

## HOW DID GOMARUS ACQUIRE THE COPY OF FLAVIUS JOSEPHUS IN GREEK FROM SCALIGER'S LIBRARY?

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*Leiden*

Franciscus Gomarus, professor of theology at Leiden (1594-1611), Saumur (1615-1618), and Groningen (1618-1641), died in Groningen on 11 January 1641.<sup>1</sup> His large library was sold in an auction sale in Leiden. The auction began on 4 October of the same year. For the auction a catalogue of Gomarus' library was drawn up and printed. It was published by the printers and publishers Abraham and Bonaventura Elzevir,<sup>2</sup> in whose bookshop the auction was to take place. The catalogue, as are so many other catalogues of private libraries, is a gold mine of historical information. However, only four copies of it, scattered over Europe, are now known to exist. Thus, the recent publication of a photographic reprint, with an introduction and indexes, can only be welcomed with gratitude.<sup>3</sup>

The introduction to the reprint edition provides much valuable information and several useful analyses. But it also contains a passage which requires reconsideration and correction. The passage concerns Gomarus as a frequent visitor of book auctions, his presence at the auction of Joseph Scaliger's library in Leiden on 11 March 1609, and his acquisition of Scaliger's copy of the *Opera omnia* of Flavius Josephus in Greek. The volume was published by H. Froben and N. Episcopius, Basel 1544, and contained manuscript annotations written by Scaliger, the great Leiden expert in chronology and classical philology (1540-1609).<sup>4</sup> It is perhaps best to begin by quoting the passage at issue here in full.

We also know that he [Gomarus] had a Flavius Josephus with MS. corrections of J.J. Scaliger, a volume now at Weimar. Contrary to the opinion of H.J. de

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<sup>1</sup> I wish to thank Profesor Antony Grafton of Princeton University for his comments on an earlier version of this note.

<sup>2</sup> *Catalogus librorum reverendi atque eximii theologi D. Francisci Gomari*, Leiden 1641.

<sup>3</sup> E. Dekker, J. Knoop, and C.M.L. Verdegaal (eds.), *The Auction Catalogue of the Library of F. Gomarus. A facsimile edition with an introduction and indexes*, Houten 1996 (Catalogi redivivi 10).

<sup>4</sup> The volume does not appear in the auction sale catalogue of Gomarus' library.

Jonge, Gomarus did not buy this at the auction of Scaliger's library, 11 March 1609. Although he [*i.e.*, Gomarus] may have been present, we cannot infer his presence from the fact that he had the book. According to Van Itterzon, we read in Scaliger's testament that the book was to be given as a "payment" to Gomarus for his future efforts in the publication of a second edition of Scaliger's *Thesaurus*.<sup>5</sup>

This passage may give rise to misunderstanding.

Firstly, I have never asserted nor even entertained the thought that Gomarus bought his copy of the Basel 1544 Josephus containing Scaliger's marginal notes at the auction of Scaliger's library. What I did claim (and still claim) is (a) that Gomarus was present at the auction mentioned, and (b) that he was in possession of the Josephus with Scaliger's manuscript emendations which is now in Weimar.<sup>6</sup> However, I did not connect these two facts in a conclusion to the effect that Gomarus bought the Josephus at the auction of Scaliger's library. The opinion now ascribed to me cannot have been mine for at least two reasons. (a) The Josephus at issue does not appear in the auction catalogue of Scaliger's library which I myself edited. It was obviously removed from the library before it was auctioned and not offered for sale. (b) The volume in question contains Gomarus' *ex libris*, which informs us that he acquired the book *ex illustris P.M. Scaligeri Testamento*.<sup>7</sup> This *ex libris* was edited by D'Ansse de Villoison in a publication to which I made reference in a footnote within the very passage criticized by Dekker and his co-authors.<sup>8</sup>

<sup>5</sup> Dekker, Knoop, and Verdegaal, p. xii, n. 30. There follow references to G.P. van Itterzon, *Franciscus Gomarus*, The Hague 1929; repr. Groningen/Castricum 1979, pp. 270-271, and to H.J. de Jonge (ed.), *The Auction Catalogue of the Library of J.J. Scaliger*, Utrecht 1977 (Catalogi redivivi 1), p. 5 and p. 8, n. 23.

<sup>6</sup> In the Zentralbibliothek der Deutschen Klassik, the former Ducal Library at Weimar.

<sup>7</sup> 'P.M.' means *piae memoriae*, *i.e.*, 'the late ....' This means that Gomarus received the book after Scaliger's death. For this reason I wrote that the volume at issue 'was later owned by Gomarus.' See *The Auction Catalogue of the Library of J.J. Scaliger*, p. 8, n. 23.

<sup>8</sup> J.B.C. d'Ansse de Villoison, *Epistolae Vinarienses*, Turici 1783, p. 80, no. V,3: 'Josephus, Basileae 1544, fol. apud Hieronymum Frobenium et Nicolaum Episcopum, cujus primae paginae quae titulum praefert, inscriptum est: *F. Gomari, ex illustris P.M. Scaligeri Testamento*, et infra: *nunc autem sum Wilhelmi Goes 1657, et denique nunc ex auctione Goesiana pervenit ad Bibliothecam Schurzfleischianam*.' As early as 1714 Schurzfleisch himself, too, mentioned the fact that his copy of Josephus, which contained Scaliger's manuscript emendations, had been bequeathed to Gomarus by Scaliger by testament. A reference to Schurzfleisch' remark occurs in the footnote in which I also referred to D'Ansse de Villoison (p. 8, n. 23). H.L. Schurzfleisch, *Acta literaria*, Vitembergae 1714, p. 20: 'Quaedam [sc. opera a Scaligero manu emendata], e quibus Josephum possideo, ad Franciscum Gomarum

Secondly, my assertion that Gomarus attended the auction of Scaliger's library was by no means based on the fact that he owned Scaliger's copy of Josephus. It was based on the fact that Gomarus' name occurs several times as that of a buyer in the margins of the former Kiel copy of the auction catalogue of Scaliger's library. In fact, it was in the context of an examination of that copy, now lost, but fortunately still readable in a photocopy kept in Leiden University Library, that I was able to enumerate some of the purchasers present at the auction. Their names appear in the margins in manuscript notes, possibly in Scrivener's handwriting. In juxtaposition to a number of the titles, the same hand also noted down the prices for which the books were sold. Among the buyers we find Gomarus, as well as G.J. Vossius, D. Heinsius, C. Mylius, J. Rutgersius, D. Baudius, W. Snellius, and others.

Meanwhile, I have checked the Leiden photocopy of the former Kiel copy once again. Gomarus' name occurs seven times, scattered all through the catalogue. He bought: Themistii Opera graeca (p. 10), Nicandri Theriaca graecolatina (p. 11), Vineti Logistica (p. 16), Dionysius Halicarnasseus, graecolatina (p. 16), Iuvenalis cum Persio (p. 35), Costumi de' Turchi (p. 43), and Marciani Heracleotae Poëma de situ Orbis (p. 48). I interpret these seven references as being evidence that Gomarus was present—evidence to which Dekker and his co-authors hardly do justice when they write, clumsily, that 'he may have been present.'

Thirdly, contrary to what Dekker *c.s.* claim, Van Itterzon does *not* state that 'we read in Scaliger's testament' that the Josephus was given by Scaliger to Gomarus in compensation for the latter's efforts in the publication of a second edition of Scaliger's *Thesaurus temporum*. What Van Itterzon states is this: 'By testamentary disposition, he [Scaliger] committed this work [of overseeing the printing of a second, corrected edition of the *Thesaurus*] to Gomarus. As a token of gratitude, Gomarus received Scaliger's private copy of Josephus.'<sup>9</sup> Thus, Van Itterzon does not state (as the authors of the introduction to the reprint say he does) that the disposition by which Scaliger bequeathed the Josephus to Gomarus figures in Scaliger's last will. In fact, this disposition occurs in no version of Scaliger's last will known to date.

No utterance of Scaliger to the effect that he gave his Josephus to Gomarus in remuneration for any service is known to be preserved.

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voluntate ejus delata sunt.'

<sup>9</sup> G.P. van Itterzon, *Franciscus Gomarus*, The Hague 1929; repr. Groningen/Castri-cum 1979, p. 270.

The question arises, therefore, how the idea that the Josephus had to serve as a token of gratitude occurred to Van Itterzon. Van Itterzon is silent about the source from which he obtained his information.<sup>10</sup> It is rather interesting, however, to compare what Van Itterzon says concerning the provenance of the Josephus copy with a passage in J. Bernays' biography of Scaliger,<sup>11</sup> a passage to which Van Itterzon does not refer, although he cites Bernays' work elsewhere.

G. P. van Itterzon, 1929 (p. 270)

'Na de eerste uitgave van zijn *'Thesaurus'* namelijk had Scaliger de tweede editie aangekondigd (Aug. 1606). Zelf had hij deze echter niet meer persklaar kunnen maken, waarom hij bij testamentaire beschikking dit werk aan Gomarus had overgedragen, waarvoor deze uit dankbaarheid Scaligers eigen exemplaar van Josephus had ontvangen.' [After the appearance of the first edition of the *Thesaurus*, Scaliger announced a second edition (August 1606). He himself, however, was unable to prepare the copy of the second edition for the press. By testamentary disposition, therefore, he committed this work to Gomarus. As a token of gratitude, Gomarus received Scaliger's private copy of Josephus.]

J. Bernays, 1855 (pp. 226-227)

'Gleich bei Uebersendung der ersten Ausgabe an Casaubonus kündigt Scaliger die zweite an in einem Briefe vom August 1606 ( ). Das fertige Manuskript war in Scaligers Testament dem Franciscus Gomarus zur Herausgabe überwiesen, und als Erkenntlichkeit für seine Mühe war ihm Scaligers durchcorrigirtes Handexemplar des Josephus vermacht.'

<sup>10</sup> In his letter to Petrus Cunaeus, rector magnificus of Leiden University, dated 24 March 1632 (Leiden, Univ. Libr., MS. C. un. 2) Gomarus discusses his task, assigned to him by Scaliger, to take care of a corrected edition of the *Thesaurus*. But he does not mention here the copy of Josephus. Gomarus also mentions the task Scaliger bestowed upon him in an undated letter to Franciscus Raphelengius, executor of Scaliger's last will, edited by G. P. van Itterzon, 'Nog twintig brieven van Gomarus,' *Nederlands Archief voor Kerkgeschiedenis*, NS 46 (1976), pp. 413-449, no. 20. In this letter Gomarus asks Raphelengius to send him a transcript of the instruction in Scaliger's last will by which Scaliger left him the task of taking care of a corrected edition of the *Thesaurus*. Gomarus writes 'cum mihi opus sit illa sententia, qua editionem Eusebii [this is the *Thesaurus temporum*] vir illustris D. Scaliger commisit, neque eius copia mihi, perturbatis meis schedis, compareat, si non molestum est, rogo ut reliquis beneficiis hoc addere velis, ut pauca illa verba, per nostrum Moullartium obsignata communique.' Van Itterzon misinterprets this request as if Gomarus was asking Raphelengius here to send him a transcript of the opening sentence of (p. 424), or some other phrase from (p. 448), the *Thesaurus temporum*. Obviously, Van Itterzon understood neither the word 'sententia', nor the word 'commisit'.

<sup>11</sup> Jacob Bernays, *Joseph Justus Scaliger*, Berlin 1855, pp. 226-227.



For his assertion that the Josephus was bequeathed to Gomarus 'als Erkenntlichkeit für seine Mühe', Bernays quotes no evidence. Van Itterzon repeats Bernays' opinion without giving him due credit. The authors of the introduction to the recent reprint of the auction catalogue of Gomarus' library try to repeat what Van Itterzon wrote, but fail to check the evidence on which it was based. Moreover, they seriously misrepresent Van Itterzon's view by making him say that the disposition by which Scaliger left his Josephus to Gomarus in compensation for his work on the second edition of the *Thesaurus*, is something 'we read in Scaliger's testament.'

What is the evidence for Bernays' statement that Scaliger bequeathed his Josephus to Gomarus out of gratitude for the latter's efforts in re-editing the *Thesaurus temporum*? Bernays himself refers to no source whatsoever. There is no other option for us than to look at what Scaliger's last will itself says about the matter.<sup>12</sup>

It may be helpful to recall here the fact that Scaliger made his last will at least three times.<sup>13</sup> His earliest testament was the one he made in January 1601.<sup>14</sup> We shall leave this testament out of consideration here since Scaliger revoked it in October 1607. Moreover, it preceded the publication of the first edition of the *Thesaurus temporum* by five years. Consequently, it cannot throw any light on the possible relationship between Gomarus' obtaining the 1544 copy of Josephus and his responsibility for a new edition of the *Thesaurus temporum*.

Scaliger's second testament is that of 25 July 1607. It is written in Latin, except for an addition or codicil dated 18 November 1608 which is in French. We shall refer to this testament as Scaliger's Latin testament of 1607.<sup>15</sup>

The third and definitive last will of Scaliger, however, was drawn up in French and dated 18 November 1608. It is a revision of the Latin

<sup>12</sup> Scaliger felt deeply miserable about the countless typographical errors in the first edition of the *Thesaurus temporum*. On this as well as his instruction that the printing of a corrected edition should be overseen by Gomarus, see now A. Grafton, *Joseph Scaliger A Study in the History of Classical Scholarship II Historical Chronology*, Oxford 1993, pp. 513-514, 750.

<sup>13</sup> H.J. de Jonge 'The Latin Testament of Joseph Scaliger, 1607', *Lias* 2 (1975), pp. 249-263. To the four copies of Scaliger's Latin testament mentioned on p. 250, a fifth one, preserved in the Bibliothèque Municipale de Bordeaux, can be added. See *Revue de l'Agenais* 77 (1951), p. 163: no. 95 'Testament de Joseph-Juste Scaliger. Texte latin. Copie du XVIIIe siècle, dans un recueil de testaments d'hommes célèbres.'

<sup>14</sup> J.J. Scaliger, *Epistolae*, Leiden 1627, Frankfurt 1628, nr. 56.

<sup>15</sup> It was edited by H.J. de Jonge, 'The Latin Testament.'

will of 1607, with many changes, on major as well as minor points. We shall refer to this definitive last will as the French testament of 1608.<sup>16</sup>

In Scaliger's Latin testament of 1607, Gomarus does not yet play a role. His name appears only in the French testament of 1608. In the latter document Scaliger gave directions to the effect that his *Thesaurus temporum* should be reprinted through the care of Gomarus—a task which the Latin testament of 1607 had assigned to Daniel Heinsius.<sup>17</sup> According to the French will of 1608, Gomarus received a large volume of Chinese paper, possibly as a sign of Scaliger's gratitude for Gomarus' involvement in the revised edition of the *Thesaurus temporum*, although Scaliger does not say so explicitly: 'La grande main de papier de la Chine ie la donne a Monsieur Gomarus, docteur et professeur en théologie de cette académie.' According to the Latin testament of 1607, this Chinese paper was to be divided equally between Heinsius and Baudius. What Gomarus did receive, with a view to his labours on the new edition of the *Thesaurus temporum*, was a set of two printed copies of that work. The one was Scaliger's desk copy containing his manuscript corrections of typographical errors; the other was a clean copy, unbound, in which Gomarus was expected to take over Scaliger's corrections in neat handwriting. The latter copy was to be presented to the printer as printer's copy.<sup>18</sup>

<sup>16</sup> The most recent edition is by P.C. Molhuysen, *Bibliotheca Universitatis Leidensis. Codices Scaligerani (praeter Orientales)*, Leiden 1910, pp. v-viii.

<sup>17</sup> 'Aussi ie prie Monsieur Gomarus, de donner ordre, que mon Eusebe [*i.e.*, the *Thesaurus temporum*, which has as its core an edition of Eusebius' Chronicle] soit reimprimé, suivant l'exemplaire par moy corrigé, car i'ay vergogne des horribles fautes que les imprimeurs y ont laissé. Mais avant que se resoudre de l'edition, il en parlera premierement a Jehan Commelin et Jude Bonnenuit son neveu, lesquels s'ils entreprennent la besogne, le dict Sieur Gomarus les obligera de la despescher le plustot que faire se pourra, si non, alors il luy sera libre de faire imprimer le livre par qui bon luy semblera. Au dict Sieur Gomarus sera delivré un exemplaire de mon Eusebius non relie, que Ionas [Scaliger's servant] luy baillera, affin qu'il puisse mettre au net les corrections que i'ay marquées en mon livre.' Molhuysen, p. vii.

