения на месте. Второй тип ориентационного полета щелкуна гребнеусого указывает на альтернативную возможность для дальней ориентации по запаху, без запускания внутренней программы изменения направления.