

Colour variation in two coastal populations of the wartbiter (*Decticus verrucivorus* (L.); Insecta: Orthoptera) in relation to biotope

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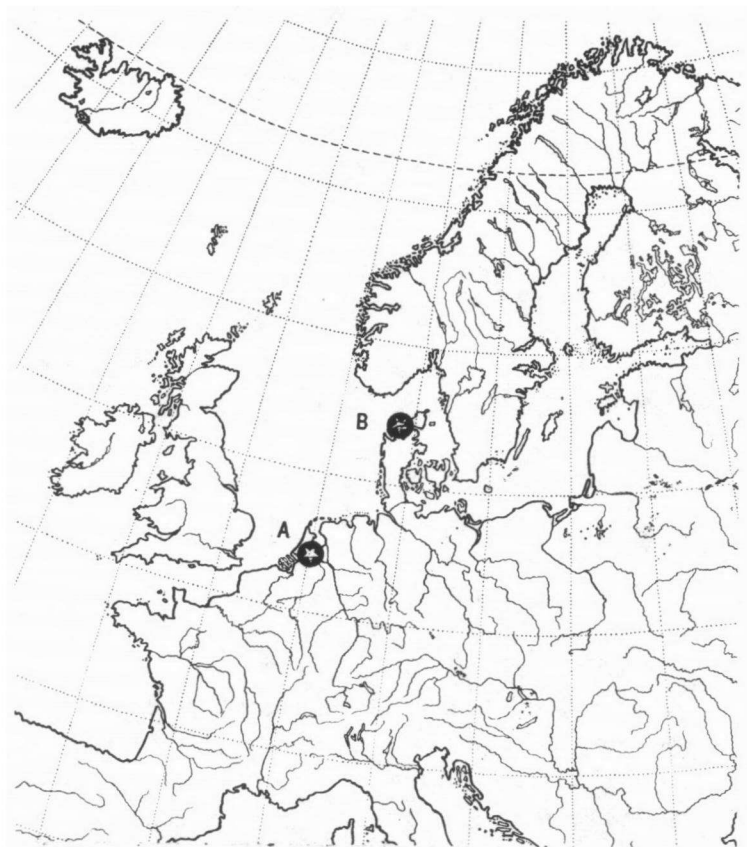
Photographs: T. Tienstra - van der Staak, except for nrs. 1, 3 and 4 by the author

Samenvatting

In de jaren '60 kwamen in het Gooi nog wrattenbijters (*Decticus verrucivorus*) voor, verdeeld over 2 populaties met elk zo'n 100 zingende mannetjes. Deze dieren hadden minimale afmetingen en waren vrijwel altijd van een donker-blauwgroene kleur. Het analis-cubitalis veld (a, foto 5) was eveneens donkergroen, of zeer donkerbruin. Toen ik in 1981 tijdens een bezoek aan het Deense Hanstholm reservaat dezelfde kleurvariëteit van de wrattenbijter aantrof, kwam ik tot de hypothese van een 'atlantische vorm', die kustheiden van Noordwest-Europa zou bewonen.

In 1992 moest ik deze veronderstelling laten vallen: in dat jaar bezocht ik grote delen van het schiereiland Thy en hoorde duizenden wrattenbijters sjirpen. Ze kwamen in verschillende biotopen voor, waren heel gevarieerd van kleur en hadden behoorlijke afmetingen. Dieren met een blauwgroene kop en pronotum werden, naast andere variaties, echter uitsluitend in de heidehabitat aangetroffen (bijlage 1).

In dit artikel probeer ik de zeer karakteristieke Gooise dieren te duiden als aanpassingen aan een zeer eenzijdige habitat, nl. de dofgroene, door menselijke invloed ontstane struikheide-akker (*Genisto anglicae-Callunetum*). De donkergroene wrattenbijters vallen hierin minder op dan de lichtgroen gekleurde. Feitelijk bestaat het biotoop van de wrattenbijter uit twee habitats, één voor de larven en één voor de volwassen dieren (tabel 1). De larvale habitat is begroeid met een nogal vochtig, lichtgroen gekleurd vegetatietype, dat afwisselend van hoogte en rijk aan structuur is. In het Gooi wordt de adulte habitat gevormd door uniforme struikheidevege-



Figuur 1. location studied sites: A. Gooi (NL), B. Thy (Den.)

tatie, die, als de schapen enige jaren geleden het betreffende perceel bezocht hebben, over grote oppervlakten tot gelijke hoogte is uitgegroeid (foto 1). Dit laatste is erg belangrijk, want hier hebben de mannetjes hun baltsplaatsen ('leks'): ze leggen er afstanden van wel 100 m per dag af, om met elkaar te rivaliseren en wijfjes te ontmoeten. Het belang van een structurele hoogte van de vegetatie ca. 25 cm boven de bodem is, dat de dracht van het mannelijke gesjirp in dat geval

meer dan twee maal zo groot is dan het op de bodem zou zijn. Vergrassing van de heide door bochtige smeie (*Deschampsia flexuosa*) hindert de dieren in hun voortbeweging, en dit is waarschijnlijk de voornaamste oorzaak geweest van het uitsterven van de wrattenbijter in het Gooi in 1989.

In Noord-Jutland zijn zowel de habitats voor de volwassen wrattenbijters als die voor de larven veel gevarieerder dan die in het Gooi (par. 3.2 en foto's 2-4). Dit is terug te vinden in het uiterlijk van de dieren (foto's 5-10).