<sup>18</sup> It cannot be ascertained whether these two copies really passed into the hands of Gomarus. True, nr. 51 in the auction catalogue of his library is a copy of Scaliger's 1606 *Thesaurus* 'cum notis Scaligeri'. But the last three words refer to Scaliger's commentary on Eusebius and Jerome printed in the *Thesaurus*, not to manuscript annotations. This appears from entry nr. 24: 'Testamentum Novum cum notis Bezae, 1588.' For several reasons it is difficult to identify nr. 51 with either of the two copies meant in Scaliger's last will. Firstly, the auction catalogue of Gomarus' library itself does not identify nr. 51 as the author's desk copy. Secondly, nr. 51 was bound, whereas the clean copy of the *Thesaurus* which Scaliger assigned to Gomarus was unbound. Thirdly, it is most likely that Gomarus

Scaliger's last will of November 1608 in French contains no further disposition by which any book from Scaliger's library is assigned specifically to Gomarus. But it does contain a passage in which Scaliger refers to a 'codicille' consisting of a list of volumes from his library, identified by their titles, which he wished to distribute to certain friends. This is what the text of the testament says:

Le catalogue de tous les livres de ma bibliothèque dont i'en distribue ceux qu'il m'a semblé bon a mes amis, en une roolle que i'ay faict signer au notaire devant tesmoins, lequel roolle ie veux qu'il ayt vigueur de codicille, est dans mon poulpitre verd, sur lequel i'ay accoustumé d'escrire.<sup>19</sup>

None of the beneficiaries is identified here by name. Nor does Gomarus' name appear in this context. No copy of the 'codicille' seems to exist any more. But from another passage in the French testament of 1608, several lines further down, it appears that the friends who were entitled to choose a number of volumes from Scaliger's library before it was auctioned, included Cornelius Mylius, Daniel Heinsius, Dominicus Baudius, as well as some other persons.

Quant aux livres qui resteront apres que les Sieurs Mylius, Heynsius, Baudius et autres miens amis en auront retiré ceux qu'il auront trié pour eux, ie veux que Jonas Rousse [Scaliger's servant] les vende a l'encan, et que l'argent qui en proviendra de la vente soit totalement a luy.<sup>20</sup>

Regrettably, it cannot be ascertained whether the 'autres miens amis' mentioned here included Gomarus. But there is indeed some probability that this was the case, since Gomarus' *ex libris* in Scaliger's copy

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already owned a copy of the *Thesaurus* (1606) before Scaliger died (1609), probably nr. 51 of the catalogue.—I do not know whether Scaliger's desk copy of the *Thesaurus* still exists. It does not appear among the 369 *libri annotati* of Scaliger listed by R. Smitskamp, *The Scaliger Collection*, Leiden 1993, pp. 103-110. W.E. van Wijk, *Het eerste leerboek der technische hydrekunde*, Leiden 1954, p. 19, speculates that it was lost in the fire of 1672 that ruined the premises of Johannes Janssonius, the publisher of the second edition of the *Thesaurus*, Amsterdam 1658. However, although this second edition was published by Janssonius in Amsterdam, according to the colophons on p. 435 and at the end of the index to the 'Animadversiones in Chronologica Eusebii', it was printed by Nicolaus Hercules in Leiden.

<sup>19</sup> Molhuysen, p. vi.

<sup>20</sup> Molhuysen, p. vi. On the disposition *ante et post mortem* of Scaliger's books, there is also the moving testimony of D. Heinsius in his letter to Casaubon, *Epistolar Scaligeri*, Frankfurt 1628, no. 453, pp. 775-776. This account, however, is not entirely in agreement with Scaliger's last will. In particular, Heinsius fails to say that Scaliger had commended the re-edition of the *Thesaurus* to the care of Gomarus. Instead, Heinsius says that Scaliger 'quae edi iterum voluit, aut emendata reliquit, fidei meae credidit,' which is only part of the truth.

of the Basel 1544 Josephus states explicitly that it passed into Gomarus' hands *ex illustris P.M. Scaligeri Testamento*.

However, the codicil appended to the French testament of November 1608 is not likely to have specified which beneficiary precisely was to receive which volume. From the Latin will of 1607 we can infer what the codicil looked like.<sup>21</sup> It consisted, firstly, of a list of titles of books Scaliger had selected from his library from which some friends were entitled to make a choice before the library was sold. Secondly, it included a short list of the names of the friends to whom Scaliger wished to accord this favour and an indication of the order in which they had to make their choice. In 1607, the number of friends was still limited to three: Mylius, Heinsius, and Baudius, and this was also the order in which they had to make their choice.

Probably, then, Gomarus' name was added to those of Mylius, Heinsius, and Baudius in the codicil added to the last will of November 1608. But even in that case Gomarus was not endowed specifically with Scaliger's Basel 1544 copy of Josephus. He was only allowed to take his turn when his name came round on the list, and to select the volumes he wanted from the ones which remained. When he took the Josephus with Scaliger's annotations, the choice of the volume was his own, not Scaliger's.

It is plain that Scaliger did not accord this favour to Gomarus until the revision of his last will in 1608. This is also the last will in which Scaliger introduced Gomarus as the intended editor of the corrected edition of the *Thesaurus temporum*. It is not entirely impossible, therefore, that Scaliger's disposition, by virtue of which Gomarus was entitled to make a selection from his library, had something to do with Scaliger's wish that Gomarus would assume the responsibility for the new edition of the *Thesaurus temporum*. But this remains a speculation, though not an improbable one.

### *Conclusion*

It is quite plausible that Scaliger added Gomarus' name in 1608 to the list of persons whom he authorized to take for themselves one or more volumes from a selection of volumes out of his library which were

<sup>21</sup> De Jonge, 'The Latin Testament,' p. 258: 'Nobilissimo viro Cornelio Mylio, huius Academiae curatori, item Heinsio, atque Baudio potestatem facio, quos velint libros de meis Graecis et Latinis eligere, ita ut post Mylium Heinsius, post Heinsium Baudius sequatur. Horum librorum catalogus repositus est in viridi pulpito, cui inniti soleo scribens.'

especially set apart for this purpose. The beneficiaries had to make their choice after Scaliger's death and before the library was auctioned. However, the authorization given to Gomarus was not recorded in Scaliger's last will proper, but, at most, in the codicil of November 1608 which is now lost. Consequently, Scaliger's disposition is no longer something we can read, let alone something we can read in his testament.

The reason why Scaliger authorized Gomarus to take for himself one or more volumes from his library may certainly have been that Scaliger wished to express his feelings of obligation towards Gomarus for the part the latter was to take in overseeing the printing of the revised edition of the *Thesaurus temporum*.

If Scaliger included Gomarus among the persons who were entitled to take one or more volumes from his library, he refrained from specifying which volume or volumes he wanted to give to Gomarus or to any other person. When Gomarus made use of Scaliger's offer, he had to make his own choice. Thus, regardless of whether or not the Josephus passed into Gomarus' hands because Scaliger wished to repay Gomarus' work on the second edition of the *Thesaurus temporum*, the volume was certainly not Scaliger's choice for Gomarus.<sup>22</sup> It was the choice of Gomarus himself.

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<sup>22</sup> Contra Dekker, Knoop, and Verdegaal, p. xii, n. 30.

# KUYPER EN DE DISPUTATIES GELEID DOOR COBET

door

H J de Jonge

*Amico suo cruditissimo Th Korteweg  
Leida heu! discessuro hoc  
qualicumque est ex Cobeti ac iuvenis  
Kuyperi urbe auferendum dat  
auctor*

Van juli 1855 tot september 1862 heeft Abraham Kuiper theologie en letteren gestudeerd aan de Leidse universiteit. Uit zijn tweede en derde studiejaar zijn enige documenten bewaard die licht werpen op zijn toenmalige activiteit en belangstelling. Naar ik meen is aan deze stukken nog niet veel aandacht geschonken. Ik doel op de theses die Kuiper in 1857 en 1858 heeft verdedigd onder leiding van professor C. G. Cobet.<sup>1</sup> Het is, dunkt me, de moeite waard, enige bladzijden aan deze theses te wijden. Men leert er niet slechts een episode uit Kuipers leven beter door kennen, zij het ook uit een fase van zijn leven die hij later als een tijd van geestelijke armoede, luchthartigheid en halfslachtigheid heeft gemeend te moeten wraken. De theses leren ook een en ander over de inrichting van het hoger onderwijs in de negentiende eeuw, een eeuw die de onze al te snel achter zich laat.

De graecus C. G. Cobet (1813-1889) werd in 1846 buitengewoon professor wijsbegeerte en Romeinse oudheden en in 1849 gewoon professor in dezelfde vakken benevens oude geschiedenis en Grieks. Hij was een indrukwekkend knap kenner van de Griekse taal en literatuur, een kundig paleograaf, een man die reden had op zijn oordeel, zijn historisch voorstellingsvermogen en zijn intuïtie te vertrouwen.<sup>2</sup> Zijn filologische arbeid was er grotendeels op gericht, de overgeleverde tekst van antieke Griekse schrijvers te toetsen en waar het hem nodig leek te emenderen.

1 Bewaard in de ingebonden collectie onder Cobet verdedigde theses aanwezig in de Leidse U.B. C. G. Cobet *Theses Philologicae* Leiden 1848-1859 (signatuur 697 C 8 en 9). Zie over de betekenis van deze theses nu ook T. Baarda, 'Het recht van de tekstemendatie bij Abraham Kuiper', in H. M. Kuitert, S. J. Noorda, e.a. edd. *In rapport met de tijd. 100 jaar theologie aan de V.U.* Kampen 1980, pp. 13-42.

2 Men zie de verhelderende en sympathieke schets van Cobets leven en werk van de competente hand van S. A. Naber, *Vier tydgenoten*. Haarlem 1894, pp. 159-357.

Daarnaast had hij aandacht voor de andere klassieke taken van de criticus: de beoordeling van de authenticiteit van de oude geschriften, en de beoordeling van hun innerlijke waarde of historische betrouwbaarheid. Bij zijn beoordeling van de tekstvorm liet hij zich leiden door zijn gedegen kennis van de Griekse taal en door zijn ervaring met oude schriftsoorten en met de taal en stijl van de auteur in kwestie. Vandaar dat hij bij voorkeur de werken bestudeerde en emendeerde van auteurs van wie behoorlijk wat bewaard is: Homerus, Herodotus, Xenophon, Plato en de Attische redenaars.

Het is achteraf makkelijk de feilen in het werk van Cobet aan te wijzen.<sup>3</sup> Ten eerste verdiepte hij zich in zijn tekstkritische activiteit als regel niet in het geheel der tekstgeschiedenis van het onderzochte geschrift, maar koos hij enkele weinige tekstgetuigen uit die hij als de minst bedorvene beschouwde, en verbeterde de lezingen die hij daarin alsnog als corrupt beschouwde onvervaard met conjecturen. Vele hiervan lijken ons nu overbodig. Veel andere zijn echter zulke notoire en briljante verbeteringen<sup>4</sup>, dat men over zijn vergissingen een toontje lager behoort te zingen dan thans de mode is onder mensen die nog niet waard waren geweest zijn schoenriem los te maken.

Ten tweede stond Cobet, zegt men, wel wat ver terzijde van de ontwikkeling der klassieke filologie die juist in zijn tijd, met name in Duitsland, veel breder begon opgevat te worden dan in Nederland gebruikelijk was. Cobet bleef zich bepalen tot de traditionele taken van de criticus, vooral de tekstkritiek, en maakte precies met zijn conjecturale tekstkritiek enorm school. De 'Altertumswissenschaft' echter stelde zich tot taak heel de antieke wereld in al haar facetten te leren kennen: historisch, archeologisch, godsdiensthistorisch, literair, sociaal-economisch en langs nog diverse andere wegen. Daarbij kregen ook provinciale streken van de Romeinse wereld, de late oudheid en de wisselwer-

3 Voor een kritische evaluatie van het werk van Cobet, zie E. J. Kenney, *The Classical Text*, Berkeley, Los Angeles, Londen 1974, pp. 117-124.

4 Voor enkele staaltjes, zie Naber, pp. 305 en 324, en elders. Er zij hier aan herinnerd, dat tot in de nieuwste uitgave van het Griekse Nieuwe Testament (Nestle-Aland, 26e editie) bij Hebr. 11:4 de prachtige conjectuur van Cobet wordt vermeld, door hem voorgesteld in *Mnemosyne* van 1860, p. 308. Deze conjectuur is als de juiste lezing bepleit door G. Zuntz, *Opuscula selecta*, Manchester 1972, p. 256. Zelf zou ik deze conjectuur uiteindelijk niet aanvaarden, maar ze heeft de verdienste, een probleem in de tekst van Hebr. 11:4 te signaleren. Die functie hadden de voorstellen van de conjecturaalcritici in het algemeen, zonder dat zij aan hun suggesties het loodzware gewicht toekenden dat men thans gewoonlijk aan conjecturen hecht.

king met het Oosten de volle aandacht. Men kan over de beweerd-e eenzijdigheid van Cobet verschillend denken. Indien zijn bearbeiding van duizend jaar literatuur, van Homerus tot Clemens Alexandrinus, als eenzijdig kan worden bestempeld, hoe moeten dan de verspreide proefboringen van tegenwoordige filologen en theologen heten? Daar komt nog iets bij. De bergen veelsoortige kennis die de Altertumswissenschaft heeft opgeleverd zijn zeker imposant. Maar teksten blijven een hoofdbron onzer beschaving en een juist oordeel inzake tekstvorm, wording en waarde van een geschrift blijft daarom een onmisbaar goed, een goed dat door de klassieke *ars critica* misschien beter gecultiveerd werd dan in de maalstroom der Altertumswissenschaft.

Wat men hiervan denke, Cobet verwierf zich in zijn tijd spoedig een schitterende reputatie. In de zestiger en zeventiger jaren was hij een der gezaghebbendste *graeci* van Europa. Hij was bovendien een begaafd spreker en uitnemend docent, geliefd en geeerd bij zijn talrijke studenten.

Elk cursusjaar gaf Cobet zeven colleges, elk daarvan gedurende twee of drie uren per week. Van deze colleges was een groot deel bestemd, niet slechts voor de zeer weinige studenten in de letteren die er waren, maar voor de studenten uit de vier andere faculteiten: de theologische, juridische, medische en natuurfilosofische faculteit. Studenten in de theologie en rechten moesten immers, alvorens het kandidaatsexamen in hun eigen faculteit te kunnen afleggen, het propaedeutisch examen in de letteren doen. Dit kon na het tweede studiejaar worden afgelegd. Het omvatte voor theologen Grieks, Latijn, Nederlands, Hebreeuws en Israëlitische oudheden, om nu te zwijgen van de *prae-examens* in de wiskunde en *testimonia* in de Semitische talen (anders dan Hebreeuws) die zij eveneens moesten halen.<sup>5</sup> Ook medici en filosofen deden een taal- en letterkundige propaedeuse, maar konden volstaan met *testimonia*. Alle studenten, en de theologen wel heel intensief, kwamen dus in aanraking met de professor Grieks Cobet, die van de propaedeutische examinering allerminst een *sinecure* maakte.<sup>6</sup> De normale studiegang van een theologisch student was kortom de volgende: twee jaar tot het propaedeutisch examen in de letteren, vervolgens twee jaar tot het kandidaats

<sup>5</sup> Een uitstekend beeld van de theologische studie omtrent het midden van de 19de eeuw te Leiden krijgt men uit H. Oort, *Herinneringen van een theologant van voor zeventig jaar*, in *Pallas Leidensis*, Leiden 1925, pp. 69-76.

<sup>6</sup> Oort, p. 70.



theologie, daarna het proponenten- of het doctoraal examen met de promotie, of een combinatie van beide.<sup>7</sup>

Voor belangstellende studenten uit alle faculteiten – en onder hen zullen wij Abraham Kuyper aantreffen – hield Cobet ook disputaties. Hij was er in 1848 mee begonnen, tegemoet komend aan de wens van studenten die zich wilden oefenen in het Latijn spreken.<sup>8</sup> Op de series lectionum heet het telkenjare: Cobet zal op donderdagen om 11 uur openbare oefeningen leiden in het disputeren, „disputandi exercitia publica moderabitur, die Iovis, hora XI”, en in 1861 kortweg: „Literarisch dispuut”. Disputaties onder leiding van professoren hadden ook nog plaats in de theologische, juridische en medische faculteit, maar alleen aan de disputaties onder Cobet werd deelgenomen door studenten uit diverse faculteiten.

