Behaviour of the wartbiter (*Decticus verrucivorus* (L.) (Orthoptera: Tettigoniidae) in relation to biotope

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Samenvatting

In dit stuk wordt het gedrag van de wrattenbijter geïnterpreteerd als funktie van de voortplanting en als aanpassing aan het bodembiotoop.
In het Gooi werd waargenomen dat *D. verrucivorus* vrijwel alleen 's ochtends sjirpt, terwijl de dieren in de Deense kustduinen dikwijls de gehele dag door sjirpen. Mogelijk dat in het Gooi 's middags het geluid van de wrattenbijter sterk wordt verzwakt door afbuigingseffekten in de verschillende luchtlagen. In de ochtend en onder de windrijkere omstandigheden in de duinen zou dit veel minder het geval zijn. Ook de keuze van de zangposten zou beschouwd kunnen worden als een aanpassing aan het bodembiotoop: op circa 25 cm boven de bodem is de dracht van het geluid enkele meters meer dan op de bodem. In de koude zomer van 1993 sjirpten de dieren echter ook op kale plekken op de grond: dit waren dan kennelijk de enige plaatsen waar de dieren voldoende konden opwarmen. Hoewel de Deense wrattenbijters dikwijls over korte afstanden vliegen, meestal binnen het cluster, bewegen de dieren zich toch vooral lopend voort. De mannetjes lopen al sjirpend rond om dan telkens voor ca. 5 minuten weer een sjirppost te bezetten. Keuper et al. (1986) beschouwen dit gedrag als een manier om de geringe dracht van het geluid te compenseren, zodat de kans om in (akoestisch) kontakt met soortgenoten te komen toeneemt.
De mannetjes zitten in clusters op vaste plaatsen bij elkaar, waarbij ze min of meer regelmatig verspreid zijn over het cluster. Hierbij proberen ze elkaar te mijden. Dikwijls echter is er agonistisch kontakt tussen twee of meer mannetjes, waarbij ze zo hard mogelijk sjirpen en copulatiebewegingen met het achterlijf maken. Waarschijnlijk speelt dit gedrag een rol bij concurrentie om vrouwtjes.
Mannetjes die kontakt met het cluster verliezen, kunnen soms heel ver hiervan verwijderd raken. Het is mogelijk dat andere clusters op deze manier genetisch verrijkt worden.

Introduction

This is my third article concerning aspects of the ecology of the warbiter. The previous articles were dealing with colour variation (Tienstra, 1992) and dimensions (Tienstra, 1993a); corrections and additions in Saltabel 10 (1993b), p. 15-16.
In this article on behaviour field observations from anthropogenic heathland sites in the Gooi, Holland and from (semi-) natural heathland and dune vegetations in Thy, northern Jylland, Denmark are discussed. By comparing these with terrarium observations and literature I put some hypotheses as to the function of behavioural traits, especially of the adult male. The requirements of the biotope to practise this behaviour are discussed.
In the field the adult males chirp in clusters. The male wartbiters don't have fixed territoria but change their chirping posts within the cluster.constantly.

Several elements of the wartbiter's behaviour, and especially those of the male, will be treated separately. I try to answer the following questions:
- What is the function of the respective element of behaviour concerning the reproductive success of the species?
- Can the behaviour be interpreted as an adaptation to ground biotope conditions?

1. Time of chirping activities

Observations

In the Gooi localities, which are 3 and 9 km removed from the IJsselmeer (formerly Zuyderzee) coast the wartbiters were observed only chirping in the morning (pers. obs. 1959-1988). In the first row of the coastal dunes of Thy (Denmark), where a strong wind is blowing most of the time, (part of?) the wartbiters are chirping here during the whole day. I have observed this many times in August 1992 with eastern wind (7-8 Bf; air temperature at 15:00 h in the afternoon ca. 25 °C) as well as in August 1993 with western wind (7-9 Bf; air temperature ca. 14 °C). At the same moment the wartbiters in Frøstrup, ca. 3 km removed from the coast, were not chirping. To the end of the afternoon a small part of the 'inland' wartbiters began chirping again.