Het biotoop van de wrattenbijter stelt complexe eisen, bovendien heeft een gezonde populatie een nogal groot oppervlak nodig (par. 2). Daardoor gaat het dan ook slecht met deze gorilla onder de sprinkhanen in het geciviliseerde Noordwest-Europa. De populatie op Thy is thans de belangrijkste van deze regio.

Ca. 5 % van de Gooise dieren is niet groen gekleurd, maar geheel of gedeeltelijk zwart, grijs, bruin of paars. Voor populaties in andere biotopen gelden vergelijkbare getallen (Sussex: kalkgrasland; Thy: gevarieerde duinvegetaties: tabel 2). De naar mijn inzicht meest bevredigende hypothese voor dit verschijnsel is, dat selectieve predatie van de larven, die zich immers in een groene habitat bevinden, een grote rol speelt.

Aantrekkelijk is het de werking van epistatische genen te veronderstellen, d.z. dominante genen die door hun invloed op meerdere loci een (te?) grote variatie binnen populaties tegengaan. Bij de bruine sprinkhaan (*Chorthippus brunneus*), waar deze genen zijn beschreven, kunnen ze m.i. populaties van deze soort 'beschermen' tegen te veel variatie in basiskleur, hoewel toch een schier eindeloze afwisseling in kleur bij een minderheid van de populatie mogelijk is. De dieren kunnen daardoor leven in biotopen met een zeer verschillende kleur en structuur, terwijl een klein aantal is aangepast aan bepaalde microhabitats.

Voor de wrattenbijter, waarvan het mannetje dagelijks grote afstanden loopt en dat gebruik maakt van vegetaties van verschillende kleur en structuur, zou te grote variatie binnen een populatie, analoog aan *Chorthippus brunneus*, nadelig kunnen zijn.

De kleur van het analis-cubitalis veld heeft waarschijnlijk de functie dat hierdoor het dier a.h.w. visueel in tweeën wordt gedeeld en derhalve minder als zodanig herkenbaar is voor predatoren, vooral als dit vleugelgedeelte geelachtig gekleurd is en het dier zich in een gra-

zige vegetatie met gedeeltelijk afgestorven grasbladen bevindt, bv. een helmgrasvegetatie (*Elymo-Ammophiletum*). De uniforme donkergroen-bruine analis-cubitalis velden van de Gooi-dieren zullen een aanpassing zijn aan het eenzijdige dofgroen gekleurde *Calluna vulgaris*-biotoop.

1. Introduction

In the 1960's hundreds of wartbiters occurred in the Gooi area, divided among two populations, one at the North and the other at the South Heath. The species is since 1989 extinct in the Gooi.

According to the notes I took and the 30 specimens or so that I collected, the animals from these two areas were very conspicuous: they were very small, and, when green, in all cases of a dark blue-green coloration. The analis-cubitalis field (a, Photo 5) at the upper edge of the elytra was either of the same dark green colour or very dark brown, never pale brown, reddish brown or yellow, like in the photograph of this species in Duijm & Kruseman (1983). The black stains on the lateral lobes of the pronotum (b) and elytra (c) and the lines on the abdomen (d) were more developed than in many continental specimens.

Except for one, incompletely labeled specimen, all the wartbiters from the Gooi present in the Entomological Museum of the University of Amsterdam have these features. They are not only collected by me, but were also by, a.o. MacGillavry, Kruseman, Piet and Troelstra between 1915 and 1967. All my specimens, and supposedly theirs too, have been collected in the heath habitat. In 1981 I visited the Hanstholm Reserve in Northern Jylland (Denmark). Here I found wartbiters with the same coloration, but of 'normal' dimensions (Photo 5). I arrived at the hypothesis of a special 'Atlantic form', which would inhabit coastal heath areas in NW Europe (Tienstra, 1992).

After I visited the SE part of this magnificent 6000 ha Reserve in 1981, I explored in the summer of 1992 the NW part of the State Reserve and the area between the Reserve and Frøstrup, part of the peninsula of Thy. I heard the chirping of at least several thousands of male *Decticus verrucivorus*. In a number of places the populations of the inland and coastal biotopes are still in contact with each other. My observations here made me drop my hypothesis: the dark-green Gooi wartbiters cannot be classified into a higher 'Atlantic form' hierarchy.

In this article the colour of the wartbiters will be discussed in relation to the biotopes in the Gooi and Thy.

2. Biotope conditions

The biotope of *Decticus verrucivorus* consists of two habitats, one for the larvae and one for the adult animals. The larval habitat is formed by a high-structured green vegetation that consists of several layers between 0 and 55 cm high: here oviposition also takes place in patches of bare sand or in those covered with a very thin vegetation (own observation, see also Cherrill & Brown, 1990b). As the diapausing eggs will starve below a humidity level of 75% (Ingrish, 1986), it is absolutely necessary that the soil is humid here all over the year: also when it seems dry on the face of it, a constant humidity at a depth from 3 cm on is indispensable. Adult females can mostly be found not very far from these 'larval' places, but in fact the exact distribution of the females during their life cycle is unknown: as they don't chirp, it is not easy to detect them in the field.

The adult males walk, while chirping, up to a 100 m daily, as part of their sexual rivalry behaviour. This walking takes place in well-defined areas, where some twenty to thirty males meddle with each other. These 'leks' (Wilson, 1980) have to meet a number of require-

ments.

As the propagation of the sound of the wartbiter is very poor at ground level - at a distance of 2-3 m. it provokes no longer a reaction of its opponent - a structural vegetation layer of 20-25 cm. high improves the transfer of the high frequencies of the walking wartbiter's chirp up to 4-5 m. and further (Keuper et al., 1986).