De disputaties van Cobet heten „openbaar”. Dit betekent, dat ze niet plaats vonden te zijnen huize aan het Steenschuur (nu nr. 5)<sup>9</sup>, maar in een zaal van de universiteit. De meeste gewone colleges gaven de professoren namelijk bij zich thuis, of in een particulier collegezaaltje in hun tuin of op zolder. Voor zulke gewone colleges betaalde elke deelnemende student zo’n f 30,— per jaar per college van twee of drie uren in de week. Met de inning van het collegegeld werd elke cursus voor elk college één der deelnemende studenten belast: de praetor, uitgekozen en aangezocht door de professor en met zijn verkiezing geplaagd door zijn collegae-studenten. Zo althans wordt de luister en misère van de praetor geschilderd in het hoogst instructieve en vermakelijke opstel „De Praetor” dat Klikspaans *Studenten-typen* besluit.<sup>10</sup> Het treft nu, dat juist ook Abraham Kuyper praetor geweest is van één van de colleges Grieks van Cobet.<sup>11</sup> Kuyper heeft blijkbaar snel Cobets aandacht en vertrouwen gewekt.

Doch voor deelneming aan de door Cobet geleide disputaties behoefden studenten niet te betalen. Er was bij gevolg ook geen lijst van betalende studenten, zoals die in de gewone colleges werd bijgehouden opdat geen van hen die het college volgden zich aan zijn financiële verplichtingen zou onttrekken. En door-

7 Oort, pp. 73-4

8 Naber, p. 346.

9 Het pand Steenschuur 5 bevat nu vierentwintig verhuurde wooneenheden. Pas in 1877 is Cobet verhuisd naar het voornamen huis Rapenburg 2, nu restaurant „De Doelen”. Daar woonde hij tot zijn dood, 25 oktober 1889.

10 In mijn exemplaar van de zevende druk, Leiden z.j., pp. 268-277.

11 J. C. Rullmann, *Kuyper-Bibliografie*, I, 's-Gravenhage 1923, p. 11.

dat zo'n collegelijst voor de disputaties niet werd bijgehouden, konden alle belangstellende cives academici, studenten en professoren van alle faculteiten, de disputaties vrijelijk bijwonen. Van deze belangstelling moet men zich vooral geen illusies maken. Een van de studenten die Cobets disputaties meemaakten, de bekende classicus S. A. Naber, deelt wel mee, dat het aan opponenten nooit ontbrak, hij voegt er echter aan toe, dat de disputeren voor de deelnemers wel leerzaam waren, „maar voor de toehoorders ver van amusant”<sup>12</sup>. In de jaren dat Abraham Kuyper tot de actieve deelnemers behoorde, waren er, als zal blijken, zo'n acht studenten die als defendens of opponens aan de disputaties meededen. Cobet zelf was steeds aanwezig als voorzitter. Het zou mij verbazen als dit gezelschap per keer meer dan een drietal belangstellenden zou hebben weten te trekken. Misschien waren dat er nog wel minder. We vernemen namelijk,<sup>13</sup> dat de disputaties van Cobet met name jongere studenten trokken en juist die hadden, in de propaedeutische fase van hun studie, hun handen vol aan colleges in de „verplichte” examen- of testimonium-vakken van het propaedeutische programma der letterenfaculteit.<sup>14</sup>

Het groepje studiosi dat uit eigen verkiezing, louter om zich te oefenen in het voeren van een Latijnse wetenschappelijke discussie, aan Cobets disputaties deelnam vormde een heel kleine elite uit het totaal der Leidse studenten. Het Latijn begon toen juist langzaam maar zeker uit de colleges en examens te verdwijnen, en deze ontwikkeling ging de meeste studenten veel te traag. In Kuypers tijd waren er te Leiden 500 studenten, daaronder 120 theologie- en 15 letteren-studenten. Aan de door Cobet geleide disputeren namen echter slechts acht of negen studenten deel: een enkele jurist, de overige voor de helft theologen, voor de helft literatoren. Hun deelneming aan deze disputaties was volstrekt supererogatoir. Er was formeel geen enkele effectus aan verbonden. Even supererogatoir was het kandidaatsexamen in de (klassieke) letteren dat menige theologische student aflegde, maar daaraan was tenminste de verlening van een graad en de toegang tot het examen voor de promotie verbonden. Kuyper deed zijn kandidaats letteren summa cum laude op 29 april 1858, nog voor het einde van zijn derde studiejaar, in welk jaar hij tevens ijverig disputeerde onder Cobet.

<sup>12</sup> Naber p. 347.

<sup>13</sup> *Leidsche studenten almanak voor 1861*. Leiden z.j. p. 230.

<sup>14</sup> Oort p. 70. Daar al die colleges (van de propaedeutische) drie uren per week gegeven werden, was het zeer moeilijk, neen, ondoenlijk ze alle getrouw te volgen.

Hoewel uit de series lectionum lijkt te volgen, dat Cobets disputaties elke week plaats hadden, is uit de bewaard gebleven theses<sup>15</sup> duidelijk, dat er, toen Kuyper tot de deelnemers behoorde, in een hele cursus zo'n veertien bijeenkomsten plaats hadden: zes vóór kerst, acht erna, en dan ongeveer om de veertien dagen, met langere onderbrekingen voor de vakanties. Het spreekt vanzelf, dat, aangezien de voertaal in deze disputen het Latijn was, het weinig talrijke publiek uitsluitend academisch was. De gang van zaken was ongeveer als volgt.

Een paar dagen voordat de disputatie plaats zou hebben deed de student die als defendens zou optreden aan de andere deelnemers en belangstellenden een samengevouwen blad papier, d.w.z. vier bladzijden, bedrukt met zo'n twintig tot vijfentwintig stellingen toekomen. Het opschrift boven de stellingen luidde gewoonlijk als volgt (ik vertaal het opschrift boven een serie stellingen verdedigd door Abraham Kuyper): „*Letterkundige stellingen* welke, onder het voorzitterschap van de zeer geëerde Heer C. G. Cobet, gewoon professor in de klassieke letteren, A. Kuyper, student in de theologie, op donderdag de 4de van de maand maart in het jaar 1858 te 11 uur in het openbaar auditorium zal voorleggen ter openbare bespreking (*disputatio*) met de medestudenten.”

De stellingen waren voor het grootste deel van de hand van professor Cobet, niet van de defendens. Meest gold het conjecturale verbeteringen in de tekst van klassieke auteurs. Zeker kon de defendens ook zelf stellingen voorstellen. Maar de deelnemers waren jongerejaars en hadden niet veel bruikbaars aan conjecturen te bieden. „Bij gebrek aan deze gaf ons Cobet uit zijn overvloed”, zegt Naber. En in de almanak van 1861 heet het bescheiden, maar misschien nog niet bescheiden genoeg: „Cobet leverde gewoonlijk de grootste helft”. Geen wonder dus, dat men de theses verdedigd onder Cobet zonder moeite terugvindt in zijn publicaties. Zo prijken onder de in mei 1858 door Kuyper verdedigde stellingen de twee volgende (ik vertaal):

## 19.

De *katègoros* (beschuldiger) van wie dikwijls sprake is in de

15 Zie onze noot 1 Baarda (cf. n. 1, bij hem pp. 21-22) heeft erop gewezen, dat Cobet jarenlang twee soorten disputaties hield: de ene donderdag werden door gevorderde classici „theses philologicae” verdedigd, de volgende donderdag werden door praekandidaten in de letteren en niet-classici „theses litterariae” verdedigd. Maar in Kuypers tijd bestond alleen nog de tweede soort.

*Memorabilia* van Xenophon is niet een werkelijke aanklager, maar de sofist Polycrates, die vele jaren na de dood van Socrates om zijn vernuft te tonen een *Aanklacht tegen Socrates* geschreven had.

20.

In Pericles' rede bij Thucydides II, 60 moet *nikoomenou* verbeterd worden in *nikoomenos* en *pooloito* in *apodoito*.

In hetzelfde jaar nu waarin Kuyper deze stellingen verdedigde, bepleitte Cobet de erin neergelegde opvattingen in het door hem geredigeerde en goeddeels door hem gevulde tijdschrift *Mnemosyne* (7, 1858, resp. p. 254 en p. 293). Het zou niet moeilijk zijn een groot deel van de overige onder Cobet verdedigde stellingen in Cobets artikelen of andere publicaties terug te vinden. Over het geheel genomen moet van de theses die tot inzet van de door Cobet voorgezeten disputaties werden gemaakt hij zelf als auctor gelden. Kennelijk vervoege de defendens zich een week of twee voor de zitting bij Cobet. Deze had bij zijn recente en lopende onderzoek een reeks observaties gemaakt, en een aantal hiervan werd nu in de vorm van stellingen gegoten. De defendens deed er wellicht nog wat van eigen vinding aan toe, en bezorgde het hele lijstje van zo'n twintig à vijfentwintig stuks bij de drukker. Tegenwoordig zou men zulk materiaal stencillen of fotokopiëren. Enige dagen voor de disputatie werden de gedrukte exemplaren bij de deelnemers rondgebracht.

Hoe de verspreiding van de theses precies in haar werk ging blijft ietwat onduidelijk. Naber zegt eenvoudig: „Een onzer had een paar dagen te voren een zeker aantal stellingen onder de *commilitones* verspreid”, maar doelt hier m.i. slechts op het feit, niet op de procedure. Als het om dissertaties ging konden studenten die wel laten rondbrengen door de pedel van het corps: men herinnert zich het fraaie portret van pedel J. Robert, in 1854 afgebeeld bij het rondbrengen van dissertaties.<sup>16</sup> Uit „De Student-auteur” in de *Studenten-typen* van Klikspaan blijkt, dat de distributie van dissertaties toenmaals ook wel het werk kon zijn „van den oppasser”,<sup>17</sup> d.w.z. van de knecht die een student ten dienste stond voor de verrichting van allerlei huishoudelijke

16 Reproductie in R.E.O. Ekkart, *Athenae Batavae*, Leiden 1975, p. 73, nr. 128.

17 In mijn exemplaar van de 7de druk, Leiden z.j., p. 122.

werkzaamheden Maar Kuyper „behoorde tot die beklagenswaardige amphibeën der academische wereld, die gedoemd zijn Student te wezen en tegelijk Leidenaar!”<sup>18</sup> Hij woonde zijn studie lang bij zijn ouders in Leiden (waar zijn vader hervormd predikant was), aan het einde van de Hogewoerd, nu nr 175.<sup>19</sup> En de „Student-Leidenaar” moest het blijkens Klikspaan stellen zonder oppasser Mogelijk bezorgde Abraham zijn theses gewoon zelf rond

In de dagen die aan het twistgesprek voorafgingen moesten de defendens en de opponenten zich uiteraard op het treffen voorbereiden Van deze voorbereiding krijgen we een vermakelijke en onthullende indruk uit opmerkingen van J J Hartman, leerling van Cobet en later professor Latijn, die recentelijk zijn opgehaald door de Latinist E J Kenney uit Cambridge.<sup>20</sup> Deze mededelingen betreffen eigenlijk een werkcollege van Cobet, maar voor de dispatatie zal de voorbereiding op vergelijkbare wijze zijn toegegaan Het komt er op neer, dat men eerst in Cobets eigen publicaties nazocht, of hij de passage in kwestie niet al eens besproken had. Want de professor vergat wel eens welke teksten hij al onder handen gehad had en gaf soms plaatsen op die hij al eerder bewerkt had Bleek dit niet het geval, „dan moest men zijn eigen verstand te baat nemen” Men beproefde zijn krachten eerst op het transcriberen van het minuskelschrift van de bedorven geachte plaats in majuskelschrift, ten einde zoveel mogelijk profijt te trekken uit paleografische argumenten Vervolgens stroopte men woordenboeken af om desnoods parallellen uit het Nieuwe Testament in dienst van een conjectuur in Herodotus te stellen En met zulk materiaal sloeg men elkaar in het dispuut om de oren

Op de dag van de dispatatie, gewoonlijk een donderdag, bij uitzondering een vrijdag of zaterdag, altijd om elf uur ’s morgens, kwamen voorzitter Cobet, de student-deelnemers en misschien nog enkele verdere belangstellenden bijeen in het „auditorium publicum”, dit is het Groot Auditorium in het academiëgebouw De academie moet men zich tot 1864 nog voorstellen als toegetakeld met het sterrenkundig observatorium op het dak Maar zoals

18 Klikspaan, *Studenten typen*, 7de dr., Leiden z j p 41

19 De almanakken plaatsen hem steeds op de Hoogewoerd, bij zijne Ouders De toenmalige adresboeken van de stad plaatsen dominee Kuyper op Hoogewoerd, nu nr 175 Thans is in het 17de-eeuwse huis gevestigd een „Yoga gezondheidscentrum”

20 Kenney, *Classical Text*, pp 122-123, Kenney put uit J J Hartman, *De Phaedri fabulis commentatio*, Leiden 1890, pp 90-91

de lezers van „Gernt Witse” weten, zag de academie er in het midden van de negentiende eeuw verder reeds ongeveer uit als thans het ijzeren hek aan het Rapenburg, het pleintje, de poort met aangepikte mededelingen, de gang met links de gewelfkamer (het „theologenhok”) en het Groot Auditorium, rechts de traptoren met de wenteltrap. Boven was het zweetkamertje, het senaculum en de faculteitskamers. Kuypers heeft dit alles gekend maar de tekeningen van Victor de Stuers op de muren langs de trap, de „Gradus ad Parnassum”, dateren van na zijn Leidse tijd, nl. uit 1865, en de zijvleugel langs de Nonnensteeg pas uit 1896. Ook de receptiekamer was er nog niet, ter plaatse was de gevel aan het pleintje geheel anders dan nu.<sup>21</sup> De inrichting van het Groot Auditorium was in hoofdzaak als thans, zoals o.a. blijkt uit de steendruk naar een tekening uit 1864 van De Stuers.<sup>22</sup> Aan de korte zuidwand stond dezelfde kathedrader als nu, met een hoger en een lager spreekgestoelte. Ter weerszijden hiervan en langs de wanden banken met lessenaar, tegenover de kathedrader in de zaal een rij losse banken zonder lessenaar achter elkaar. Het geheel leek in Kuypers studietijd sprekend op de huidige toestand, doordat bij de in 1914-1915 uitgevoerde restauratie het oude interieur tot leidraad diende. Het zag er in de dagen van Kuypers alleen veel gewoner uit: er heerste nog niet die voorgewende deftigheid en steriele opgedofte keurigheid van nu. De almanak van 1829 zegt ervan (p. 76): „Het Groot-Auditorium is veranderd. Er zijn eenige banken geplaatst, om aan vele toehoorders plaats te kunnen verschaffen, met het gelukkige gevolg dat thans ruim een derde gedeelte van hen, die plaatsen behoorden te vinden, hoe opeengepakt dan ook, kunnen zitten. Sommigen vinden die verandering eene, der eerste hoogeschool onzes lands waardige, verbetering, anderen meenen eene slaafsche navolging van de timmerorde *eener armenkerk* te ontdekken.”

Over de precieze toedracht van de disputaties onder Cobet zijn naar mijn weten geen berichten bewaard. Maar het moet ongeveer zijn toegegaan als bij het ritueel voorafgaand aan de toenma-

21 J. J. Terwen en anderen: *Universiteit en architectuur*, tentoonstellingscatalogus Leiden 1979, pp. 5-9, aldaar verdere literatuur.

22 Gereproduceerd in *Minerva*, Feestnummer 1 maart 1889, p. LI (Leiden: Gem. Arch. Bibliotheek Leiden 41073 fd); zie ook de pentekening door De Stuers van de professorenbank links van de kathedrader, gereproduceerd in *Vox Studiosorum*, feestnummer juni 1880, z. pag. (ibid. 37954 pl.) en foto's van het Groot Auditorium in de prentenverzameling van het Leidse Gem. Arch., nrs. 12569 en 12590. Voor de huidige inrichting zie de foto in Ekkart: *Athenae Batavae*, p. 99, nr. 192.

lige promotie, dat goed beschreven is.<sup>23</sup> Naar analogie daarvan kan men zich het volgende voorstellen.