Discussion

Keuper et al. (1988) provide a possible explanation for these observations. In the afternoon a negative temperature gradient in the air exists, i.e. the temperature decreases with increasing height, so the sound waves are bent away from the ground to the layers with a lower temperature. In the so-called shadow-zones the higher frequencies are especially strong attenuated. This could be detrimental to the sound propagation of the wartbiter, of which the frequencies range from 12,4 to ca. 80 kHz. So maybe the singing of *Decticus verrucivorus* in inland sites is mainly restricted to the mornings (8.00 - 13.00), because the microclimatic conditions for sound propagation are favourable then. In the afternoon these conditions occurr less often.

Because of the stronge winds in the first row of the coastal dunes in Thy the negative temperature gradient might not exist and therefore *Decticus* is able to sing all day long.

2. Song perches

Observations

In the warm summer of 1992 I observed singing male wartbiters mostly on top of *Ammophiletum* or *Callunetum* vegetations ca. 25 cm above ground level in horizontal position, as well as sitting vertically on stems, e.g. of *Rumex acetosa* plants. In the cold 1993 summer however they were nearly exclusively singing on patches of bare sand between the vegetation (coastal dunes) or on very low vegetation mainly consisting of the grass *Agrostis*, recently grazed by rabbits, resp. on mosses spec. div. (*Pleurozium*, *Hypnum*, *Polytrichum*) (inland sites in Thy, northern Denmark).

Discussion

The song of *Decticus verrucivorus*, with prominent frequencies of 12-16 kHz and 30-55 kHz (Kalmring et al., 1990), seems not to be adapted to the acoustic properties of the soil biotope, where frequencies higher than 10 kHz are more strongly attenuated than those below this pitch (Michelsen & Larsen, 1983). As the propagation of the sound is enhanced with several meters the wartbiter preferably chooses higher song perches (Keuper et al., 1986). In cold weather however patches with bare sand and short turf seem to be the only places which are warm enough for reproductive behaviour.

3. Clustering

Observations

Clusters were found especially on warm places, e.g. SE exposed slopes of dunes, and always adjacent to or in humid 'green' areas (Tienstra, 1992), where egg deposition and development of the larvae takes place.

The diameter of a cluster of some 20 males depends on the structure and acoustic properties of the vegetation. In the Gooi area the diameter of the three big clusters on the North Heath was about 100 m in the middle of August (fig. 1). They occurred on open vegetation with relatively favourable acoustic properties (*Genisto anglicae-Callunetum*: Tienstra, 1992). In Thy, the clusters on SE exposed dune slopes mostly are twice as small (10 clusters, ca. same number of chirping males). This might be caused by smaller acoustic range on these sites. Refraction, reflection, multiple scattering of the