For this purpose the uniform anthropogenic *Genisto anglicae-Callunetum*-vegetation (see de Smidt, 1981) (Photo 1) of the Gooi is very fit. When a flock of sheep grazed a particular area several years ago, all the heather-plants grew out to the same height, thus making possible the daily wanderings of the wartbiters at a constant distance from the ground.

Though this large bushcricket has very small fore and midlegs - probably to avoid obstruction by grasses -, a too grassy habitat, and especially the rigid flowering stems of the grass *Deschampsia flexuosa*, may impede its daily walking tours and thus its sexual (rivalry) contacts. Therefore, in many places the males find themselves in dry areas for their leks, the vegetation here being so scarce that they can wander, using the scattered tussocks of e.g. the grass *Corynephorus canescens* as a chirping post. In the Thy dunes a 'structural' vegetation layer of flat-lying leaves of the dune-grass *Ammophila*



Photo 1. The Gooi, South Heath, 1964. *Genisto anglicae-Callunetum*; this vegetation has a function for the leks of the wartbiter. In the distance, 30 m. lower, the humid 'green' breeding places of the larvae can be seen. La Gooi, Lande méridionale, 1964. *Genisto anglicae-Callunetum*; cette végétation a une certaine fonction pour les "leks". A l'arrière-plan, 30m plus bas, le biotope humide des juvéniles.

larval habitat

Verge of cycle track:

little hole that collects rain water from track; height of vegetation 0-10-30 cm, coverage about 90%.

Main plant species
Agrostis capillaris
Plantago lanceolata
Campanula rotundifolia
Dactylis glomerata
Holcus lanatus
Molinia caerulea
Galium mollugo
Trifolium repens
Cirsium arvense
Artemisia vulgaris
Rubus cf. fruticosus

Orthoptera
Decticus verrucivorus
Tettigonia viridissima
Chorthippus brunneus
C. mollis
C. albomarginatus
Gryllus campestris

Larval and adult habitat

Southeast exposed slope of loam pit, veg. *Festuco-Thymetum serpylli* (Westhoff & den Held, 1969)
height of vegetation: 0-3-15-25-35-55 cm, coverage 95%

Main plant species
Calamagrostis epigejos
Hypericum perforatum
Agrostis capillaris
Festuca rubra
Festuca ovina
Ononis spinosa
Pimpinella saxifraga
Thymus serpyllum
Polygala vulgaris
Galium verum ssp. maritimum
Linum catharticum
Lotus corniculatus
Viola canina
Calluna vulgaris
Erigeron acer
Antennaria dioica
Achillea millefolium
Plantago lanceolata

Orthoptera
Decticus verrucivorus
Chorthippus brunneus
C. biguttulus
C. mollis
Omocestus viridulus
Stenobothrus stigmaticus
Nemobius sylvestris

Adult habitat (used as lek):

veg. *Genista anglica*-*Callunetum* (Photo 1)
height of vegetation: uniform 0 and 30 cm, coverage 80%

Main plant species
Calluna vulgaris (cov. 80%)
Genista anglica
G. pilosa
Festuca ovina ssp. tenuifolia
Nardus stricta
Deschampsia flexuosa (rare)
in open places a.o.:
Cladonia
Polytrichum piliferum
Dicranum scoparium

Orthoptera
Decticus verrucivorus
Chorthippus biguttulus
Myrm. maculatus
Oed. caerulescens

Table 1. Examples of larval and adult habitats of *Decticus verrucivorus* in the Gooi: the main plant species and the Orthoptera-fauna in the localities (data: Tienstra, 1992). Biotope de *Decticus verrucivorus* au Gooi.

arenaria is also used as such.

Because of all these conditions the leks can be found at fixed places. In most landscapes only a very small part of an extensive area is used by the wartbiters: they not only need lek territories with a not to luxuriant vegetation, but also humid places for egg deposition and 'green' vegetations for larval development in their neighbourhood.

If I put the case that a minimum of some 50 to 60 chirping males, to be divided among 2-5 leks, and which mutually can enrich the populations of each other as to their genetical composition, is necessary for the long-term survival of the wartbiters, then the 'vital space' (Lensink, 1963) in the more uniform landscape of the Gooi area is 1,5-2 sq. km and in part of the Thy dunes, with the highest degree of variation, 4-5 ha, as I observed in the field in the respective areas.

The maximum diameter of a large lek is about 150 m: in the Gooi, where the larval areas were situated especially along paths etc., the distribution of the leks also created linear figures with a maximum length of 3 km; in the differentiated Thy dunes the usage of the area by the wartbiters can be more economical, so that the vital space can be smaller here. Nevertheless, this is also a large area for a ground-dwelling insect.

On account of the complex biotope conditions the wartbiter has strongly declined in NW Europe, especially in the last two decades, in several countries nearly to extinction. The Thy populations undoubtedly is the most important of the region.

3. The biotopes in the two areas

3.1. The biotope in the Gooi (Photo 1)

In the 1960's the wartbiters exclusively used a small part of the 1000 ha grey-brown podzolic soil occupied by a uniform *Genista anglica*-*Callunetum* vegetation, a result of five ages of human wood cutting and sheep grazing. Here the animals had their leks. These were situated near the 'green' larval places, which were lying either along the main cycle track, where water from the track was led into undeeep holes and ditches, or in loam pits (Table 1): very vulnerable localities in the crowded Gooi area because of tourist recreation, and even more as these were very limited areas in the monoculture of *Calluna vulgaris*.