Om kwart over elf besteed Cobet het hogere, de defendens het lagere spreekgestoelte van de kathedra. Cobet sprak een kort openingswoord, waarna de defendens alle aanwezigen uitnodigde hun bezwaren met redenen omkleed en duidelijk te doen kennen. Daarna nam één der studenten het woord en kritiseerde deze of gene stelling, waarop de defendens repliceerde. Vervolgens kregen andere opposanten hun kans. Aangezien de meeste stellingen „moeijelijk door een ander konden verdedigd worden” dan door Cobet, naar de almanak van 1861 zegt, zal hij als voorzitter met zijn sprankelend Latijn en levendige voordracht geëgeld in de discussie hebben ingegrepen en van het dispuut een college hebben gemaakt.

Na een uur, misschien anderhalf uur<sup>24</sup>, als iedereen het zijne wel gezegd had, moet men naar het déjeuner hebben verlangd en blij geweest zijn, dat men kon opbreken, doch niet dan nadat afspraken voor de volgende bijeenkomst waren gemaakt (betreffende datum en defendens) en Cobet een kort slotwoord had gesproken. Onmogelijk konden alle voorgelegde stellingen aan bod zijn gekomen. De frustraties waren, blijkt bij de afschaffing van deze disputaties kort na Kuypers deelneming eraan, dat het aantal stellingen waarop men geprepareerd moest zijn steeds te groot (ca. 25) was, dat het verlossende woord toch meestal slechts van Cobet zelf moest komen, en dat de jonge deelnemers, nog te onervaren als tekstcritici, en aan het disputeren niet gewoon, dit meestal deden met het vaste voornemen om nooit iemand gelijk te geven. In 1859 loopt het met deze disputaties van Cobet af. Ze waren ingesteld in 1848. De almanak van 1861 zegt vrijmoedig, dat gebrek aan belangstelling de oorzaak van de opheffing dezer disputaties is.<sup>25</sup>

23 Oort, p. 74

24 De disputaties geleid door prof. C. J. van Assen, jurist, staan op de series aangegeven als gedurende één uur, donderdags van drie tot vier, *Studenten-almanak voor het jaar 1858*, Leyden z. j., p. 120 voor Cobets disputaties ken ik zo'n gegeven niet

25 *Leidsche studenten-almanak voor 1861*, Leiden z. j., p. 230. „Het publiek dispuut, onder leiding van Prof. Cobet, is dit jaar (1859/60) niet gehouden. Gebrek aan deelneming is hiervan de reden, het vorige jaar (1858/9) toch was het getal der gewone defendenten en opposanten niet grooter dan zes. De zaak was geheel in handen van de jongere studiosi, die zich nog minder goed in de conjecturaal-critiek te huis gevoelen en die, niet aan het disputeren gewoon, dit meestal doen met het vaste voornemen, om nooit iemand gelijk te geven. Ook was het getal theses te groot. Prof. Cobet leverde gewoonlyk de grootste helft, die moeijelijk door een ander konden verdedigd worden, terwijl het de bestrijders niet aanmoedigde.”

Het bericht uit de almanak is niet zonder belang. Het zegt, dat er in 1858/9 slechts zes deelnemers waren, d w z gewone defendenten en opponenten, naast voorzitter Cobet. Volgens de bewaard gebleven gedrukte theses hadden in die cursus echter elf bijeenkomsten plaats waarin acht verschillende defendenten optraden, vier theologen, twee juristen en twee literatoren. Het door de kroniekschrijver van de almanak genoemde getal van zes is dus wat al te somber, al kan het aantal deelnemers tegen het einde van de cursus natuurlijk tot zes gedaald zijn. Toch is het verschil tussen de informatie uit de almanak en die vervat in de bewaarde theses zo gering, dat men mag aannemen dat op grond van de theses een redelijk betrouwbaar beeld van de door Cobet geleide disputaties en van de kring van deelnemers kan worden gevormd.

Afgaande dan op de gedrukte theses van de jaren waarin Abraham Kuyper aan de disputaties van Cobet deelnam, kan men het volgende opmerken:

Kuyper nam deel in de cursussen 1856/7 en 1857/8, toen hij tweede- en derdejaars student was, doch niet meer in de daarop volgende cursus die de laatste zou worden waarin de disputaties plaats hadden.

De deelnemers van 1856/7 waren de volgende:

- 16-10-1856 defendens J. L. Sirks, student klassieke talen,
- 30-10-1856 defendens H. E. Moltzer, student theologie,
- 13-11-1856 defendens J. G. F. Herfs, student klassieke talen,
- 27-11-1856 defendens G. Smit Sibinga, student klassieke talen,<sup>26</sup>
- 11-12-1856 defendens J. L. Sirks, student klassieke talen,
- 22- 1-1857 defendens H. E. Moltzer, student theologie,
- 19- 2-1857 defendens H. Smits, student klassieke talen,
- 2- 4-1857 defendens A. Rutgers, student theologie,
- 23- 4-1857 defendens A. F. L. Gregory, juridisch student,
- 7- 5-1857 defendens J. L. Sirks, student klassieke talen,
- 22- 5-1857 defendens H. E. Moltzer, student theologie,
- 13- 6-1857 defendens A. Kuyper, student theologie.

Er waren in dit eerste jaar waarin Kuyper meedeed dus negen deelnemers, allen jongerejaars, geen van allen kandidaat. Vier waren classici, vier theologen en één jurist. Er hadden veertien bijeenkomsten plaats. Kuyper defendeerde slechts een keer en wel in de allerlaatste disputatie. Hij was toen negentien jaar. De

<sup>26</sup> De overgrootvader van J. Smit Sibinga, professor Nieuwe Testament aan de Universiteit van Amsterdam sinds 1969. G. deed ook in 1857/8 mee.



door hem voorgelegde stellingen bestaan uit een vierentwintigtal conjecturen in Lysias, waarvan ongetwijfeld alleen Cobet de auteur is.

Trad Kuyper het eerste jaar slechts éénmaal op als defendens, het volgende jaar deed hij dit vier maal. In dat jaar, 1857/8, ziet de lijst van deelnemers er als volgt uit:

- 1-10-1857: defendens: H. E. Moltzer, student theologie, die vooraf een korte toespraak houdt, vermoedelijk om te wijzen op het belang van het disputeren en de wenselijkheid van een talrijkere deelnemerskring,
- 15-10-1857: defendens: A. Kuyper, student theologie,
- 29-10-1857: defendens: J. Rutgers, student theologie,<sup>27</sup>
- 12-11-1857: defendens: G. Smit Sibinga, student klassieke talen,
- 26-11-1857: defendens: H. W. van der Meij, student klassieke talen,
- 10-12-1857: defendens: J. A. Lublink Schröder, student klassieke talen,
- 28- 1-1858: defendens: A. Kuyper, student theologie,
- 18- 2-1858: defendens: H. E. Moltzer, kandidaat klassieke talen en student theologie,
- 4- 3-1858: defendens: A. Kuyper, student theologie,
- 18- 3-1858: defendens: J. Rutgers, kandidaat klassieke talen,
- 29- 4-1858: defendens: G. Smit Sibinga, kandidaat klassieke talen,
- 14- 5-1858: defendens: O. Geerts, student theologie,
- 28- 5-1858: defendens: A. Kuyper, kandidaat klassieke talen en student theologie,
- 10- 6-1858: defendens: J. J. Cornelissen, student klassieke talen.

Deze cursus waren er acht deelnemers: vier classici en vier theologen. Van de vier theologen haalden er drie in de loop van het jaar hun kandidaats in de letteren: H. E. Moltzer, J. Rutgers en A. Kuyper. Er vonden opnieuw veertien bijeenkomsten plaats.

De 23 stellingen die Kuyper op 15 oktober 1857 voor zijn rekening nam behelzen negentien conjecturen in Livius en vier in Demosthenes. Ze zijn alle van Cobet. Met Livius hield deze zich bezig ten behoeve van zijn college Romeinse oudheden, waarvan hij zeer veel werk placht te maken.

Op 28 januari 1858 presenteerde Kuyper 27 stellingen: acht waren conjecturen en interpretaties van Tacitus, acht conjecturen in Plato's *Symposium*, acht conjecturen in Homerus. Ik denk niet dat er iets van Kuypers hand bij is.

27 Broer van A. (zie bij 1856/7) en van F. L. Rutgers (de medeoprichter van de V.U.); de drie waren zoons van de Leidse professor Hebreuws en O.T. Antonie Rutgers. Ze woonden bij hun vader op het Rapenburg.

Onder de twintig stellingen die Kuyper op 4 maart 1858 aanbod komen conjecturen voor op Herodotus, Livius, Gellius en Thucydides Die op Herodotus VII, 15 (*dele kaleunta*) en Thucydides (boven genoemd) publiceerde Cobet ook in *Mnemosyne*, evenals de interpretatie van *ho kategoros* in Xenophons *Memorabilia* <sup>28</sup> De lijst bevat deze keer ook stellingen van onverwacht algemene strekking bv nr 2 „In zijn beschrijving van de Joodse geschiedenis toont Tacitus zich geen historicus” Zou hierin misschien een opinie van Kuyper zelf schuil gaan?

De laatste serie stellingen die Kuyper proponeerde bevatten weer de typisch Cobetiaanse conjecturen op Demosthenes, Aeschines, Dinarchus, Aristophanes en Lysias Voorts acht theses op het terrein der Romeinse oudheden Alleen in de allerlaatste twee kan men wellicht de hand van Kuyper vermoeden, nr 19 „Het is volstrekt noodzakelijk, dat theologische studenten, die immers het Nieuwe Testament zullen gaan verklaren, uit de Romeinse geschiedenis die dingen gedoceerd krijgen die strekken tot beter begrip van de toestand ener Romeinse provincie omtrent het begin onzer jaartelling” en nr 20 „Men moet het oneens zijn met de geleerde Burger, die oordeelt dat in de gymnasia de lezing van het Nieuwe Testament hersteld moet worden” Met deze twee beweringen is de lijst van in totaal 114 stellingen die Kuyper onder Cobet ter discussie stelde en verdedigde ten einde

De historische notities hierboven geven tot heel wat overwegingen aanleiding Terughoudendheid lijkt verkieslijk

Wat Kuyper betreft het wordt, ten overvloede, duidelijk, dat hij te Leiden tot de kring van Cobets zeer goede en ijverige leerlingen behoorde <sup>29</sup> Dit disputeren was geen verplichting hij deed

<sup>28</sup> *Mnemosyne* 6 (1857) p 48 over Herodotus VII 15 7 (1858) p 293 over Thucydides II 60 7 (1858) p 254 over *ho kategoros* Een voortgezet onderzoek in Cobets verdere publicaties is nodig voor een nauwkeuiger bepaling van het auteurschap van de door Kuyper gepresenteerde stellingen Vgl reeds Baarda (cf n 1) p 27 n 52

<sup>29</sup> Ik maak van de gelegenheid gebruik om iets aan te vullen bij wat L Praamsma in zijn *Abraham Kuyper als kerkhistoricus* diss V U Kampen 1945 heeft vermeld over Kuypers betrekkingen met Ed Reuss de bekende Straatsburgse oud- en nieuwtestamenticus Reuss werkte in de zestiger jaren aan zijn *Bibliotheca Novi Testamenti Graeci* een bibliografie van alle gedrukte uitgaven van het Griekse Nieuwe Testament met bepalingen van hun onderlinge afhankelijkheid Uit vele streken van de wereld had Reuss inlichtingen gevraagd en gekregen In Nederland was zijn informant Abraham Kuyper Praamsma behandelt in een bijlage de correspondentie van Reuss en Kuyper en vermeldt in een noot op p 171 dat Kuyper in

het vrijwillig, hoewel het naast zijn studie voor het propaedeutisch en het kandidaats een extra last betekende. Latijn leren spreken is niet veel moeilijker dan Frans of Engels leren spreken. Maar welke tweede- of derdejaars student neemt anno 1980 de moeite, zich te oefenen in het correct gebruik van wetenschappelijk Frans of Engels?

En wat de disputaties betreft, wat is er niet verloren gegaan sinds die tijd waarin literatoren, juristen en theologen nog met elkaar debatteerden over een literatuur en een geschiedenis die naar hun correct besef hun allen aanging. Momenteel is het gesprek tussen exegeet en dogmaticus al haast onmogelijk, laat staan tussen theoloog en jurist, uitzonderingen daargelaten. Oorzaak is de verlating van een gemeenschappelijke grondslag die voor allen waarde heeft. Deze eeuwen oude grondslag laat zich blijkbaar niet opheffen dan op straffe van desintegratie en voortgaande geestes- en spraakverwarring. Wie kan hierin winst of vooruitgang zien? Het is, vreemd genoeg, niet zeker, dat Kuyper de ontwikkeling niet zelf heeft versneld. Hij heeft zijn Leidse jaren niet zo maar verloochend. De antirevolutionair Kuyper heeft de revolutie gediend. Maar dat hebben zeker anderen al betoogd.

Leiden, 25 juni 1980

het voorwoord tot Reuss' boek, verschenen te Brunswijk in 1872, wordt bedankt. Dat is juist, maar in het boek zelf worden Kuypers inlichtingen bovendien met vermelding van zijn naam geregistreerd, zo (behalve op p. 9) op pp. 52, 89, 143, 217 („humanissimus Kuyper”) en 288. De meeste informatie komt uit de Leidse U B. Ook wanneer Kuypers naam niet genoemd wordt zijn Reuss' gegevens over in Nederland voorhanden exemplaren van Griekse Nieuwe Testamenten als regel van Kuyper afkomstig.

# The character of Erasmus' translation of the New Testament as reflected in his translation of Hebrews 9

H. J. DE JONGE

In the sixteenth and seventeenth centuries the Latin translation of the New Testament by Erasmus of Rotterdam was the most widely used Latin text of the New Testament next to the Vulgate. Erasmus' translation was printed in about 220 editions and reprints in several countries in Europe.<sup>1</sup> Given the wide circulation of this translation and the important role it has played, it is strange that its nature does not seem to have been subjected to a systematic investigation.<sup>2</sup> The present contribution is a condensed account of such an investigation, based on an exhaustive analysis of Erasmus' translation of Heb. 9 as published in his fifth and final edition of the New Testament (Basle, 1535). In this edition, thirty years of work found their completion. We shall focus on the result of this work rather than on the eventful development which led to it.

Erasmus' translation must always be considered against the background of the Vulgate (Vg.), not only because it was the first alternative Latin text of the complete N.T. that could rival it but also because Erasmus himself regarded and presented his translation as a "revision and improved edition"<sup>3</sup> of the current Latin text, that is, the Vg. Since Erasmus' fifth edition of the N.T. does not contain a text of the Vg.,

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1. Jac. le Long, C. F. Boerner, A. G. Masch, *Bibliotheca sacra*, 3 vols., Halae 1778-1785<sup>3</sup>, III, 591-608.

2. Useful remarks on the character of Erasmus' translation can be found in Richard Simon, *Histoire critique des versions du Nouveau Testament* (Rotterdam, 1690; rpt., Frankfurt, 1967), chs. 21 and 22, pp. 242-64; Fr. Kaulen, *Geschichte der Vulgata* (Mainz, 1868), pp. 319-22; A. Bludau, *Die beiden ersten Erasmus-Ausgaben des Neuen Testaments und ihre Gegner* (Freiburg im Br., 1902), pp. 33-48; and B. Hall, 'Erasmus: Biblical Scholar and Reformer,' in T. A. Dorey, ed., *Erasmus*, Studies in Latin Literature and Its Influence (London, 1970), pp. 81-113; at pp. 98-100.

3. Thus the title of Erasmus' editions of the N.T.: *Novum Instrumentum omne, diligenter ab Erasmo Roterodamo recognitum et emendatum* (Basle, 1516). In later editions *Instrumentum* was changed to *Testamentum*. As there were no Greek editions of the N.T. that could be "revised and improved" in 1516, the title of Erasmus' editions of the N.T. announced only his Latin translation, not his edition of the Greek.

we took the Vg. text included in his fourth edition (Basle, 1527) as the standard for comparing Erasmus' translation with the Vg.