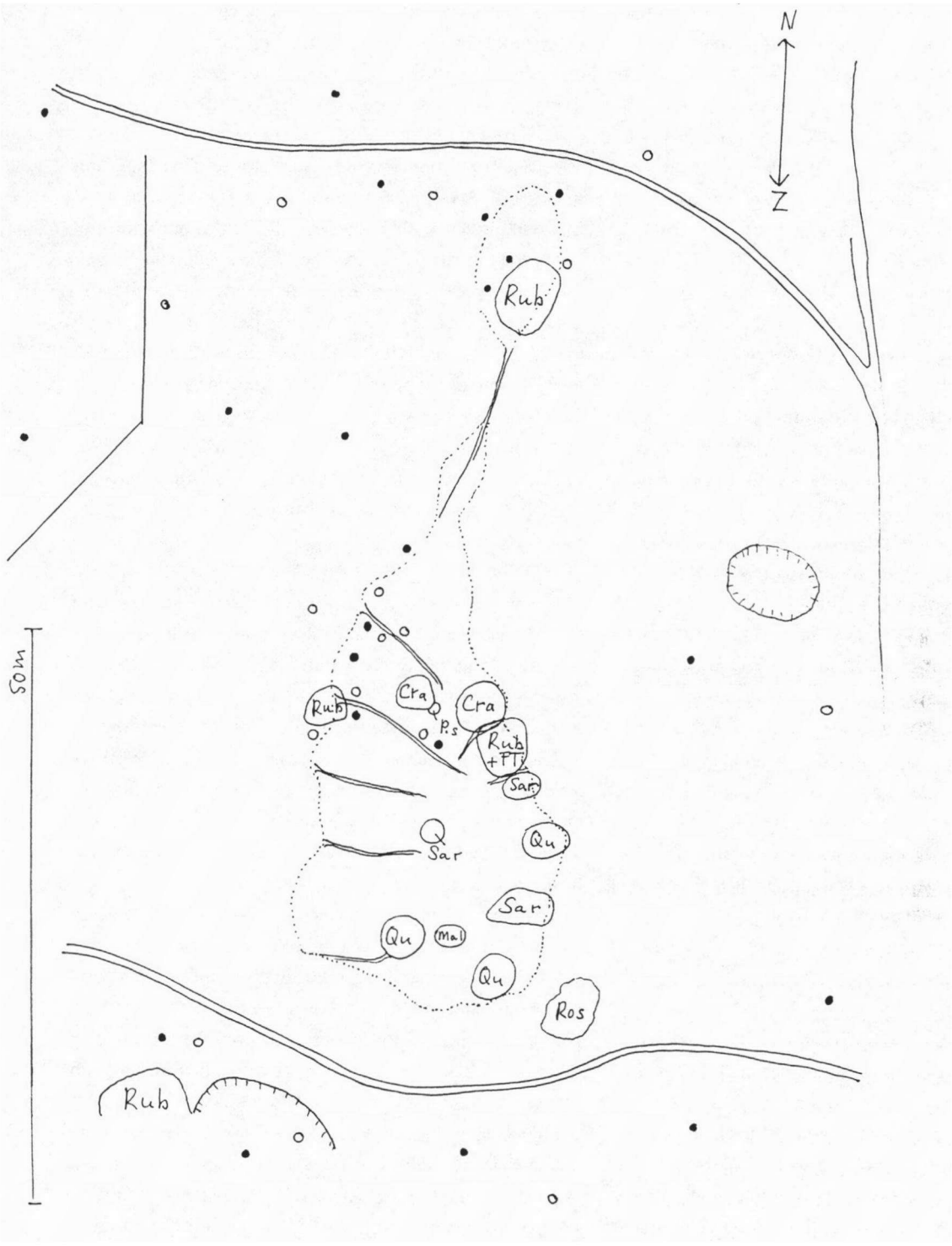

Fig. 1. Positions of chirping *Decticus verrucivorus* in a loam pit on the north Heath, het Gooi, the Netherlands.

● : singing males on August 15th, 1966 at 11:00 a.m.
o : singing males on August 16th, 1966 at 11:00 a.m.

Vegetation in and around the pit: *Festuco-Thymetum serpylli*, to the edge of the cluster: *Genisto anglicae-Callunetum* (see Table 1, Tienstra, 1992). The following shrubs are indicated in the circles: *Malus sylvestris*, *Prunus spinosa* (P.s.), *Quercus robur*, *Rosa eglanteria*, *Rubus* spec. div., *Sarothamnus scoparius*, *Crataegus monogyna* and *C. oxyacantha*. The concentration of wartbiters on the SE exposed slope of the pit probably is correlated to the highly structured vegetation and the favourable microclimatological conditions.

sound waves of the song will weaken it, as a substantial part of the wavelength of this sound corresponds to the sizes of vegetations structures, notably grass leaves in *Ammophiletum* vegetation (a.o. of the grasses *Ammophila*, *Calamagrostis*, *Festuca* and *Agrostis*) (Tienstra, 1992; Keuper & Kühne, 1983). Later on in the season the diameter of the clusters of male wartbiters increases, with the growing inter-individual distances (par. 6).

Discussion

Acoustic systems with silent females, like in *Decticus verrucivorus*, more or less imply acoustic communication between the males. In this case, the acoustic information not only has a function in attracting females but also in premating selection (Latimer & Schatral, 1986). Clustering of males in so-called 'leks' (Wilson, 1980) offers possibilities to this (Schatral et al., 1985; Tienstra, 1992, 1993a). Moreover acoustic information may give rise to regular dispersion of the males in a cluster, to avoid agonistic contacts (Schatral et al., 1985; Latimer, 1980; Latimer & Schatral, 1986), thus creating opportunities for undisturbed copulation.

Singing of bushcrickets also has a visual component: the elytra moving in sunshine are conspicuous for predators, especially for birds of prey which have very sharp senses of sight (see also Tienstra, 1992). Clustering of singing males in large aggregations probably reduces the risk of predation for single individuals, as the whole cluster will be warned by a stop of the chirping activities of one of the males.