3.2 The biotope at Thy (see for the Orthopterofaunas Appendix 1)

3.2.1 Coastal heath (Photo 3)

In Denmark the natural heath habitat, consisting of *Carici arenariae-Empetretum* (de Smidt, 1981) has a lot of variety: it contains, except for *Carex arenaria* and *Empetrum nigrum*, plant species like *Polypodium vul-*

gare, *Hieracium umbellatum* and *Ammophila arenaria*. Scattered over the area you can find many low, grassy places with a.o. *Calamagrostis epigejos*, *Pimpinella saxifraga*, *Ophioglossum vulgatum* and in the wettest places, unfit for the wartbiter, *Hydrocotyle vulgaris*, Orchidaceae div. spec. and *Gentiana pneumonanthe*.

I suppose that egg deposition takes place in the border zones of these small areas, where a.o. *Plantago coronopus*,

Armeria maritima, *Ononis spinosa* and *Odontites verna* indicate a form of *Plantago coronopus-Carex distans*-association (Westhoff & Den Held, 1969). On the bare, sandy ridges of the soil here the females may deposit their eggs. This vegetation also indicates that the water level is rather high.



Photo 2. Thy, 1992, Inland heath near Frøstrup: a mosaic of patches with a.o. *Vaccinium uliginosum*, *Calluna vulgaris*, *Empetrum nigrum* with *Ammophila arenaria*, *Erica tetralix*. A little 'spoiled' by the grass *Deschampsia flexuosa*. The population density of the wartbiters is small in the heath, as compared to that in the verge of the road (front of photo), which functions as a corridor between heath areas. Thy, 1992. Lande près de Frøstrup: végétation mosaïque de *Vaccinium uliginosum*, *Calluna vulgaris*, *Empetrum nigrum*, *Ammophila arenaria*, *Erica tetralix*. Une partie est envahie par *Deschampsia flexuosa*. La densité de la population de *Decticus verrucivorus* est petite dans la lande, en comparaison avec le bord de la route, qui fait fonction de corridor entre deux parties de la lande.

3.2.2. Coastal dunes (Photo 3)

The same can be said of the coastal dunes, where the wartbiters occur in greater population densities. Here too, the soil is always moist and males as well as females can be found in the superficially uniform-looking vegetation, which however demonstrates a subtle, nearly mosaiclike diversity: the dunes on the weather side are covered with an *Elymo-Ammophiletum*-vegetation, var. with *Elymus arenarius* and *Lathyrus japonicus* (= *maritimus*) (low population density of wartbiters) and off the wind side with the variety of this plant-association with a.o. *Festuca rubra*, *Hieracium umbellatum* with patches of *Carici arenariae-Empetretum* and *Violo-Corynephorum* (Westhoff & den Held, 1969) in between (very high population density of wartbiters); in Appendix 1 these lee side plant-associations are presented together under the heading '*Carici arenariae-Empetretum* (+ *Ammophiletum aren.*, etc.....)', so to be considered as part of the heath habitat.

The leks are mostly on SE exposed slopes, often with an *Ammophiletum*-vegetation.



Photo 3. Hansholme Reserve, 1981. Coastal heath and dunes. A mosaic of *Elymo-Ammophiletum*, *Carici arenariae-Empetrum* and *Violo-Corynephorum* functions as a walking area for the male wartbiters; most leks can be found in SE exposed *Ammophiletea*. On the left in the distance a 'green' place, which I suppose to be fit for larval wartbiters. Landes et dunes à la côte. Végétation mosaïque de *Elymo-Ammophiletum*, *Carici arenariae-Empetrum* et *Violo-Corynephorum* fait fonction d'aire de "promenade" pour les mâles. La plupart des "leks" se trouvent sur *Ammophiletea*, exposés au sud-est. À gauche une zone "verte", biotope des juvéniles.



Photo 4. Thy, 1992. Verge of road 6 km. east of Hjarðemál. Dry ditch with a.o. *Heracleum spondylium*, *Equisetum arvense*, *Urtica dioica*; next to it scanty former 'productive' grassland. In the area in-between, parallel to the wire, chirping males and (egg-lying) females in a linear configuration. Bord de route, 6km à l'est de Hjarðemál. Fossé sec à *Heracleum spondylium*, *Equisetum arvense*, *Urtica dioica*. À côté: petite pelouse abandonnée. Entre les deux, mâles chantants et femelles pondants sur une ligne.

Sussex population (chalk grassland) (Cherrill & Brown, 1991) males and females		
1987	95.2	(n=334)
1988	86.5	(n=266)
1989	100	(n=201)

Gooi population (dry <i>Callunetum</i>) own observations, only males		
1966	93.4	(n=91)
1967	94.5	(n=73)
1969	100	(n=63)

Table 2. Percentage of green animals (adult) in two populations of *Decticus verrucivorus*. Pourcentage d'adulte de couleur verte dans deux populations de *Decticus verrucivorus*

3.2.3. Inland heath (Photo 2)

On the more inland heaths vegetation is denser and higher; the *Calluna vulgaris* and *Empetrum nigrum* plants are up to 45 cm high (the 'ideal' height for the walking/chirping male *Decticus*' is about 20 cm, par. 2).

The vegetations are often mixed with the grass *Deschampsia flexuosa*, of which, as stated above, the rigid flowering stems impede the males in their daily walking tours to challenge the other males and to meet females. So this grass, the result here of the decline of wind influences because of *Pinus*-plantations, and the end of sheep grazing, directly destructs the structure of the lek. All the heath areas in north Jylland with more than approximately 30% *Deschampsia* had no wartbiters at all.

Another cause of their absence may be the fact that the areas of bare soil are minimal here, so that the females cannot deposit their eggs.