The most conspicuous and striking feature of Erasmus' translation is its resemblance to the Vg., both in choice of words and in syntactical structure. In Heb. 9, Erasmus' version runs to 470 words; 283 out of these 470 words are identical with those in the Vg. This means that for exactly 60 percent, Erasmus' translation concurs with the Vg. Erasmus also agrees with the Vg. in passages where his Greek text could or even should have occasioned a different translation. In v. 16, for instance, the Vg. gives no adequate translation of *φέρεσθαι*.<sup>4</sup> The Greek means that it is necessary for a death to be "recorded, reported, officially registered." The Vg. has *intercedat*, which is not correct. But Erasmus retained it. A most interesting case occurs in v. 21, where Erasmus' Greek text as printed in his last three editions (1522, 1527, 1535) has a second *πάντα*, inserted between *αἵματι* and *ὁμοίως*. This second *πάντα* is absent from most, if not all known Greek manuscripts; it is probably a misprint in Erasmus' Greek text. The Vg. has nothing that corresponds to it. But Erasmus ought of course to have translated this second *πάντα*. Yet he does not do so, obviously because he simply followed the Vg., even in this case where his own Greek text differs from it. Other instances of Erasmus' adherence to the Vg. in defiance of his Greek text are his word order *noui testamenti* in v. 15 (contra his Greek *διαθήκης καινῆς*) and his word order *secundum legem . . . purificantur* (Vg. *mundantur*; contra the Byzantine Greek text *καθαρίζεται κατὰ τὸν νόμον*) in v. 22.<sup>5</sup> In the latter two cases the Vg. is based on a Greek reading different to the one known to Erasmus. Nevertheless he followed the Vg., in defiance of his own Greek text. He also followed the Vg. in translating *μήποτε* in v. 17 by *nondum*<sup>6</sup> and *θανάτου γενομένου* in v. 15 by *morte intercedente*. It is clear that, in the chapter under consideration, Erasmus' translation is not an independent version, but a revision of the Vg. with the aid of Greek manuscripts. Erasmus changed the Vg. text wherever this seemed to him to be necessary or desirable, but otherwise he left it as it stood. Thus he also retained the traditional translation *testamentum* for *διαθήκη*, al-

4. The reader is requested to have at hand an edition of the *textus receptus* of the N.T., e.g., the one printed with Erasmus' Latin translation in Vol. VI of his *Opera omnia*, ed. J. Clericus (Lugduni Batavorum, 1705); space forbids me to quote extensively.

5. That Erasmus did not regard such matters of word order as insignificant can be concluded from his modifications in v. 3.

6. Cf. v. 8, where, both in the Vg. and Erasmus, *nondum* is the translation of *μήπω*.

though he rightly observed in his Annotations at Heb. 9:16, "διαθήκη Graecis *dispositionem* sonat magis quam *testamentum*."<sup>7</sup>

The only other Latin translation which can have influenced Erasmus is the translation of Paul's Epistles by Jacques Lefèvre d'Étaples, published first in 1512 and for the second time in 1515.<sup>8</sup> In Heb. 9 Erasmus and Lefèvre agree in 48 deviations from the Vg. We quote some examples:

<i>Vulgate</i>	<i>Lefèvre and Erasmus</i>
v. 1 saeculare	mundanum
v. 4 fronduerat	germinaverat
v. 8 propalatam	manifestatam
v. 9 parabola	similitudo

However, all the readings in which Erasmus' translation of 1535 agrees with that of Lefèvre as against the Vg. can also be found in Erasmus' earliest Latin translation of the N.T. (1506-9) which, although preserved in manuscript, remained unpublished during Erasmus' lifetime.<sup>9</sup> The agreements between Erasmus and Lefèvre cannot be explained, therefore, as due to the influence of Lefèvre on Erasmus. But they can all be accounted for as the result, *either* of Erasmus' and Lefèvre's being indebted to the same exegetical sources or traditions—e.g., Mutianus Scholasticus' Latin translation of Chrysostom's commentary on Heb., Ps.-Ambrose's (i.e., Alcuin's) commentary on Hebrews, L. Valla's *Annotationes in N.T.*—or of their following a Greek reading different to the one translated in the Vg., or again, of their adherence to the same translation principles (e.g., avoidance of Greek loan words). All in all, there is no reason to assume that Lefèvre exercised any direct influence on Erasmus' translation.

The changes which Erasmus introduced in the text of the current Latin version (the Vg.) in order to bring about his own "revised and improved" translation, can be classed under seven heads, according to the reason or the purpose for which each alteration was made. Several

7. *LB* (this is the usual designation of the Leiden edition mentioned in n. 4 above), VI, 1007F.

8. J. Faber Stapulensis, *Contenta. Epistola ad Rhomanos . . . Epistola ad Hebraeos, In hac secunda emissionem obiter relegendo commentarios: castigata sunt nonnulla* (Paris, 1515).

9. See now H. Gibaud, *Un Inédit d'Erasmus: la première version du Nouveau Testament . . . 1506-09* (Angers, 1982). I am grateful to Dr. Gibaud for sending me photostats of the pp. 575-76 (containing Heb. 9) of his book when it had not yet been published.

of Erasmus' changes reflect a mixture of motives. Consequently, there is some overlap between the seven categories of alterations with which I shall deal here in the order of their frequency.

(i) In 39 cases Erasmus' alteration reflects his striving for a grammatically better, more classical (i.e., broadly Ciceronian) Latin. A fine example is his use of *manifestatam* in v. 8, where it replaces *propalatam* of the Vg. In classical Latin the verb *propalare* does not mean 'to manifest,' but 'to stake out (a plant).' Only in post-classical Latin does it mean 'to make public, to throw open.' In the Vg. it occurs only here. Obviously, Erasmus wanted to avoid the dubious term and replaced it by a good classical word.<sup>10</sup> In vv. 22 and 25 Erasmus changed the Semitic turn of phrase *in sanguine* into a simple instrumental ablative *sanguine*, v. 22, and into the good Latin expression *per sanguinem*, v. 25. Another marked improvement is Erasmus' use of the accusative in substitution for the ablative after the preposition of direction *in*: in v. 6 he wrote *in prius . . . tabernaculum* instead of *in priori . . . tabernaculo* of the Vg.

(ii) A second group of alterations, represented by 26 instances, mirrors Erasmus' intention of enhancing the elegance of the Latin translation. A good specimen is his substitution of *reperita* for *inventita* in v. 12. In his *Paraphrases in Elegantias Vallae* Erasmus explains that *invenire* is 'to find either by chance or after searching,' whereas *reperire* is specifically 'to find what one has not looked for.'<sup>11</sup> Erasmus' *reperita* in v. 12 is certainly meant to be more accurate and more elegant than *inventita*. Typically Erasmian elegance is to be found in *siquidem*, in lieu of *enim*, in vv. 2 and 16, and in *quatenus* for *quemadmodum* in v. 27. In the *Paraphr. in Eleg. Vallae* Erasmus states that Cicero used *quatenus* for *in quantum*.<sup>12</sup> The Greek of v. 27 has καθ' ὅσον, literally *in quantum*. But Erasmus prefers the Ciceronian synonym *quatenus*. Another example is Erasmus' turn of phrase *a condito mundo* instead of *ab origine mundi* in v. 26. Finally there is that nicety in v. 27, where the Vg. has *statutum est hominibus*. From Valla's *Elegantiae* Erasmus had learned that *statutum est mihi* means *apud me cogitando firmatum est*.<sup>13</sup> In Heb. 9:27 this cannot be the meaning intended by the author. The

10. Erasmus (and Lefèvre d'Étaples) may have found *manifestatam* in the Old Latin version by Mutianus Scholasticus of Chrysostom's commentary on Hebrews (Migne PG 63, 336).

11. Erasmus, *Opera omnia* (Amsterdam 1969-) cited below as ASD, I, 4, p. 264, lines 564-65, and p. 310, lines 848-50. It does not matter here that the distinction cannot be substantiated from good classical sources.

12. ASD, I, 4, p. 307, line 764.

13. ASD, I, 4, p. 240, lines 911-12.

Greek ἀποκείται means: 'it is in store, in prospect for all people.' Consequently, according to Ciceronian standards, the rendering *statutum est* is impossible. Erasmus corrected it by introducing an elegant verb with the required meaning: *manere*. As he explained in his *Paraphr. in Eleg. Vallae*, *manere* means *futurum esse*.<sup>14</sup> He adds by way of illustration: eternal punishments await those who are guilty. This is a splendid example of how Erasmus' knowledge of the subtleties of Ciceronian Latin enabled and inspired him to add to the elegance of the Latin Bible.

(iii) There are 26 further changes which show that Erasmus also aimed to make the Latin translation correspond more closely to the Greek. Examples are the addition of *Igitur* in v. 1, corresponding to οὖν, the rendering of the plural ἀγνοημάτων in v. 7 by the plural *ignorantiis* instead of *ignorantia*, and the substitution of *quandoquidem* for *alioquin* as a translation of the causal conjunction ἐπεὶ in v. 17.

(iv) In a fourth group of Erasmian changes, once again 26 instances, one perceives Erasmus' attempts at greater clarity of translation. Under this category we have to class his replacement of *modo* by *nunc* in v. 5, and the insertion of the copula in vv. 3 (*erat*) and 20 (*est*), where the copula was missing in the Vg.

(v) In 9 cases Erasmus' translation differs from the Vg. because he believed he could give expression to an improved exegesis. In reality, virtually all these changes are, from an exegetical point of view, deteriorations. This applies, e.g., to Erasmus' replacement of *iustificaciones culturae* in v. 1 by *iustificaciones*, (*sic*: a comma) *cultus*, as if λατρείας were an accusative, not a genitive.

(vi) A sixth group of alterations consists of 7 cases in which Erasmus removed a textual corruption of the Vg. In v. 5, e.g., *quae* in the Vg. is a corruption of *-que*, which renders a Greek δέ. Erasmus removed the source of the corruption by translating δέ as *autem*. He also restored *offer* instead of *offerret* in v. 7, the future of *purgabit* instead of the perfect of *emendavit* in v. 14, and *vestram* instead of *nostram* in the same verse. In all 7 cases Erasmus recovered the original reading of the Vg. with the aid of the Greek text.

(vii) A seventh category of changes is made up of 5 cases in which Erasmus translated a Greek reading different to the one underlying the Vg. Here we are confronted with a very serious drawback of Erasmus' translation. In fact, the Greek manuscripts he used were all of the Byzantine branch of the textual tradition, but the Vg. contains

14. ASD, I, 4, p. 274, lines 872-75.



many readings that are older than and superior to the corresponding Byzantine variants. In revising the Vg. (which remained the basis of Erasmus' version) after Byzantine manuscripts, Erasmus not only confused different branches of the textual tradition, he also replaced good early readings transmitted in the Vg. by inferior ones from the Byzantine text. Remarkably, Erasmus was well aware of this embarrassing effect of his procedure. But since he had undertaken to translate from the Greek whatever his Greek manuscripts might give, he did not feel free to retain readings of the Vg. which in his view were better than the Byzantine variants. "There are readings in which the Vulgate or the Vetus Latina of Ambrose is to be preferred to the Greek manuscripts," Erasmus declared.<sup>15</sup> But "I am translating what the Greek manuscripts give."<sup>16</sup> Unfortunately, Erasmus did not realize that, as he did not make a fresh translation but only a revision of the Vg., he inadvertently retained (as we mentioned above) several typical Vg. readings at places where his Greek manuscripts required another translation. As a result, Erasmus' translation is a monstrous mixture of Vg. and Byzantine elements.

In Heb. 9, Erasmus replaced five times the Vg. reading by a Byzantine reading:

<i>Vulgate</i>	<i>Erasmus following the Byzantine text</i>
v. 9 iuxta quam < καθ' ἣν	in quo < καθ' ὅν
v. 13 hircorum . . . tauro-	taurorum . . . hircorum <
rum < τράγων . . . ταύρων	ταύρων . . . τράγων
v. 14 sanctum < ἁγίου	aeternum < αἰωνίου
v. 14 nostram < ἡμῶν	vestram < ὑμῶν
v. 26 suam < αὐτοῦ	sui-ipsius < αὐτοῦ

In four out of these five cases the Byzantine reading translated by Erasmus is inferior to that of the Vg. The exception is *aeternum* in v. 14; here the Byzantine reading is original, so that in this case Erasmus had the good fortune to produce a better Latin reading than the Vg.

15. Erasmus, *Apologia*, ed. H. Holborn, *Des. Erasmus Rot., Ausgewählte Werke* (Munich, 1933; reprint, 1964), pp. 170-71; LB VI, fo.\*\*3, lines 2-3.

16. Erasmus, *Apolog. resp. lac. Lop. Stum.*, LB IX, 287C-D: "ubique clamo . . . me vertere quod habetur in Graecorum voluminibus, nec usquequaque mihi probari lectionem illorum." That Erasmus was aware that the readings of the Vg. might in some places be better than those of his Greek manuscripts has rightly been noticed by Bludau, *Die beiden ersten Erasmus-Ausgaben*, p. 41, and W. Schwartz, *Principles and Problems of Biblical Translation* (Cambridge, 1955), p. 143.

This one improvement does not counter-balance, however, the great disadvantage of Erasmus' version, that is, his systematic confusion of Byzantine and Vg. readings. For the rest it should be remembered that the Vg. too is a blend of textual traditions; Erasmus did nothing worse than the makers of the Vg. had done eleven centuries before.

### *Conclusion*

The main feature of Erasmus' translation of Heb. 9 is its dependence on the Vg., to which it owes 60 percent of its text. Its further characteristics are in order of numerical importance:

1. A striving for grammatically more correct, more classical Latin;
2. A striving for more elegant Latin;
3. A striving for closer agreement with the Greek text;
4. A striving for greater clarity and avoidance of ambiguity;
5. Attempts to give an exegetically better translation, without great success;
6. Successful attempts to correct textual corruptions in the Vg.;
7. The adoption of Byzantine readings in substitution for readings of the Vg.

Both from an exegetical and a text-critical viewpoint Erasmus' version is a failure. Only linguistically, by the standards of humanistic Latin, is it an improvement.



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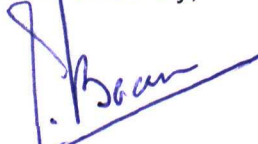
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Yours sincerely,



Drs. J. Baars  
General Manager

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DIGITISATION OF 35MM REELS  
“THE WOMEN’S (LATER QUEEN MARY’S)  
ARMY AUXILIARY CORPS: SERVICE RECORDS 1917 1920”  
WO 398**

**MicroFormat Systems B.V.  
PO Box 287  
2160 AG LISSE  
The Netherlands**



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Based on our information the number of images to be scanned is approximately 263,900. Our calculation of the project is based on 250,000 images.

**TRANSPORT**

Our estimate is based on the presumption that all 240 reels of film can be collected by our own transport at the start of the project and returned at the end of the project. Therefore only twice a transport is needed.

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## PRICES

The prices are the "best and final" costing for the project

Digitisation per scan	£ 0.049
Transport per collection or delivery	£ 400.00
Price per CD	£ 3.85
Option 1: price per DVD	£ 5.50
Option 2: Use of portable hard disk, excluding postage costs	£ 350.00

Example calculation of the project with images stored on CD

250,000 images: 0.049 per image	£ 12,250.00
2 transports: 400.00 per transport	£ 800.00
1800 CD's: 3.85 per CD	<u>£ 6,930.00</u>
The total costs for digitisation this project will be	£ 19,980.00

Example calculation of the project with images stored on DVD

250,000 images: 0.049 per image	£ 12,250.00
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260 DVD's: 5.50 per DVD	<u>£ 1,430.00</u>
The total costs for digitisation this project will be	£ 14,480.00

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## GENERAL TERMS

- all mentioned prices are exclusive of VAT
- delivery times in mutual agreement
- these prices are valid until 31st December 2005



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The National Archives  
Attn. Gary K. Flatman  
Digitisation Manager  
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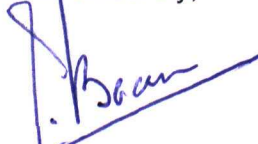
Lisse, 28 June 2005  
ref. JB/7020/205162

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Drs. J. Baars  
General Manager

Encl. Quotation for Digitisation project (WO 398)

ABN•AMRO Bank 56 80 31 148  
KvK nr. 28067736

Algemene Leveringsvoorwaarden gedeponeerd  
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tent gewerkt aan deze etnische democratiseringspolitiek, hoewel niet zonder problemen. De vroegere marxistische ideologie, die de TPLF tot eind 1990 nog in haar vaandel had, werd opgegeven voor een meer pragmatische visie, vooral in de sociaal-economische sfeer. In de politieke sfeer kan men echter nog met die ideologie verwante organisatieprincipes herkennen (bijv. 'duale structuren' van regering en bestuur en een soort democratisch centralisme). De politiek van TGE en EPRDF tot nu toe toont een opvallende continuïteit met het al in de periode van de gewapende strijd uitgestippelde programma.

### Resultaten en problemen van het Ethiopische experiment

Enige resultaten en problemen van de nieuwe politiek zijn de volgende.