4. Locomotion

Observations

I observed wartbiters in Thy flying off the dunes over longer distances in the warm 1992 summer (Tienstra, 1993a). In the cool summer of 1993 I only saw *D. verrucivorus* males flying within their own cluster from one bare sandy place to another, over a distance of 5-10 m, just above the vegetation, in the same way as acridid grasshoppers like *Chorthippus brunneus* do. The wartbiters demonstrated this behaviour not only when they were disturbed by me, but also spontaneously. I didn't see females flying in the 1993 summer. The flying behaviour could be observed especially on SE exposed dune slopes.

However, the most important ways of locomotion for *Decticus verrucivorus* are walking and jumping. I consider the shape of the legs as an adaptation to ground life. The hind legs are very long and therefore suitable for pushing off during walking. The fore and mid legs are relatively short, compared to those of the shrub-living *Decticus albifrons*. In the field I many times observed animals pushing themselves through grassy vegetation, pulling with nearly stretched hind legs, not impeded by too long mid and fore legs.

In Denmark the males covered 30-80 m in one morning on a meadow with very short grass (*Poo-Lolietum*: Tienstra, photo 4, 1992), in the dunes on *Ammophiletum* vegetation this distance was rarely more than 15 m. In the last habitat the females covered 5 m at the most in the same period. In the Gooi area, Holland, I observed a maximum transposition of a wartbiter male of 100 m in one day. The uniformly grazed *Callunetum* vegetation, which was present here in the 1960s, is very suitable for walking of the wartbiter.

Discussion

The structure of the vegetation will turn the scale of the distance covered: eventually it may impede locomotion of the animals nearly completely, e.g. when by lack of grazing the grass *Deschampsia flexuosa* has strongly increased. The animals will become entangled in the rigid flowering stems of this grass (Tienstra, 1992). A lot of daily walking is an essential feature of the wartbiter's behaviour, especially in the males. *D. verrucivorus* does not occupy fixed song perches, like other big bushcrickets. It takes such a post for 5-10 minutes and then moves on while stridulating with a lower intensity during 1-2 minutes (Keuper et al., 1986) until it reaches a suitable song perch for more intense singing. In relation to the bad propagation of the sound of *D. verrucivorus* the walking activities may be considered as a way to enhance the number of (acoustic) encounters with conspecifics (Keuper et al., 1986). The evolution of behavioural traits might have been accomplished more easily than adaptation of the sound to the unfavourable acoustic properties of the ground biotope, because of morphological restrictions of the chirping apparatus (Keuper et al., 1986).

The colour variation of *D. verrucivorus* helps in reducing predation of a mobile insect like *D. verrucivorus* (Tienstra, 1992).