3.2.4. Road verges (Photo 2 and 4)

Where wartbiters in inland heath areas do occur, they can be found in anthropogenic biotopes, like the road verge of Photo 2, respectively on the edge of a Poo-Lolietum (Westhoff & den Held, 1969), a former 'productive meadow' (Photo 4), which, as a consequence of poverty of the soil and a dry spring, looks more like a savannah vegetation at the end of the dry season. I found chirping males here in a linear constellation, backed by the high herbs of the dry ditch. On this ridge long, sandy patches, traces of former ploughing, could be seen. In this place I observed an egg-lying female. As a consequence of the linear position of the animals

the social structure of the lek must have been weak, also because the males were chirping here at soil level, a condition with very unfavourable acoustic properties.

In many places however these long anthropogenic structures have a function as corridors between distinct areas.

4. Colour variation in the two areas

4.1 The Gooi

The coloration of the green specimens was described in par. 1 of this article. A small percentage of the adult wartbiters did not have the overall blue-green colour. This quantity globally agrees with that of the Sussex-population and the Denmark-data (Appendix 1).

I found the following not-green varieties:

- sides of the animal pale grey (upper side of head, pronotum and elytra, including analis-cubitalis field, blue-green)
- animals of overall dark grey, nearly black coloration
- overall purple
- overall pale brown
- overall reddish brown
- overall dark brown

All colour variations demonstrate the characteristic white stripe, with black and mostly also white spots on the elytra. I collected specimens of most varieties. As I prepared them with formaldehyde 10% they maintained their colours pretty well.

4.2 Thy

In 1992 I didn't find specimens with an overall blue-green coloration like those of my 1981 visit and as described in par. 1 (Photo 5). Nevertheless, in the area I visited this summer animals with blue-green head and pronotum but with pale green coloured elytra could be found (Photo 6). This variation however was only present in the heath habitat, while I saw all-over pale green wartbiters (Photo 7) in all habitats. The colour of the analis-cubitalis field at the upper edge of the elytra (a, Photo 5) was, of the animals from the heath, as well as those from the other habitats, green, pale brown or dark brown (Photos 5-10). A good number of specimens had lateral pronotum lobes with, except for the 'traditional' black spot, an olive brown or ditto green coloration (a, Photo 8). This feature was always coupled with a frontal spot (b) on the hind femora in this olive colour set-

ting, which is an argument for linked genes or pleiotropy.

I saw one specimen of an overall dark brown coloration (Photo 9).

5. Discussion

5.1. Varieties in the green body colour

The biotope of the wartbiter at Thy is, including the heath habitat, much more varied than that in the Gooi. The presence and/or lack of distinct body colour varieties in these areas must be considered as selective answers to their respective circumstances.

Investigations of a number of Acrididae demonstrate the importance of a large phenotypic variation for ground-dwelling grasshoppers, as vegetations of this biotope are spatially and temporally very variable in our climate. Moreover, grasshoppers with a large phenotypic variation have been demonstrated to choose actively for habitats that agree with their own body coloration

(Rubztov, 1935). Both phenomena together enhance the fitness of these populations, as they are better able to exploit their environment than monomorphic populations.

The exclusively (?) blue-green coloration of the Gooi-warbiters in green colour setting might lead to the conclusion that amputation of their biotope on account of the building of houses upon the communal meadows at the end of the last and the beginning of this century led to gene flow and consequently to impoverishment of the gene pools of the populations. The usual lag between the state of the environment and the adaptive state of the population had probably become substantial in the Gooi area, so that the animals must have been vulnerable. Although the Gooi populations had accomplished maximum crypsis because of the development of an overall dark blue-green colour in nearly all individuals-, they were however still conspicuous in the dull-green *Calluna vulgaris*-habitat, at least to human eyes. Nevertheless, the flossy purple inflorescence seemed to



Photo 5. Hanstholm Reserve, 1981. All-over dark blue-green male of *Decticus verrucivorus*. The elytra with the analis-cubitalis field (a) also have this coloration; the black spots on lateral lobes of pronotum (b) and elytra (c) are well-developed, as well as the black striping (d) on the abdomen. Mâle vert foncé de *Decticus verrucivorus*. Les élytres et le champ anal-cubital (a) de même coloration; les tâches noires sur les lobes du pronotum (b) et sur les élytres (c) sont bien développées, de même que les anneaux noirs sur l'abdomen (d).



Photo 6. Frøstrup Heath, 1992. Male of *Decticus verrucivorus*. Animals from the heath are often smaller, more markedly stained and striped and of a darker green than those from other biotopes. Head, upper sides of pronotum and abdomen: dark blue-green; lateral lobes of pronotum and front of hind femora olive brown; elytra green; analis-cubitalis field pale brown. Mâle de *Decticus verrucivorus*. Les animaux vivant sur les landes sont plus petits, de couleur plus foncée, que celles des autres biotopes. Tête, partie supérieure du pronotum et abdomen vert foncé; lobes du pronotum et fémurs postérieurs buns olives; élytres verts; champ anal-cubital brun clair.

