

Dimensions in two coastal populations of the wartbiter (*Decticus verrucivorus* (L.)) in relation to biotope

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Samenvatting

In een vorig artikel (Tienstra, 1992a) heb ik de kleurvariatie binnen de wrattenbijterpopulaties van het Gooi en Thy (Denemarken) besproken.

Hier komt het verschil in afmetingen tussen dieren van deze locaties aan de orde.

De Gooise wrattenbijters hebben minimale afmetingen (tabel 1). Dit kan te maken hebben met het ontbreken van voldoende eiwitrijke voeding in de arme *Genista anglica* - *Callunetum* vegetatie, de door eeuwenlange begrazing met schaapskudden ontstane heide-akker, die in het Gooi in de jaren '60, vóórdat vergrassing en verbossing toesloegen, de belangrijkste habitat was van de volwassen dieren. Op Thy bevinden de dieren zich in een zeer gevarieerd biotoop en ze hebben dan ook flinke afmetingen. De dieren van de heidehabitat lijken hier eveneens iets kleiner te zijn (tabel 1). De vleugels van de Thy'se wrattenbijters zijn flink ontwikkeld, ze vliegen van de hoge duinen naar beneden. In dit heuvelachtige gebied zullen dieren met lange vleugels enig selectief voordeel hebben, doordat ze ook op deze wijze naar andere baltsplaatsen kunnen gaan.

Introduction

In a previous article (Tienstra, 1992a) I have compared the colour variability of wartbiters in the Gooi area (Holland) and at Thy (Denmark). I have put forward the hypothesis that the preponderance of the dark blue-green colour of the Gooi animals was due to the uniform anthropogenic scanty *Genista anglica* - *Callunetum* heathland

biotope (see De Smidt, 1981), as opposed to the greater variability of the Thy animals, caused by a much more varied biotope, consisting of heathland, dunes and former agricultural vegetation.

In this article I will treat the differences in dimensions of the animals from these two areas.

1. Size

The Gooi wartbiters were extremely small (Table 1). I consider this to be another result of differences in their biotope. The larvae of *Decticus verrucivorus* are probably predominantly carnivorous (Cherrill, 1989); the adults, probably out of sheer necessity, are herbivorous: in captivity they immediately hunt for *Chorthippus brunneus* and *C. albomarginatus*, and this from the very start of their captivity. In their natural habitat in the Gooi area, a dry *Callunetum*, I did observe them eating only the growing tips of the heather plants; their faeces were invariably dry, fibrous and greenish.

Undoubtedly a sufficient quantity of animal food is absent in the *Callunetum typicum* during late August and September, when *Decticus* needs many proteins for its progeny, as this period has the highest reproduction rate. The Gooi wartbiters - and to a lesser extent those from the heathland habitats of Thy, although not the Thy animals from the "green" habitats (in the middle of August in the dry 1992 summer (Tienstra, 1992a)) - had very lean appearance, with shrunk abdomen. This leads me to believe that the heathland habitat, especially the dry *Callunetum typicum* of the Gooi area, is too scant for the wartbiter.

males	hind femur	pronotum	elytron		n
Harz ¹	25.3-35.0	6.9-10.5	21.3-25.0		-
't Gooi (1915-1967) ² heath-habitat	26.3 (25.0-28.6)	7.6 (6.5-8.9)	24.7 (20.8-27.3)		10
Thy (1992) ³ heath-habitat	28.5 (28.0-29.0)	7.8 (7.0-8.5)	27.9 (27.0-29.0)		4
Thy (1992) green-habitat	31.7 (28-34)	8.7 (8.0-9.0)	30.9 (23.0-34.0)		13
females	hind femur	pronotum	elytron	ovipositor	n
Harz	28.0-37.0	7.7-11.0	23.0-30.0(38.0)	17.0-26.0	-
't Gooi (1940-1967) heath-habitat	28.3 (26.0-32.6)	7.7 (6.8-8.9)	23.1 (21.0-27.8)	18.3 (15.9-21.0)	10
Thy (1992) heath-habitat	32.0	8.5	28.5	22.5	1
Thy (1992) green-habitat	37.0	9.0	34.0	37.0	1

¹Harz, 1960

²Tienstra, 1992b

³Tienstra, 1992a

Table 1. Measures in two coastal populations of *Decticus verrucivorus* (L.) and in literature (in mm)

As well as other bushcrickets the male wartbiter offers a nuptial present to the female before copulation: a spermatophore, containing two little ampullae with sperm, together with a spermatophylax, rich in proteins. The spermatophore is attached to the abdomen of the female and assures the transfer of the sperm into the female body while she is eating the spermatophylax. Moreover, the female will not copulate with another male during this time.

A very large spermatophylax, such as of the bushcricket *Ruspolia verticalis*, may function as a parental investment, favouring the survival rate of the progeny by increased fertility (Gwynne, 1984 in Wedell, 1991), as well as by larger eggs, larvae and adults (Gwynne, 1988 in Gwynne, 1990).

Wedell and Arak (1989) however have proven that the spermatophylax of *Decticus verrucivorus* has the right size for the transfer of the ejaculate to be accomplished,

although the possibility of parental investment cannot completely be excluded. The spermatophylax size per se failed to show any effect on female reproduction. Instead, it was found that the volume of ejaculate transferred to the female is the factor controlling female receptivity and oviposition behaviour. Thus the main function of nuptial feeding may be defined in this species as sperm protection.