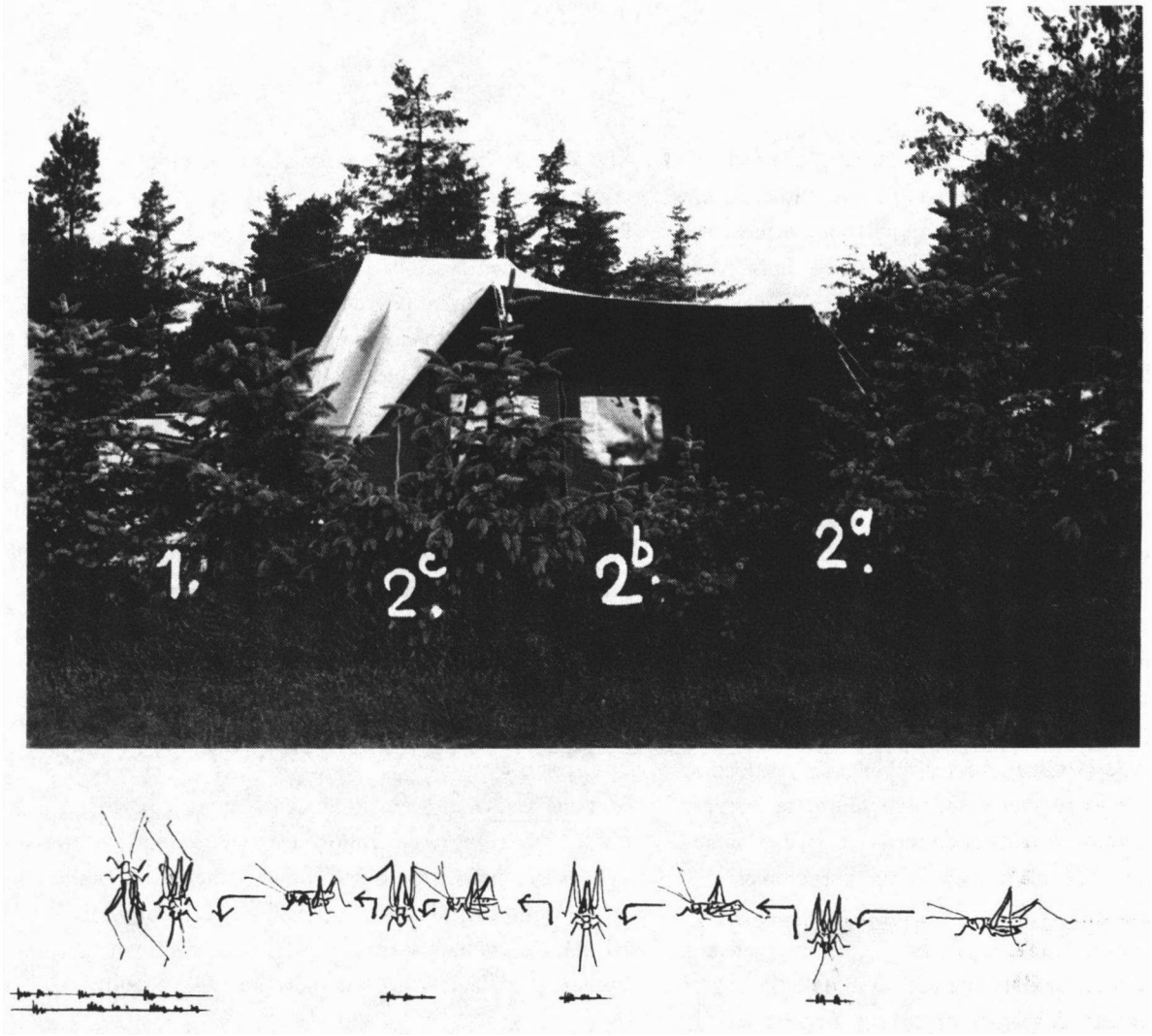

Photo 1. Arena of two male *Decticus verrucivorus*, Hjardemål Klit Plantage, camping, Aug. 1992.
Chirping male nr. 1 had been approached by nr. 2, which stopped four times at posts 2a, 2b, 2c, and 1 respectively. When chirping ardently during ca. 1 minute in each stop, it again and again turned its right side, which produces a higher sound intensity, to nr. 1 and vice versa. I observed this 'directional' behaviour several times, but always in conditions without wind.

5. Acoustic rivalry

Observations

In the morning, when after sunrise the soil is warming up, the males in a cluster produce single chirps, in which they distinctly respond to each other. As temperature rises, they begin to walk and, when stopping, to chirp more ardently. In their behaviour they distinctly react upon each other acoustically, also when synchronously chirping with their rival(s). I'd like to circumscribe this synchronous chirping as 'accidental', analogous to the synchrony in *Pholidoptera griseoaptera* during prolonged chirps (Jones, 1966).

In richly structured vegetations with many high herbs and patches of bare sand and low-tufted grasses interindividual distances between chirping males are relatively small, e.g. in the industrial area of Frøstrup, Denmark 3-7 m on 7 August 1993 (n = 27). Though constantly changing, the mutual distances between the males were always within this range (see also fig. 1). Low densities in a population however may lead to agonistic contact between acoustically interfering males. I observed on three occasions from 25 observed duets and trios that during this behaviour the 'owner' of the chirping post and the 'invader' turned each other their right sides (photo 1). As the right elytron contains the sound producing speculum, a higher sound intensity is measured on the right and upper sides of chirping bush-crickets (Keuper et al., 1986; Rheinländer & Römer, 1990). I observed this behaviour only in conditions without wind, but never in the terrarium.

Two acoustically rivaling males (or 3: Bulbjerg 1993; up to 5 rivaling males in the terrarium pers. obs.) chirp together during some minutes, while moving their abdomen in a way that resembles copulation movements. When males get very close to each other, with touching antennae and legs, 'defence' movements of the legs clearly play a role in damping aggression. In the terrarium I observed that old individuals with incomplete 'defence' caused by legs broken off were attacked and even eaten.