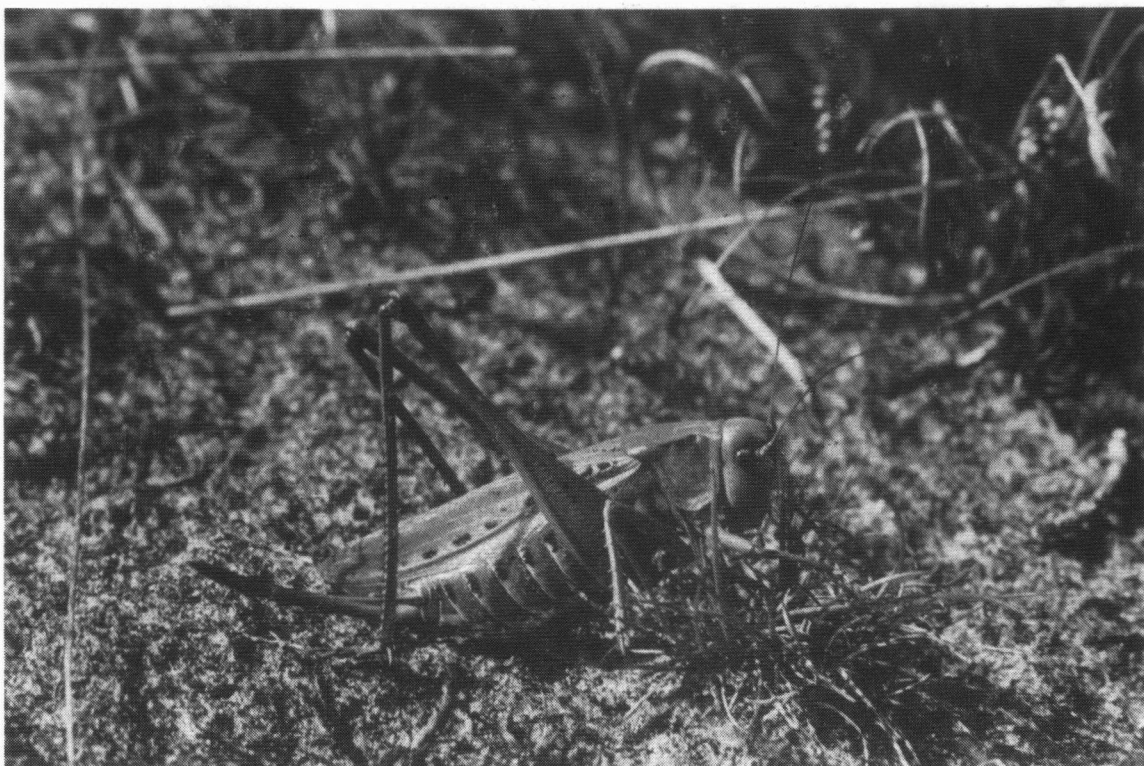


Photo 7. This weakly stained and striped, all-over pale green female of *Decticus verrucivorus* was found in a dry *Callunetum*-vegetation near Frøstrup. Femelle de couleur verte claire vivant dans une végétation de *Callunetum*.



Photo 8. Hjardemål, male of the verge of photo 4. The wartbiters in these biotopes are mostly somewhat bigger and have a more pale green coloration. Colour: overall green, also the analis-cubitalis field; lateral lobes of pronotum (a) and front of hind femora (b) show the (so characteristic for the Thy peninsula) olive brown coloration. n mâle du bord de route de la photo 4. Les animaux de ce biotope sont plus grands et de couleur plus claire. Coloration: vert, également le champ anal-cubital; lobes du pronotum (a) et fémurs postérieurs (b) bruns clairs.



Photo 9. Hanstholm Reserve, 1992. This big male was found in the first line of sea-side dunes, in *Ammophiletum*. Overall body colour dark brown, except for analis-cubitalis field (pale brown) and lateral lobes of pronotum/front of hind femora (dark olive brown). Ce grand mâle a été observé dans la première rangée de dunes côtières, dans un *Ammophiletum*. Coloration: corps brun foncé, à l'exception du champ anal-cubital (brun clair) et des lobes du pronotum et des fémurs postérieurs (brun-olive foncé).



Photo 11. Hjørdemål Klit, 1992. This big female was found near to the male of photo 9. However, it flew off when disturbed and covered some 15 m in a nearly horizontal line. Colour: overall pale green, except for the analis-cubitalis field (pale brown); black staining and stripes at pronotum, elytra and abdomen minimally developed; one hindleg missing. Cette grande femelle a été observée près du mâle de la photo 9. Elle s'envolait sur une distance de 15 m. Coloration: vert clair, à l'exception du champ anal-cubital (brun foncé); coloration foncée et tâches sur le pronotum; élytres et abdomen peu développés; une patte postérieure manque.

favour crypsis. Also in Denmark the animals with a (partly) blue-green coloration were probably - the material is statistically insufficient - restricted to the heath habitat. The 1992 findings in this habitat were made in places up to 300 m from dunes or other 'green' vegetations. The overall blue-green specimens of my 1981 visit to the Hanstholm Reserve occurred in a large heath area, 3 km removed from coastal and 'green' vegetations like road verges, meadows etc.

These observations led me to my selection hypothesis concerning the blue-green Gooi animals.

Ofcourse predation of adult individuals by vertebrates must play an important role in this, but I honestly admit that my own observations of predation are scarce: in the Gooi the sparrow hawk (*Accipiter nisus*) skims over the heath, catching insects, but I didn't collect concrete data.

Cherrill & Brown (1990b) report the kestrel (*Falco tinnunculus*) as a potential predator.

They record 5.2 % of the adults of the 1987 Sussex-population with severed hind femora, hind tibiae or ovi-positors; a further 13.0 % had an entire hind leg missing, while an adult female was found with triangular

beak marks on her abdomen. In Denmark birds of prey seemed to be nearly completely absent at the moment, I suppose as a consequence of the intensive corn culture over extended areas.

Besides mammals the big lizard (*Lacerta agilis*), which is very common at Thy, may be a potential predator.