Experiments with doubly mated females (Wedell, 1991) strongly suggest that sperm mixing occurs within the wartbiter, numerical sperm competition being the acting mechanism. Fertilization success seems to be directly related to the size of the spermatophylax, which in turn is correlated to the volume of ejaculate transferred. Thus, when the second male provides the female with a larger spermatophylax relative to the first male, his volume of ejaculate will be larger and there will be a numerical superiority of his sperm. Hormones in the

ejaculate may cause the postmating unreceptivity period of the female, hasten the onset of oviposition and increase the rate of egg-laying (Wedell & Arak, 1989).

Cherrill & Brown (1990) report dramatic increases in weight of adult females during the month of August. This is probably caused by the maturation of the eggs and the accumulation of body fat. At the end of August the females attain their maximum body weight, so that they should not reach a peak in potential fecundity until early in September (Sussex population, 1987 and 1988). In addition, Cherrill & Brown state that the weight increase of the male *Decticus* after larval development is bigger than can be accounted for by the production of a single spermatophore. Therefore they suggest that the males accumulate sufficient material to enable them to produce a number of spermatophores in rapid succession.

However, I doubt if the mechanisms described will often occur in the field in the Gooi biotope: if the summer is dry during the second half of August and in September - as is often the case - and, if not, the weather may be so bad in this northern Atlantic climate as to exclude nearly all copulation opportunities, it may be virtually impossible for the wartbiter to find enough proteins at all. Cynical coincidence: this period of the wartbiter's highest reproduction rate is the summer holiday period in Holland; in the densely populated urban Gooi area, 30 km. east of Amsterdam, not a *conditio sine cura* for the wartbiter.

South Heath (5 leks)		North Heath (5 leks)	
11 August 1966	29	15 August 1966	62
		16 August 1966	62
21 August 1967	22	22 August 1967	51
		23 August 1967	51
9 August 1969	22	9 August 1969	41
		10 August 1969	41
31 August 1988	0?	31 August 1988	4?
22 August 1989	0!	22 August 1989	0!
13 August 1991	0*	13 August 1991	0*

Table 2. Numbers of chirping males in two areas of the Gooi, counted in the best conditions: between 10.00 hr and 13.00 hr, temperature above 25° C, sunny weather. The equal numbers in two consecutive days indicate the reliability of the method. * = sunny periods.

These circumstances suggest a limited fecundity and a restricted copulation frequency. Moreover, they may have caused a decline in genetic diversity within the Gooi populations, as double matings hardly occurred, especially in the preceding three decades, when population densities fell dramatically.

Table 2 provides data on the Gooi populations up to their extinction in 1989. During the mid 1960's the populations had already been reduced, especially on the South Heath, where some 20 males were divided over 5 leks occupying an area of 2 sq. kms. In fact every chirping male could be considered to be an isolated one. On the North Heath 2 of the 5 clusters of animals were not yet desintegrated.

The situation can be regarded as an example for other heathland areas in our country. Though these biotopes were probably not that scant - the wartbiter specimens collected from heathland areas in the central part of our country do not indicate such small size as those from the Gooi area (University Museum of Amsterdam) - the wartbiter was already extinct in the 1960's in most localities where it had previously been known. A possible explanation for the longer survival of the Gooi populations may be the continuous presence of flocks of sheep until 1966, i.e. two decades later than elsewhere. In this case, recreation in the urbanised Gooi had a favourable effect! The sheep prevented the expansion of the grass *Deschampsia flexuosa* and the germination of foliage trees, especially of the aggressive exotic *Prunus serotina* (see also Tienstra, 1992a).

At the moment, three very small populations of wartbiter still occur in the Netherlands, of which only one is more or less subject to any conservancy management.

Summarizing, the scanty Gooi habitat may have been the clue to the small dimensions of the wartbiters and perhaps also to the greater vulnerability of the populations, compared to those of e.g. Thy. The Thy heathland animals however also suggest a tendency - the material is statistically insufficient - to somewhat smaller dimensions than those from the "green" habitats (table 1). Another explanation for smaller dimensions of wartbiters from heathland habitats may of course be their different physiology as a consequence of the food availability for the adults and perhaps also the larvae.

2. Wing length

The wings of the Jylland animals are well developed (Table 1). At several occasions I witnessed male wartbiters taking off from the dunes - sometimes from very high ones (Bulbjerg, 47 m), covering sandstone and limestone rocks - and fly slowly downwards, up to a distance of a hundred meters. The only female I observed flying covered 15 m in this way (Photo 10, Tienstra 1992a).

This disparity can not only be explained by the difference in body weight, but also by the fact that the muscles used for the male's chirping are also its flying muscles. While chirping, the frequency of movement is very high. By endothermy the body temperature can be 10° Celsius above the environmental level. This probably universal phenomenon is demonstrated in the nearctic bushcricket *Neoconocephalus* by Heath & Josephson (1970, in Greenfield, 1990). It also explains why female bushcrickets often are much easier to catch than chirping males.

In the Gooi area the male wartbiters used their wings exclusively, as far as I could observe, in a flying movement without "concrete" results, when they were disturbed during chirping. The females only jumped. It is also important to note that steep slopes, as in Jylland, are lacking in the Gooi. Because of the hilly character of the Thy dunes and the great population density, the long wings, apart from causing a higher sound intensity, may give any selective advantage for the distribution of the males from their own lek to other ones.

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Résumé

La variabilité des dimensions de *Decticus verrucivorus* de la région 'het Gooi' (Pays-Bas) et de Thy (Danmark) est étudié. Les animaux des landes uniformes sont de beaucoup plus petits que celles des végétations plus variées. Ceci peut être le résultat du manque de protéines dans le régime alimentaire.