Discussion

Bailey (1985) demonstrated that the intensities of the high frequency peaks in the song of bushcrickets are very directional. The fact that especially higher frequencies of the song are more attenuated (Keuper et al., 1986), may account for the lack of the above described 'directional' behaviour in windy occasions. Directional hearing may be distorted under such circumstances. Rivalry motivation also may play a role. In all of the three observations of this behaviour 'isolated' males were concerned. In the terrarium resonance of the sound against the glass walls could have played a role.

I consider the copulation-like movements during rivaling to be averted behaviour, because encounters between males form an essential part of the social behaviour of this ground-living species. Different from other bushcrickets like *Tettigonia viridissima* and *T. cantans*, rivalry between males of the wartbiter does not lead to biting and chasing away of the subordinate male. Anyone who ever felt a bite of the wartbiter can imagine what the function is of this apparent biting block.

The function of the duets and trios of chirping males is not clear. Female premating selection on account of acoustic information seems very likely. For instance in *T. cantans* lower prominent sound frequencies (which are mostly the result of tegminal resonance) seemed to favour dominance more than high values for sound intensity and body weight (Latimer & Schatral, 1986). A high sensibility in the Central Nerve System of the wartbiter for the vibration frequency of 100 Hz might have a special function in drawing the attention of the female (Kühne te al., 1980). Each closure of the tegmina may induce vibration in the body of the singing insect which is then transmitted to the underground. When two individuals, males and/or females, are very near to each other, preferably on the same plant, this vibration frequency might play a stimulating role in the sexual behaviour.

6. Reproductive strategies in a cluster

Observations

In the second half of July and the beginning of August the clusters of *Decticus verrucivorus* are still relatively dense and stable with inter-individual distances between the males of ca. 3 - 15 m. (fig. 1). In this situation nearly all the individuals have acoustic contacts with their neighbours. The distances covered during the daily walking tours of the males are more limited than later in the season. This pattern can also be found in other Tettigoniidae that live in shrubs and trees like *Tettigonia viridissima* and *T. cantans* (pers. obs.). Males of the wartbiter may get removed from the cluster, probably caused by loss of acoustic contact with group members. By the end of the summer roughly half of the original number of males will still be present in the cluster, but with greater inter-individual distances. In the terrarium some individuals are constantly walking more than others. This seems to be independent on the presence and/or absence of other individuals. In the field the same individuals (recognizable by means of their coloration) covered great distances again and again, also when they were brought back in the cluster (n=10).

Discussion

Walking behaviour seems to be partly genetically determined. Part of the males follow a safe reproductive strategy by staying in the cluster. The 'wandering' males may enrich other clusters genetically. They can be called to have a 'quality strategy', with far less favourable reproductive chances but with new genetic possibilities.

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Résumé

Comportement de Decticus verrucivorus dans deux sites à la côte

Le comportement de Decticus verrucivorus est interpreté en fonction de la reproduction et de l'adaptation à son biotope. Dans la région Het Gooi (Pays–Bas) *D. verrucivorus* chantait uniquement le matin; à Thy (Danemark) le chant est entendu toute la journée. Dans la population hollandaise, l'absence de chant l'après–midi pourrait être la conséquence d'un effet d'écartement du bruit dans les différentes couches d'air dans un site plus continental que celui des dunes à Thy. Les choix des postes de chant peut également différer en fonction du biotope. A une hauteur de 25 cm, le chant prote plusieurs mètres plus loin qu'au sol. Pendant l'été froid de 1993, les animaux chantants se trouvaient également à des endroits dénudés, qui se chauffent plus vite que des endroits à végétation.

Bien que les animaux étudiés au Danemark volent sur de petites distances, leurs mouvements prennent généralement la forme de marches sur le sol. Les mâles marchent en chantant, puis ils s'installent durant env. 5 minutes à un endroit pour chanter. Ce comportement est expliqué par les efforts pour atteindre les femmeles, compensant ainsi la faible portée du chant. Les mâles sont généralement groupés, mais à l'intérieur d'un groupe, ils sont espacés et ils évitent le contact avec d'autre mâles. Lorsqu'ils se rencontrent, ils se comportement de façon spéciale, en chantant fortement et en simulant des mouvements de copulation.

En captivité, les femelles peuvent être fécondées plusieurs fois, à condition ue la nourriture contient beaucoup de protéines.

Les mâles qui perdent contact avec leur groupe, peuvent s'écarter beaucoup du groupe. Ainsi, les autres groupes subissent un enrichement génétique.