5.2. Percentage of a not-green basic body coloration

In par. 4 (Table 2) I pointed out that a minority of adult specimens from the Gooi, Sussex and Thy populations didn't have the overall blue-green, green or pale green body colour. I suggest that this may have to do with predation of the larvae. Just after hatching the larvae have a greyish coloration (Cherrill & Brown, 1991). During their development they generate the green colour more and more, especially from stage 4 on. While they find themselves in their green larval habitat during this period, selective predation of the not-green colour varieties seems likely. In any case the mortality rate of the larvae is very high: in the 1988 Sussex-population 99.3 % ! (Cherrill & Brown, 1990a). Candidates for this feat might be the crested lark (*Galerida cristata*), the wheatear (*Oenanthe oenanthe*) and groups

of wandering starlings (*Sturnus vulgaris*). Although occurring in the area then, I never saw the black grouse (*Lyrurus tetrix*) and the pheasant (*Phasianus colchicus*) in the neighbourhood of the breeding places, contrary to the small lizard (*Lacerta vivipara*), which is very common in the Gooi as well as in the Thy area.

Considering the data of the Gooi, England and Denmark, which agree as to the percentage of green individuals in these populations, predation of adult warbiters may not play an important role in the 95/5 body colour ratio.

Another possible explanation for this might be the working of epistatic genes, i.e. dominant genes that exhibit interactions with other loci, thus 'protecting' the populations of the warbiter from too much variation and nevertheless making possible an enormous variation in a minority of it (analogous to *Chorthippus parallelus* (Sansome & La Cour, 1935) and *C. brunneus* (Gill, 1981). One may imagine that maximum crypsis for a large bushcricket like *Decticus verrucivorus*, which occupies habitats of diverse colours and structures (e.g. the colour and diameter of leaflets in poor vs. more luxuriant vegetations), will be realised by not too much variation. The males of this species walk around in the sunshine, while chirping, covering distances up to 100 m a day. During these activities they make use of diverse vegetations (see also Photos 1-4), in which a not-green basal coloration might be disadvantageous.

Crypsis with less uniformity is to be found with little grasshoppers like *Myrmeleotettix maculatus* which presents an almost endless variety in body colour and detailed spotted and striped markings. This small xerophilic grasshopper, occurring exclusively in the heath habitat, is, in its variety, very well adapted to many microhabitats of the heath biotope, where it dwells all its life.

Chorthippus brunneus however, which can be found in a variety of biotopes, has predominantly a brown body colour; other colour varieties are only demonstrated by a minority in most populations as adaptations to specific microhabitats, thus enlarging the fitness of these populations as a whole. In this species the working of epistatic genes has been confirmed (Gill, 1981). *Decticus verrucivorus* lives in habitats with a large diversity too. An analogous hypothesis can be offered for this wandering insect.

5.3. Colour of analis-cubitalis field

The colour of the analis-cubitalis field at the upper edge of the elytra undoubtedly plays an important role in crypsis. When the animal is in a resting position, the clear green lateral sides are not easily visible. Seen from above, the brown colour of the area mentioned favours crypsis of the animal in more luxuriant grassy vegetations, as it presents itself in the form of a linear structure. Because of this the rectangular form of the green pronotum and head may look less conspicuous, as the animal is, so to say, divided in two elements.

In the dull dark green *Calluna vulgaris*-monoculture, which was formerly so abundant in the Gooi heaths, a dark green or dark brown an.-cub. area would favour crypsis, a pale coloured one would make the animals very conspicuous. This might explain the complete (?) absence of the pale brown coloration of this area in the individuals of the Gooi populations, according to my own observations and as demonstrated by the material collected in Amsterdam, while it is present in a number of the Jylland warbiters, as well as in those from other Dutch populations (e.g. Hoge Veluwe, Nunspeet, Drongelen, Hoog-Buurolo). The biotopes in these places are more varied in structure and colour of vegetation than that of the uniform *Calluna*-habitat in the Gooi, which became nearly the only open type of vegetation in this area until the 1970's, when the expansion of the grass *Deschampsia flexuosa* and of the exotic *Prunus serotina* had begun, results of increased N-deposition and the end of sheep grazing.

The variety in colour of the analis-cubitalis field in the Jylland populations (Appendix 1) is certainly correlated here to the diversity of biotopes and a certain disequilibrium of the regulating genes.

5.4. Black staining and stripes

The black stains on pronotum and elytra, and ditto lines on the abdomen also can be considered as adaptations with a crypsis function of this ground-dwelling bushcricket. I could not find a significant difference in the amount of staining between 'heath' and 'green' habitat animals (Appendix 1).

5.5. Genetic characteristics of respective colour features
Stains on elytra and body, and also the (for the Danish specimens rather typical) combination of dark olive brown lateral lobes of pronotum and olive brown stains on hind femora 'shine through' the green basic colour.

Even in the brown, grey, violet, etc. specimens these features are visible. This argues for different gene complexes of these genes respectively: the overall body colour is superimposed on other polychromatic variations in detail.

5.6. Alternative hypotheses

The basic body colour, notably the adult (blue-)green, might, besides genetic and selective correlates, be the result of modification. Young wartbiters have a greyish coloration; during their larval development they generate their green body colour.

Laboratory experiments with *Schistocerca vagans* demonstrated that low humidity during earlier larval stages result in a high proportion of green hoppers turning brown in later instars, whereas high humidity result in most hoppers retaining their green coloration (Rowell & Cannis, 1972). Analogous to this, the young larvae of the Gooi wartbiters may have generated a darker green body colour during their development in distinctly drier habitats than the Jylland animals in what I suppose to be their 'breeding areas'.

Homochromic responses, i.e. grasshoppers developing pigments within a very short period so that they can survive at a substratum whose colour has suddenly changed, e.g. after a fire, can be excluded for the wart-biter. This phenomenon only seems to involve black, yellow and orange pigments and apparently these are not produced on green backgrounds (Rowell, 1971). Moreover, the greyish colour of the young *Decticus* larvae changes to green from stage 4 on, as the larvae still find themselves in their green larval habitats.