\* Aangezien het EPRDF uitgaat van het federatieve en niet van het unitaire model voor de Ethiopische staat, was een van de eerste maatregelen invoering van een nieuwe regio-indeling, gebaseerd op de verspreiding van etnische groepen. De grenzen van de regio's waren niet geheel ondubbelzinnig te trekken, maar het ideaal was dat in elke regio één groep duidelijk de numerieke meerderheid zou hebben. Aldus onstonden 14 regio's, vele met etnische namen. Bij voorkeur zouden mensen met 'allochtone achtergrond', in het bijzonder de afstammelingen van Amhara, die vooral sinds de verovering en incorporatie van de zuidelijke gebieden aan het eind van de vorige eeuw (door keizer Minilik II) arriveerden, daar niet moeten wonen. Leidende functies en kaderposities zouden ook uiteindelijk ingenomen moeten worden door leden van de dominante etnische groep in die regio.

\* Vooral in de eerste twee jaar (1991-1992) had de aanmoedigingspolitiek van etnische regio- en identiteitsvorming veel geweld tot gevolg: op het platteland ontstond een chaotische sfeer van rivaliteit en machtsstrijd. In sommige gebieden leek dit soms verdacht veel op een campagne van 'etnische zuivering', waarbij vele Amhara, Gurage en andere 'immigranten' werden verjaagd of gedood en hun bezittingen vernietigd. Dit soort gewelddaden wordt nu tegengegaan, maar lokale tactieken van uitsluiting en intimidatie komen nog voor. Een onderliggende dreiging van gewelddadig conflict blijft aanwezig.

\* Het proces van 'democratisering' – partijvorming en partij-activiteit, toegang tot de media, het opzetten van representatieve fora – wordt nauwgezet gecontroleerd door het EPRDF en de TGE. Deze maken

ook het beleid, krijgen hun voorstellen door de COR en ontwijken serieuze discussie met oppositiegroepen. De COR was feitelijk ook geen autonome wetgevende vergadering (gezien o.a. zijn status als niet-gekozen lichaam). De minderheidspartijen in de COR, evenmin als de oppositie erbuiten, hebben geen politieke invloed. Het Oromo Liberation Front (OLF), dat in 1991 deel uitmaakte van de COR en de TGE, beging wellicht een vergissing door in juni 1992 uit te treden (vanwege serieuze problemen met het TPLF). Zijn stelling dat de TGE, als een 'overgangsregering' gebaseerd op het Charter van 1991, moet proberen een algemeen aanvaardbare politiek te formuleren met bestaande groepen, heeft daardoor aan kracht verloren. De EPRDF doet echter geen poging meer oppositiegroepen (en zeker niet degenen die zijn uitgetreden of ook verwijderd uit de COR) bij haar beleid te betrekken. Dit leidt volgens vele waarnemers tot meer en meer autocratisch optreden.<sup>5</sup>

\* De relatie van de zittende machthebbers met de nieuwe politieke partijen en oppositiekrachten is dus problematisch. Hoewel de regering de vorming van etno-politieke partijen onder bepaalde condities toeliet, is men niet gelukkig met alle groeperingen. Wanneer deze bewegingen het Charter onderschrijven en niet oproepen tot geweld, kunnen ze niet worden geweerd. Maar de TGE/EPRDF poogt ze te marginaliseren. De onafhankelijke pers maakt geregeld melding van intimidatie door soldaten, van huiszoekingen, arrestaties op vage gronden, dubieuze rechtspraak, en van kidnapping of ombrengen van oppositieleiden.<sup>6</sup>

Daarnaast heeft het EPRDF sinds 1990 ook een soort parallel-partijen opgericht om de etnische groepen vertegenwoordigd door bovengenoemde partijen te 'co-opteren': deze alternatieve partijen<sup>7</sup> moeten concurreren met deze oppositiegroepen. Een goed voorbeeld is de OPDO (Oromo People's Democratic Organisation), die eind 1990 werd opgezet om het OLF en het IFLO (Islamic Front for the Liberation of Oromia) de wind uit te zeilen te nemen, hetgeen vaak lukt, want de steun van de grote en cultureel en sociaal zeer diverse Oromo-bevolking voor deze bewegingen is geenszins vanzelfsprekend. De OPDO fungeert ook als partij die kader levert voor de Oromia Regio. Een ander goed voorbeeld is de ANDM (Amhara People's Democratic Movement) van premier Tamrat Layne en deel van EPRDF. Men kan, bijna vier jaar na het begin van de 'overgangperiode' (die in beginsel slechts gold tot januari 1994), zeker nog niet spreken van een maatschappelijk gewortelde democratische cultuur.

\* Het voorbereiden van een nieuwe Grondwet werd gedomineerd door de EPRDF/TGE. De angekondigde brede democratische discussie, bijv. in de lokale bewonersassociaties (*k'ebelles*), leidde niet

professor in de geneeskunde en leider van de AAPPO. Hij kreeg twee jaar gevangenisstraf vanwege 'geplande gewelddadige aanvallen op de regering'. Volgens Amnesty International (1 juli 1994) waren het bewijsmateriaal en de rechtsgang uiterst dubieus. Op grond van de vele incidenten (gedocumenteerd in de EHRC- en Amnesty-rapporten) kan men stellen dat bijv. voor de beoordeling van Ethiopische *asielzoekers* in dit verband een zeer zorgvuldige afweging per geval nodig is; men kan niet categorisch zeggen dat Ethiopie een 'veilig land' is.

<sup>7</sup> Bekend staand als de PDO's (zie voor een bijna complete lijst de *Ethiopian Herald* (Addis Ababa), 5 juni 1994, blz. 7).



# Differential winter mortality and seasonal selection in the polymorphic ladybird *Adalia bipunctata* (L) in the Netherlands

PAUL M. BRAKEFIELD\*

Department of Population and Evolutionary Biology, University of Utrecht,  
Padualaan 8, Utrecht, The Netherlands

Accepted for publication 12 April 1984

Seasonal selection acting on the melanic polymorphism in the two-spot ladybird *Adalia bipunctata* was investigated in The Netherlands. An increase in melanic frequency over the spring–summer reproductive period was quantified. The selective advantage gained by melanics averaged 9%, but significant heterogeneity occurred between populations. Adult hibernation behaviour is described. The beetles when outdoors show a highly clumped distribution both between and within trees. The distribution of the morph classes between aggregations is random. Survivorship in a hibernating cohort (initial  $n = 1898$ ) on a grid of 70 lime trees near Utrecht was monitored by making three counts over the winter of 1981–1982. Intense selection favouring each melanic morph occurred during December and January. The relative fitness of non-melanics was 0.55 (melanics = 1). The discovery of dead beetles in late January (about 5% of total losses) and the absence of spatially density-dependent mortality were consistent with a climatic stress rather than selective predation. The period of selection was associated with very cold temperatures averaging up to 4°C below normal and an overall mortality of nearly 75%. There was no change in morph frequency, near normal temperatures and a lower mortality from February to early April. Examination of groups of nearby trees in late January strongly suggested that similar differential mortality had occurred except on some willows. This difference was probably due to the more protected hibernation sites available on these trees. Samples of hibernating cohorts at three other sites showed no evidence of differential mortality. Laboratory experiments with hibernating beetles found no difference in survivorship or rate of weight loss between starved non-melanics and melanics in temperature regimes with and without periods of adult activity. It is concluded that the intense winter selection on the study limes is probably exceptional. Examination of changes in morph frequency through the annual cycle suggests that at some sites the selection favouring melanics during reproduction is counterbalanced by selection against melanics in late summer or early autumn. The results are discussed in relation to mathematical models of cyclical selection and to other field studies including that of Timofëeff-Ressovsky (1940), who found large decreases in melanic frequency during hibernation in Berlin.

KEY WORDS:—Coccinellidae – *Adalia bipunctata* – melanism – polymorphism – seasonal selection – cyclical selection – reproduction – selective advantage – hibernation – differential mortality.

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## INTRODUCTION

Timoféeff-Ressovsky (1940) found that the frequency of the melanic forms of the two-spot ladybird *Adalia bipunctata* declined substantially over the period of winter hibernation in Berlin (see also Timoféeff-Ressovsky & Svirezhev, 1966). His study provides one of the most striking examples of the operation of seasonal selection. Such cyclical patterns of selection are of considerable interest because theoretical work has shown that they can maintain polymorphism or at least delay the time to fixation (e.g. Haldane & Jayakar, 1963; Hedrick, 1974; Hoekstra, 1975). However, the conditions necessary for protected polymorphism are usually very restricted but are much less so when gene frequencies are intermediate and selection coefficients large. These conditions prevailed in the population studied by Timoféeff-Ressovsky.

The polymorphism in *A. bipunctata* is controlled by a number of alleles at a single gene locus with melanics dominant to non-melanics (Lus, 1928, 1932). Timoféeff-Ressovsky (1940) sampled a population at the beginning and end of the winter at hibernacula in crevices between the stone blocks of a ruined church. He obtained large samples in each of the 12 consecutive years, 1929–1940, with a single gap in spring, 1932. The consistent decrease in melanic frequency during hibernation averaged about 20%. In each of three years Timoféeff-Ressovsky collected all the *A. bipunctata* from an area of wall prior to the end of hibernation. Comparison of living and dead beetles demonstrated that the change in melanic frequency was due to differential mortality. Some other workers have obtained considerably fewer data for hibernating populations of *A. bipunctata*, which have not indicated a difference in winter survivorship between the morph classes (Bengtson & Hagen, 1975; Honek, 1975; Zakharov & Sergievsky, 1980).

My study of *A. bipunctata* in The Netherlands was designed to examine the dynamics of the polymorphism in more detail than previous workers (Brakefield, 1984a, b, c). Comparisons of mating and non-mating *A. bipunctata* at sites along clines have shown that melanics gain a mating advantage in post-hibernation populations (Brakefield, 1984c). Analysis of frequency data for sites where large numbers of mating animals were found strongly suggested that this mating advantage resulted in an increase in melanic frequency in the next generation. More extensive data sets are analysed in this study which confirm that such an increase occurs over the reproductive period in The Netherlands. The survivorship of cohorts of hibernating *A. bipunctata* is then examined to determine whether differential winter mortality counterbalances this increase. Finally, the changes in melanic frequency which occur through the whole annual cycle of the species are followed.

## MATERIALS AND METHODS

*Sampling in the summer*

The study sites were on four transects which traversed an area between a region of low, and one of high melanic frequency. Details of the sites, methods of sampling, geographical variation of melanism and population biology are given in Brakefield (1984a, b). Sequences of samples from each summer generation were obtained from a number of sites with differing frequencies. Their analysis examines the combined data for the two melanic morphs, *quadrimaculata* and *sempustulata*, and those for the non-melanic *typica*.

*Sampling in the winter*

The main study site for hibernating *A. bipunctata* was Utrecht E. (site 11, Brakefield, 1984a) in the central region of The Netherlands. This is a recreation area of roads, grass and planted trees just outside the city boundary. In the winter of 1981–1982 three separate counts of hibernating beetles were made on grid L<sub>1</sub> of 70 lime trees (*Tilia* sp.) planted in two, or sometimes three, rows (Fig. 1A). The trees were about 40 years old. Since beetles were rarely completely hidden (Fig. 1B & C) a thorough search of the bole and main branches of each tree revealed most, if not all, of them. The beetles were not disturbed. During the mid-winter visit collections of all beetles were made from surrounding groups of trees.

A similar series of counts were made of a smaller cohort on a grid of 48 poplar trees (*Populus alba*) at the nearby site of De Uithof (no. 12). Some samples of hibernating beetles were collected from an eight-storey building and surrounding walls and trees at this site.

*Laboratory studies of survivorship*

Some hibernating *A. bipunctata* were used to investigate survivorship of the morph classes in the laboratory. Beetles were assigned at random to cohorts of at least 90 individuals of each morph class. They were weighed and placed in stoppered 9 ml glass vials. Survivorship and loss of weight (in two cohorts) were then examined at regular intervals. Cohorts of each morph class were kept without feeding in three controlled environment rooms.

## RESULTS

*Selection during summer reproduction*

The combined frequency data for 26 post-hibernation adult populations and for their offspring collected as pupae or adults are given in the Appendix. In some years and at some sites the later samples include members of a second summer generation (Brakefield, 1984a). Some of the samples of adults collected after emergence from pupae began, included surviving adults of the parental generation. This source of error is excluded when the 'second' generation samples are made up of pupae only. Figure 2 shows that there is a trend of increasing melanic frequency over the reproductive period. The changes in

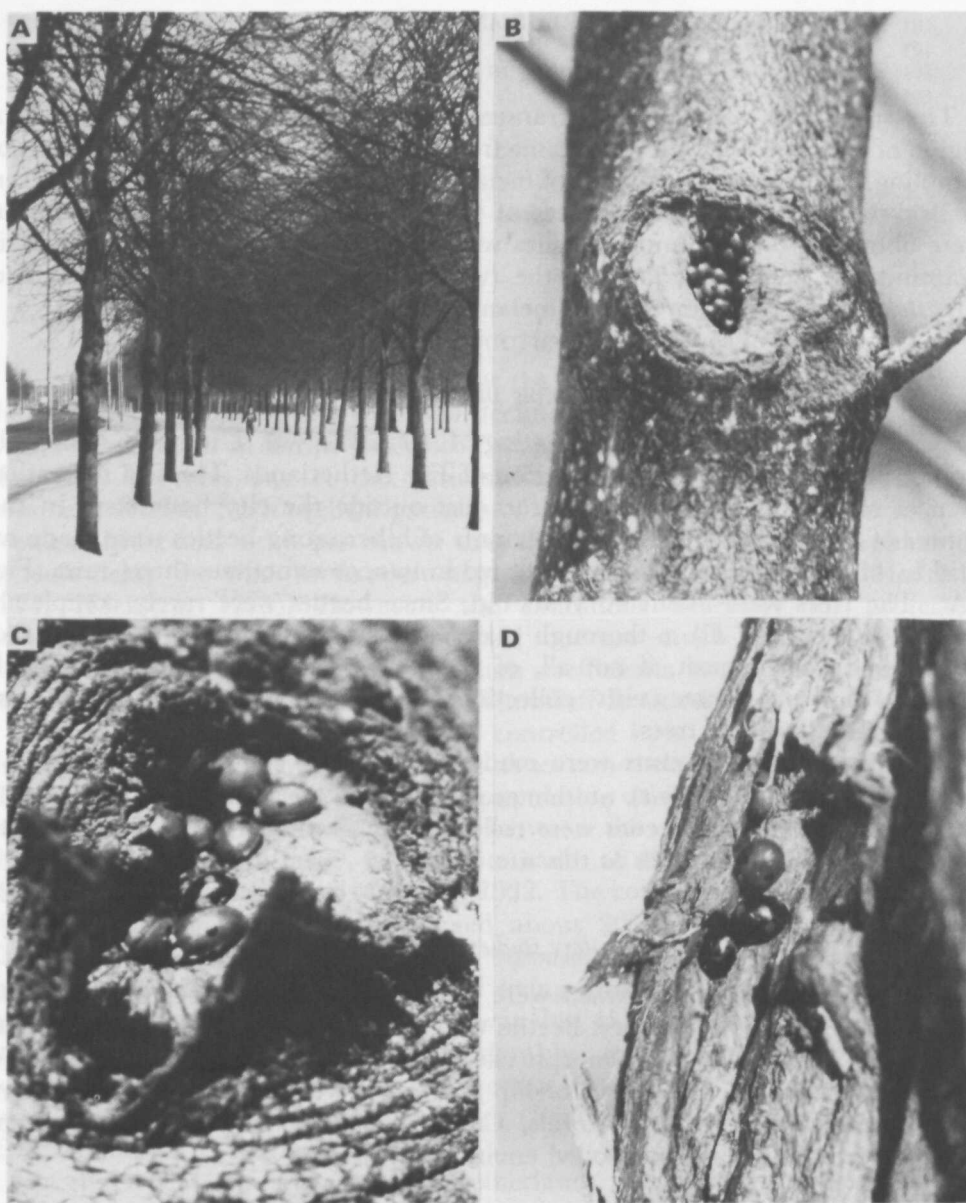


Figure 1. A, Lime trees on grid L, at Utrecht E in December 1981 (looking NE); B and C, examples of hibernating aggregations of polymorphic *Adalia bipunctata* on the limes; D, a group of beetles on *Salix alba* exposed after removal of bark.

melanic frequency are quite small, averaging 3.2% for all data. The magnitudes of these changes are not strictly comparable since overall melanic frequencies ranged from 3 to 58% (see Appendix). Figure 2 includes frequency distributions of estimates of the selective advantage gained by melanics over the reproductive period. For all data this advantage averages 9%.