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Résumé

Deux populations de *Decticus verrucivorus*, une du Gooi (Pays-Bas) et une de Thy (Danemark) ont été étudiées. Au Gooi, presque exclusivement des animaux verts foncé ont été observés, tandis qu'à Thy il y avait plus de variabilité dans la coloration de l'animal (vert clair, vert foncé, brun olive) et des élytres (champ anal-cubital), mais la proportion d'animaux verts est également 95%. Les animaux du Gooi étaient également de taille extrêmement petite, ce qui est probablement dû au biotope peu varié, consistant d'une lande à *Calluna*. A Thy, les animaux volaient facilement. L'espèce est en déclin dans le nord-ouest de l'Europe. La population du Gooi n'existe plus depuis 1990. Celle de Thy est probablement la plus grande de la région.

Appendix 1

Data of *Decticus verrucivorus* from northern Jylland, collected by R. Tienstra, august 1992
Données concernant *Decticus verrucivorus* dans le nord de Jylland en août 1992.

'green' habitat									
sex	pronotum	elytron	hindfemur	ovipositor	body color	pron. lat lobes	black stains elytra	color an.-cub	locality
♂	9.0	23	32.5	-	d. green		+++	p. brown	A
♂	9.0	30	32	-	d. green		+++	p. brown	B
♂	8.5	28	28	-	d. green		++	d. brown	C
♂	8.5	31	31	-	p. green		+++	p. green	D
♂	8.5	31	32	-	p. green		+	p. brown	D
♂	9.0	33	34	-	p. green	olive green	+	p. brown	D
♂	8.0	34	33	-	p. green	olive green	+	p. brown	E
♂	8.0	31	31	-	p. green		++	p. green	F
♂	9.0	33	33	-	p. green		+++	p. brown	F
♂	8.5	30	31	-	p. green		++	p. brown	F
♂	9.0	32	31	-	p. green	olive brown	++	p. brown	F
♂	9.0	33	31	-	d. brown	olive brown	+++	p. brown	G
♂	8.5	32	32	-	p. green	olive brown	++	p. green	H
mean	8.7	31	32						
extr	8-9	23-34	28-34						
(N=13)									
♀	9	34	37	23	green		++	p. brown	F
Heath habitat									
♂	8.0	27.5	28	-	p. green		+	p. brown	I
♂	8.5	29	29	-	p. green*		+++	p. brown	I
♂	7.5	28	29	-	p. green	olive brown	++	green	I
♂	7.0	27	28	-	p. green*		++	green	I
mean	7.8	28	29						
extr	7-8.5	27-29	28-29						
(N=4)									
♀	8.5	28.5	32	22.5	p. green		+	p. green	J

* head + pronotum blue-green

Description habitat

- A. Hjardeå Klit Hotel; grassy vegetation along verge (photo 4); other Orthoptera - *Chorthippus brunneus*
- B. Hjardeå Klit Hotel; grassy vegetation along verge (other locality than A); other Orthoptera - *C. brunneus*, *C. biguttulus*
- C. Frøstrup; verge of road near *Cariciarenariae-Empetretum*, *Callunetum* & *Ericetum* (photo 2); vegetation cov. 100%, 30 cm high: *Carex arenaria*, *Ammophila*, *Festuca rubra*, *Armeria maritima*; other Orthoptera - *C. brunneus*, *C. biguttulus*
- D. near Hjardeå Klit Hotel; verge of road near *Cariciarenariae-Empetretum*, *Callunetum* & *Ericetum* (photo 2); vegetation cov. 100%, 30 cm high: *Carex arenaria*, *Ammophila*, *Festuca rubra*, *Armeria maritima*; other Orthoptera - *C. brunneus*, *C. biguttulus*, *Omocestus viridulus*
- E. Frøstrup, near Hjardeå Klit Hotel; vegetation cover 100%; verge along field (*Ammophila*, *Elytrigia repens*, *Galium verum*, *Campanula*); other Orthoptera - *C. brunneus*, *C. biguttulus*, *O. viridulus*
- F. Hjardeå Klit Beach; Dunes along the North Sea beach: *Elymo-Ammophiletum* with *Rosa pimpinellifolia*, *Galium verum*, *Pimpinella saxifraga*, *Lathyrus japonica*; other Orthoptera - *C. brunneus*, *C. biguttulus*, *C. albomarginatus*, *O. viridulus*
- G. Hanstholm Reserve; dunes along the North Sea beach: *Elymo-Ammophiletum* with *Rosa pimpinellifolia*, *Galium verum*, *Pimpinella saxifraga*, *Lathyrus japonica*; other Orthoptera - *C. brunneus*, *C. biguttulus*, *C. albomarginatus*, *O. viridulus*
- H. Hjardeå Klit Camping; verge of field with *Calluna vulgaris*, *Carex arenaria*, *Ammophila*, *Festuca rubra*, *Holcus lanatus*; other Orthoptera - *C. brunneus*, *C. biguttulus*
- I. Hanstholm Reserve; *Carici arenariae-Empetretum* (+ *Ammophila arenaria*, *Corynephorus canescens*, *Potypodium vulgaris*, *Viola canina*, *Hieracium umbellatum*, Lichenes) (photo 3); other Orthoptera - *C. brunneus*, *C. biguttulus*, *Myrmeleotettix maculatus*
- J. Frøstrup; *Carici arenariae-Empetretum*, *Callunetum*, *Ericetum*, with a.o. *Vaccinium uliginosum* (photo 2)