The data presented in Fig. 2 involve the factors: site (*S*), generation (*G*) and frequency (*F*). The statistical significance of the changes in melanic frequency is

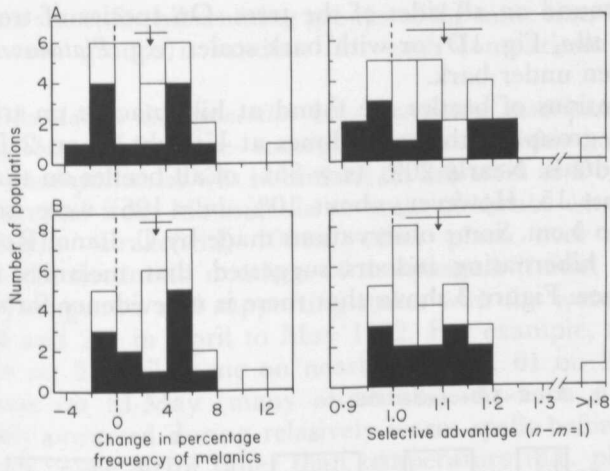


Figure 2. Frequency distributions for the change in frequency of melanic *Adalia bipunctata*, and the selective advantage of melanics (non-melanics = 1) over the period from post-hibernation adults to their progeny collected either as A pupae or B pupae and adults, at individual sites. Shaded histograms show sites for which sequential samples were obtained in each generation. Mean  $\pm$  95% C.L. are shown for each total distribution.

examined using a 3-way  $G$  test (Sokal & Rohlf, 1981) to analyse: (a) the full data set; and (b) those data for sites at which sequential samples were obtained in each generation and including only pupae in generation 2. These analyses show that the change in melanic frequency between generations is significant but that it is not independent of site ((a)  $G_{(S)GF} = 145.2$ ,  $df = 26$ ,  $P < 0.001$ ;  $G_{SGF} = 47.21$ ,  $df = 25$ ,  $P < 0.01$  and (b)  $G_{(S)GF} = 56.30$ ,  $df = 12$ ,  $P < 0.001$ ;  $G_{SGF} = 30.40$ ,  $df = 11$ ,  $P < 0.01$ ). Thus there are differences between sites in the selective advantage gained by melanics over the reproductive period. Nevertheless, the increase in melanic frequency over this period is consistent with the occurrence of seasonal selection in The Netherlands similar to that in Berlin (Timoféeff-Ressovsky, 1940) but involving considerably smaller changes in frequency.

### Hibernation behaviour

Adult *Adalia bipunctata* in The Netherlands hibernate from late October or early November until April or early May. In many built-up urban areas they usually hibernate inside buildings. At De Uithof where modern multistorey buildings are surrounded by large planted areas, some beetles enter the buildings while others remain on trees or are found in crevices on the concrete blocks of the buildings' walls. In villages and smaller towns a similar diversity of hibernation sites occurs. In more rural areas with few buildings most beetles hibernate on trees; particularly species of lime (*Tilia*), willow (*Salix*), poplar (*Populus*) and plane (*Platanus*), but also others including hawthorn (*Crataegus*), ash (*Fraxinus*) and oak (*Quercus*).

*Adalia bipunctata* hibernating on young lime trees (Fig. 1A) are usually more or less exposed in small crevices or cavities on the bole or beneath large branches (Fig. 1B and C). They are found from about 60 cm up to several



metres above ground on all sides of the trees. On species of tree with fissured bark (e.g. *Salix alba*, Fig. 1D) or with bark scales (e.g. *Platanus X hispanica*) the beetles are hidden under bark.

Small aggregations of beetles are found at hibernacula on trees (Fig. 1B to D). The largest group on the study limes at Utrecht E. on 2 December 1981 was of 59 individuals. Nearly 20% ( $n = 351$ ) of all beetles on that date were in groups of at least 15. However, about 10% ( $n = 196$ ) were isolated with no neighbour within 5 cm. Some observations made by C. Lane (Rothschild, 1962) on *A. bipunctata* hibernating indoors suggested that melanics might tend to aggregate together. Figure 3 shows that there is no evidence for such behaviour

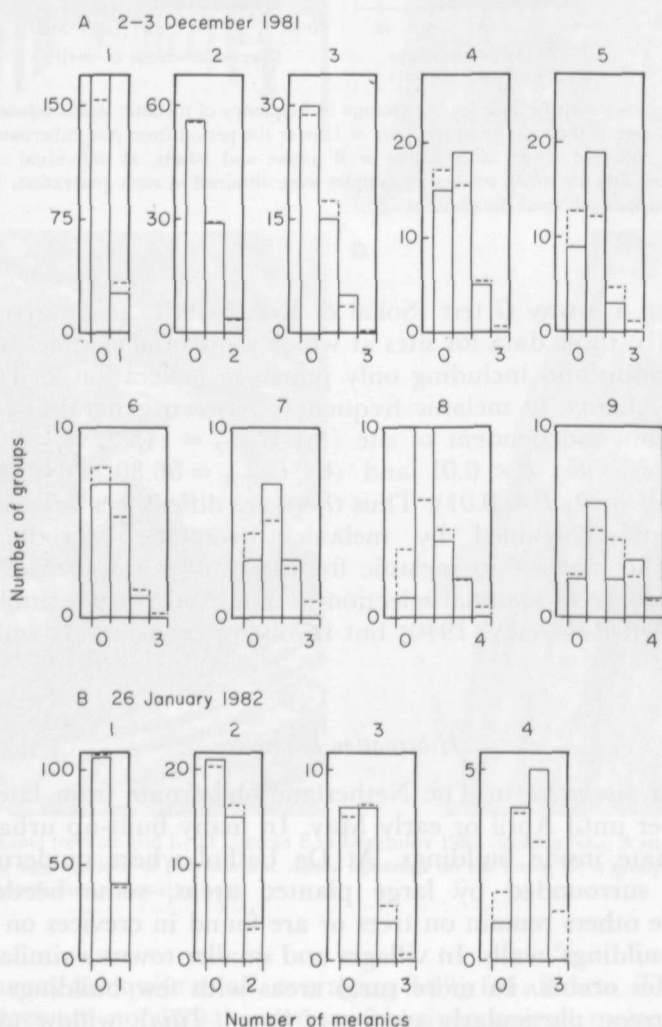


Figure 3. Comparison by group size of frequency distributions of aggregations of hibernating *Adalia bipunctata* with differing numbers of melanics. Group size is given above each histogram. Solid histograms show observed frequencies and broken ones expected frequencies calculated for single beetles from overall melanic frequency and for groups from a binomial distribution (where necessary expecteds are combined for higher numbers of melanics). Data are for grid L<sub>1</sub> of lime trees at Utrecht E. on the dates indicated for all group sizes with at least ten aggregations.

on the study limes since, for hibernating groups of the same size, the distribution of melanics between groups is random (for each comparison by chi-square,  $P > 0.05$ ).

The coccinellids *Adalia decempunctata* (L.), *Exochomus quadripustulatus* (L.) and *Synharmonia conglobata* (L.) were sometimes found within aggregations of *A. bipunctata*. *E. quadripustulatus* was abundant on ash trees at De Uithof.

The spring dispersal from hibernacula to areas of shrubs where feeding and reproduction begins (Brakefield, 1984a) takes place over several weeks. Observations on the decline in numbers of *A. bipunctata* (initial total = 634) at hibernacula on young trees and supporting stakes with ties were made at three sites (nos 12, 23 and 25) in April to May 1982. For example, at site 25 there were 121 beetles on 3 April (none on nearby shrubs), 61 on 23 April, 54 on 10 May and none on 13 May (many on shrubs). At each site most of the dispersal probably occurred during relatively warm spells before 23 April and 13 May. However, some factor other than temperature (e.g. photoperiod, see Hodek, 1973) appears to be involved in initiating dispersal since there was no emigration on warm days in late March. There was no evidence at any of the sites that the timing of dispersal differed between the morph classes (heterogeneity chi-square tests,  $P > 0.1$ ). Movement to hibernacula in the autumn was not closely monitored (one marked melanic released on lime trees at De Uithof on 15 September 1980 was found on a concrete wall about 75 m away on 8 April 1981, see Brakefield, 1984a).

#### *Selection during winter hibernation*

*Survivorship of a cohort:* Table 1 gives the frequency data for the three winter counts of *A. bipunctata* on the study limes at Utrecht E. There was a highly significant increase in the proportion of each melanic morph between early December and late January. During this period nearly 75% of all beetles died. The following period of similar length extending nearly to the commencement of dispersal from hibernacula was associated with much lower mortality (33%) and no further change in morph frequency.

The number of beetles per tree in December varied widely (range = 0–76, mean = 27.1) with an extremely clumped distribution ( $s^2/\bar{x} = 15.51$ ). Because of this variability and the presence of many trees with few or no beetles, the effects of selection are analysed further by dividing the linear grid of trees into eight

Table 1. Changes in the frequency of the non-melanic and melanic morphs of *Adalia bipunctata* in a hibernating cohort on grid L<sub>1</sub> of limes at Utrecht E

Date	Number of non-melanics	Number of melanics <sup>a</sup> quad.	semp.	Total (n)	% melanic	Chi-sq. (df = 2)
2–3 Dec. 1981	1581	224	93	1898	16.70	26.39***
26 Jan. 1982	362	89	42	493	26.57	2.60
1 April 1982	237	47	36	320	25.94	

<sup>a</sup>, quad. = *quadrimaculata*; semp. = *sempustulata*.

\*\*\* $P < 0.001$ .

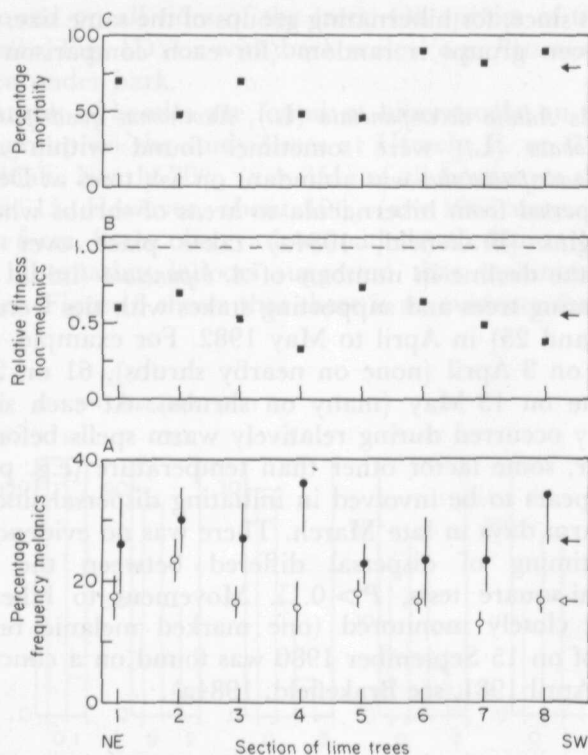


Figure 4. Analysis of counts of *Adalia bipunctata* made on 2-3 December 1981 (○) and on 26 January 1982 (●) in sections of grid  $L_1$  of lime trees at Utrecht E. A, frequency of melanics on each data; B, relative fitness of non-melanics (melanics = 1) over the study period; and C, percentage mortality over the study period. Vertical ranges show standard errors and arrows indicate mean values.

sections of roughly equal length and of six to ten trees. Figure 4 shows that the change in melanic frequency between early December and late January occurred in each of these sections. Application of a 3-way  $G$  test shows that this change was significant ( $G_8 = 23.17$ ,  $P < 0.01$ ) and independent of selection (3-way  $G_7 = 4.34$ ,  $P > 0.1$ ). The mean relative fitness ( $\pm$  S.E.) of non-melanics is  $0.554 \pm 0.052$  (melanics = 1) which is equal to the overall mean.

The mortality of *A. bipunctata* over the first period was considerably higher in three sections of trees at one end of the grid (overall  $\chi^2_1 = 141.1$ ). There is no evidence of a relationship between mortality and intensity of selection for the eight sections (Fig. 4;  $r = +0.28$ ,  $P > 0.1$ ). A comparison of melanic frequency between the two groups of sections with differing mortality showed no significant differences before or after selection ( $\chi^2_1 = 2.71$  and 0.01 respectively).

Although *A. bipunctata* is distasteful and warningly-coloured some predation by birds occurs (refs in Muggleton, 1978; Brakefield, 1984a). Furthermore, Betts (1955) showed by gut analysis that the closely related *A. decempunctata* can form a substantial component of the winter diet of great tits *Parus major* in oak woodland. Titmice and other insectivorous birds were present at Utrecht E. I have no direct data on the involvement of bird predators in the differential mortality in the hibernating cohort of *A. bipunctata*. However, there is no relationship between the number of beetles on a tree in early December and the



percentage mortality up to late January (minimum five beetles and arcsin transformation:  $b = -0.014$ ,  $F_{(1,61)} = 0.02$ ,  $P > 0.1$ ). This argues against a major rôle of predation by birds since they would be expected to act in a density-dependent manner. Thus, studies of predation by titmice have found strong spatially density-dependent mortality of overwintering larvae of the moths *Ernarmonia conicolana* in pine cones (Gibb, 1958), and *Cydia pomonella* under the bark of apple logs placed within trees (Solomon & Glen, 1979; and see other refs therein). The range in density and mortality in Solomon and Glen's experiments was similar to that at Utrecht E.

The presence of some dead *A. bipunctata* lodged in cavities on trees within the study area in late January was consistent with mortality associated with a climatic stress. The 59 dead beetles on the study limes represented less than 5% of those disappearing since early December. The total dead beetles ( $n = 185$ ) showed no difference in melanic frequency to the counts of all living beetles made in December or January ( $\chi^2_1 = 0.47$  and  $1.59$  respectively). A sample collected on 11 March 1982 inside a building at De Uithof similarly showed no differences between living and dead beetles ( $\chi^2_1 = 0.01$ , with  $n = 366$  and  $244$  respectively), although in this case there was also no evidence of a change in melanic frequency over the winter.

Lusis (1961) suggested that greater changes of body temperature in melanics than non-melanics, as recently demonstrated by Brakefield & Willmer (1984) for *A. bipunctata* under illumination, is involved in winter selection on the polymorphism. Differential activity is one expected consequence of the differing thermal properties. Some slow locomotory activity was observed on the study limes on sunny winter days. This will lead to turnover in the hibernating aggregation in addition to losses due to death. If differential activity occurs, changes in the distribution of melanics between aggregations of different sizes may be expected (for example, an accumulation of melanics as isolated individuals or within small groups). Figure 5 shows no indication of such changes. There is no significant heterogeneity in melanic frequency between the size classes shown in Fig. 5 (Dec.:  $\chi^2_{14} = 9.87$ ; Jan.:  $\chi^2_7 = 3.35$ ).

*Winter climate:* Some climatic data for the period of hibernation are summarized in Table 2 for De Bilt 4 km north-east of Utrecht E. Extreme cold conditions occurred in December 1981 and January 1982 with temperatures averaging up to 4°C below normal. Temperatures of below -12°C were recorded in each of these months. Continuous periods of days with a frost occurred from 7-28 December and 5-24 January. Thus the period of intense selection and high mortality of *A. bipunctata* at Utrecht E. coincided with a time of extreme cold. In other months, including February and March 1982, when no selection and lower mortality occurred, temperatures were similar to normal.

*Survivorship of laboratory cohorts:* Details of the conditions used in the laboratory experiments are given in Fig. 6. The three regimes represent one in which no beetle activity occurred (A), one in which periods of days with activity alternated with those without (B), and one with constantly high temperatures and high illumination during the hours of light (C). The survivorship curves of the cohorts of non-melanic and melanic *A. bipunctata* were closely similar in each regime (Fig. 6). Furthermore, the loss of body weight in cohorts A and B was

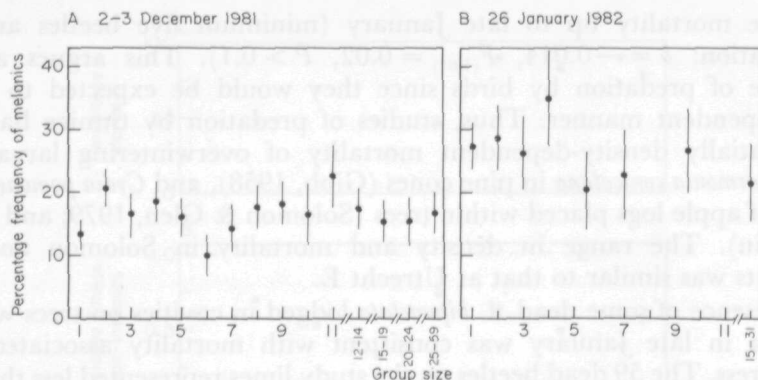


Figure 5. Frequency of melanic *Adalia bipunctata* in combined counts for hibernating aggregations of different sizes on grid  $L_1$  of lime trees at Utrecht E. on the dates indicated. Vertical ranges show standard errors.

similar for each morph class (see Fig. 6). Comparisons of the initial weights of beetles dying up to the last date when mortality was  $< 25\%$  (see Fig. 6) with those surviving, show that smaller beetles tend to die earlier (A:  $t_{183} = 8.46$ ; B:  $t_{182} = 6.88$ , with  $P < 0.001$ ). The percentage of initial weight lost over this period by surviving beetles decreases with size, although the relationship is only significant for cohort B (A:  $b = -0.439$ ,  $F_{1,139} = 4.02$ ,  $P \cong 0.1$ ; B:  $b = -0.445$ ,  $F_{1,149} = 7.30$ ,  $P < 0.05$ ). A general increase in mortality rate with higher temperatures is evident in Fig. 6.

*Survivorship in other natural cohorts:* The spatial variation in melanic frequency in late January on surrounding trees to the main grid of study limes ( $L_1$ ) at Utrecht E. is shown in Fig. 7. The three areas of limes have homogeneous frequencies ( $\chi^2_2 = 3.06$ , overall = 24.9% mel.). However, those for all the areas of trees are heterogeneous ( $\chi^2_9 = 22.84$ ,  $P < 0.01$ ). Examination of Fig. 7 suggests

Table 2. The winter climate at De Bilt. Mean monthly figures for daily maximum and minimum temperature and relative humidity are given for 1981–1982 together with differences to the 30-year means for 1951–1980 in parentheses. The number of days with maximum and minimum temperatures below  $0^\circ\text{C}$  are included

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Maximum $^\circ\text{C}$	11.9 (-2.4)	9.8 (+1.1)	1.7 (-4.0)	4.3 (-0.1)	6.1 (+0.7)	9.6 (+0.8)	12.6 (+0.1)
Minimum $^\circ\text{C}$	4.8 (-1.6)	3.2 (+0.3)	-3.4 (-3.9)	-2.4 (-1.7)	-0.5 (+0.2)	1.2 (+0.1)	2.6 (-0.7)
Days with max. $< 0^\circ\text{C}$	0 (0)	0 (-1)	10 (+7)	7 (+3)	1 (+3)	0 (-1)	0 (0)
Days with min. $< 0^\circ\text{C}$	2 (0)	8 (0)	23 (+10)	21 (+6)	16 (+1)	11 (-3)	3 (-2)
R.H. %	87 (+1)	85 (-3)	93 (+4)	87 (-2)	82 (-4)	80 (-1)	74 (-4)

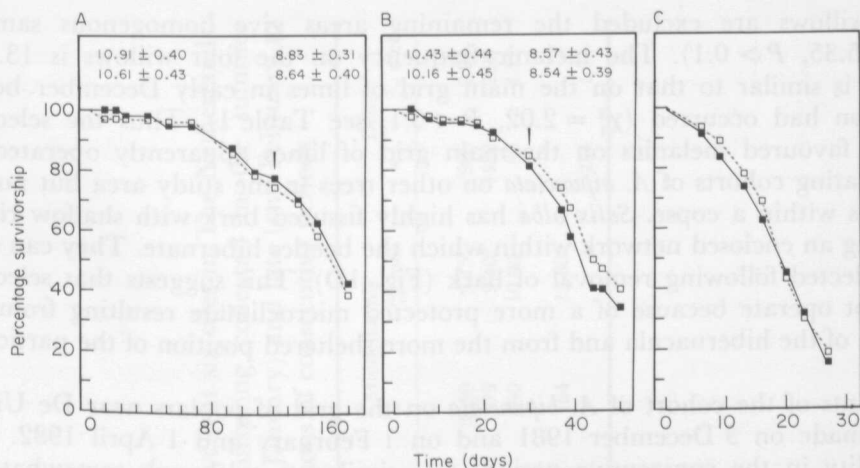


Figure 6. Survivorship of cohorts of non-melanic (□) and melanic (■) *Adalia bipunctata* in controlled environment rooms. A, 4°C with 12:12 h light:dark; B, 2 days at 18°C: 5 d at 4°C, 12 L: 12 D; C, 16 h L at 25°C and 60% R.H.: 8 h D at 16°C and 90% R.H. Initial fresh weights in mg (mean ± 95% C.L.) and those on the latest dates when mortality was < 25% (see arrows) are shown for non-melanics (above) and melanics in cohorts A and B. Note that the time axes are not directly comparable.

that there is a lower frequency on each of four large willows, *Salix alba*, within a copse of trees with few or no coccinellids. These four trees give homogeneous frequencies ( $\chi^2_3 = 0.14$ ), but the combined sample is different from those for all other areas ( $\chi^2_1 = 16.64$ ,  $P < 0.001$ ) and for the three other willows which are isolated and alongside a canal ( $\chi^2_1 = 11.69$ ,  $P < 0.001$ , see Fig. 7). When the

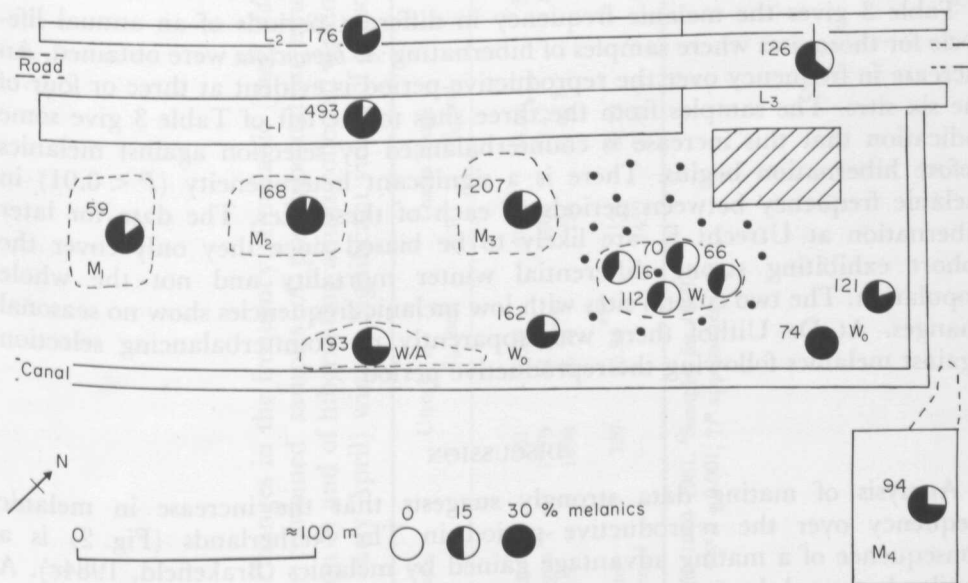


Figure 7. Sketch map of the study area at Utrecht E. showing the frequency of melanic *Adalia bipunctata* with sample sizes, for different habitats on 20–27 January 1982. L, grid of lime trees; M, group of mixed trees including ash and oak; W/A, group of willow and ash; W<sub>0</sub>, isolated willows and W<sub>1</sub>, four willows within other trees with no hibernacula (●).

four willows are excluded the remaining areas give homogenous samples ( $\chi^2_8 = 5.35$ ,  $P > 0.1$ ). The melanic frequency on the four willows is 13.3%, which is similar to that on the main grid of limes in early December before selection had occurred ( $\chi^2_1 = 2.02$ ,  $P < 0.1$ , see Table 1). Thus the selection which favoured melanics on the main grid of limes apparently operated on hibernating cohorts of *A. bipunctata* on other trees in the study area but not on willows within a copse. *Salix alba* has highly fissured bark with shallow ridges forming an enclosed network within which the beetles hibernate. They can only be collected following removal of bark (Fig. 1D). This suggests that selection did not operate because of a more protected microclimate resulting from the nature of the hibernacula and from the more sheltered position of the particular trees.

Counts of the cohort of *A. bipunctata* on the grid of poplars near De Uithof were made on 3 December 1981 and on 1 February and 1 April 1982. The mortality in the consecutive periods was similar to, although somewhat less intense than on, the study limes at Utrecht E. (49.5 and 22.1%). There was no heterogeneity in melanic frequency between counts ( $\chi^2_2 = 0.09$ ; with consecutive melanic frequencies of 24.27% ( $n = 206$ ), 25.00% (104) and 25.93% (81)). Thus although this cohort was hibernating in similarly exposed positions on trees close to the limes at the main study site, there is no corresponding differential mortality.

Table 3 includes some details of counts of *A. bipunctata* made on trees at Middelharnis and Oude-Tonge near the coast in early January and early April. At neither site was there a change in melanic frequency.

#### *Overall seasonal changes in melanic frequency*

Table 3 gives the melanic frequency in different periods of an annual life-cycle for those sites where samples of hibernating *A. bipunctata* were obtained. An increase in frequency over the reproductive period is evident at three or four of the six sites. The samples from the three sites to the left of Table 3 give some indication that this increase is counterbalanced by selection against melanics before hibernation begins. There is a significant heterogeneity ( $P < 0.01$ ) in melanic frequency between periods at each of these sites. The data for later hibernation at Utrecht E. are likely to be biased since they only cover the cohort exhibiting strong differential winter mortality and not the whole population. The two coastal sites with low melanic frequencies show no seasonal changes. At De Uithof there was apparently no counterbalancing selection against melanics following the reproductive period.

#### DISCUSSION

Analysis of mating data strongly suggests that the increase in melanic frequency over the reproductive period in The Netherlands (Fig. 2) is a consequence of a mating advantage gained by melanics (Brakefield, 1984c). A similar but much larger increase presumably occurs in Berlin to counterbalance the higher winter mortality of melanics (Timoféeff-Ressovsky, 1940 and see Lusi, 1961). There are apparently three annual generations in Berlin as against one or two in The Netherlands (Timoféeff-Ressovsky & Svirezhev, 1966;





Brakefield, 1984a). Samples collected at different times in the summer period of adult activity by other workers in various regions of Europe have provided little evidence of changes in melanic frequency (Meissner, 1907a, b, 1909, 1910; Creed, 1966, 1975; Lusi, 1973; Bengtson & Hagen, 1975; Honek, 1975; Muggleton, 1978; Zakharov & Sergievsky, 1980; Klausnitzer & Schummer, 1983). However, many samples are small and comparisons often involve single sampling occasions or grouped data for 'early' and 'late' periods which cover only part of the whole reproductive period. The occurrence of overlapping generations and of spatial and temporal heterogeneity in morph frequency within generations (Brakefield, 1984a, b) means that care is necessary in interpreting such data.

My observations in The Netherlands indicate a similar diversity of hibernation sites to those found in Britain (Benham & Muggleton, 1978). The aggregative behaviour is characteristic of the species (see Hodek, 1973).

This study shows that differences in survivorship between non-melanic and melanic *A. bipunctata* may occur in hibernating cohorts in The Netherlands, but that they are probably exceptional. The only cohorts which exhibited such a difference were associated with exposed hibernacula at a single study site and experienced particularly harsh climatic conditions. The subpopulation with differential mortality showed an increase in melanic frequency from about 17 to 27% over the mid-winter period of powerful selection and heavy mortality. This selective advantage contrasts with the intense winter selection against melanics in Berlin observed by Timoféeff-Ressovsky (1940). Some samples of hibernating *A. bipunctata* obtained by other workers have provided no examples of differential winter mortality (Zakharov & Sergievsky, 1980; see also Bengtson & Hagen, 1975; Honek, 1975). Thus, although differences in winter survivorship of the morphs may occur in some populations of *A. bipunctata*, there is no indication that they are a general phenomenon. Evidence of changes in the frequency of melanic forms during hibernation has been obtained in two other species of coccinellids (Tan, 1948; Parry & Peddie, 1981).

The winter climate in Berlin is usually colder than in The Netherlands (Table 4). However, the difference was considerably less during the mid-winter period of selection at Utrecht E. (cf. Table 2). Thus general differences in climate are unlikely to account for the difference in direction of selection at Utrecht E. and Berlin or for the absence of selection in other cohorts in The Netherlands.

Hibernating coccinellids, including *A. bipunctata*, characteristically have high levels of stored fat and glycogen, inactive ovaries and reduced respiration rates. They can have very low supercooling points which may change with time (see,

Table 4. Comparison of the mid-winter climates at De Bilt and Berlin. Figures are 30-year means for 1931–1960

	Maximum daily temperature (°C)			Minimum daily temperature (°C)			Relative humidity (%)		
	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.
De Bilt	5.4	4.3	5.3	0.6	−0.8	−0.8	88	86	83
Berlin	3.1	1.7	2.9	−1.4	−3.5	−3.1	88	84	82

e.g. Hariri, 1966; Hodek, 1973; Parry, 1980). Factors other than temperature and energy reserves are likely to influence overwintering survivorship in *A. bipunctata*. One such factor is moisture in the air, since insects freeze internally at higher temperatures when their surfaces are wet than when they are dry (Salt, 1936). The extreme period of cold in December 1981 in The Netherlands coincided with relative humidities which were higher than normal in the study area or Berlin (Tables 2 and 4). This may then have contributed to the climatic stress experienced by *A. bipunctata* at some exposed sites. Further laboratory experiments on winter survivorship using very low temperatures would be valuable. However, the significance of the results would be difficult to interpret without more understanding of the microclimates at hibernacula.

The data collected for some sites in The Netherlands (Table 3) suggest that the increase in melanic frequency over the reproductive period is counterbalanced by selection against melanics before hibernation commences. More data sets which include large samples taken in early hibernation are necessary to establish how general this pattern of selection is. Brakefield & Willmer (1984) found that the temperature excess over ambient air reached by larger melanic *A. bipunctata* under illumination similar to bright sunlight can be  $> 10^{\circ}\text{C}$  (compared to  $7^{\circ}\text{C}$  for non-melanics). Thus a possible causal mechanism for the selection against melanics is the occurrence of greater heat stress in conditions of prolonged sunshine and very high ambient temperatures. Unfortunately the late summer and early autumn period of the life-cycle is the least well understood (see Brakefield, 1984a). Field observations in The Netherlands suggest that the species becomes less active and more widely dispersed during this period. They may tend to aestivate in diapause (see Ipert, 1966).

The relevance of mathematical models of cyclical selection (e.g. Haldane & Jayakar, 1963; Hedrick, 1974; Hoekstra, 1975) to the dynamics of melanism in *A. bipunctata* in populations in The Netherlands is unclear, since a second annual generation probably does not always occur and, in such cases, the period of selection in opposing directions must operate within single generations (see Goux, 1978; Pasteur, 1977). In regions with more than one annual generation adults from each one probably overwinter and are subject to opposing selection pressures when these occur. The moderate nature of the selection coefficients involved in seasonal selection in The Netherlands (Fig. 2) and their variability between populations (see also Brakefield, 1984c) suggests that in any case they are unlikely to provide a unitary explanation for the polymorphism. Seasonal selection may, however, contribute in some regions to maintaining the polymorphism by interacting with other factors such as a balance between migration and selection or frequency-dependent effects introduced by forms of sexual selection or differential timing of reproduction (see Brakefield, 1984b; O'Donald *et al.*, 1984).

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## APPENDIX

Numbers of non-melanic (n-m) and melanic (mel) *Adalia bipunctata* in the combined samples for each generation in the summer period of reproductive activity for sites in The Netherlands. The twelve sites at which sequential samples were obtained in each generation are given above (see text for details)

no.	Site name	Year	Generation 1		Generation 2 pupae		Generation 2 adults		Overall % mel
			n-m	mel	n-m	mel	n-m	mel	
23	Middelharnis	1979	901	76	689	58	569	60	8.24
4	Delft	1980	879	27	1052	31	394	11	2.88
10	Utrecht C.	1980	902	223	1786	357	966	249	18.49
12	De Uithof	1980	1367	407	373	148	1814	727	26.51
23	Middelharnis	1980	3316	334	521	47	366	45	9.20
28	Willemstad	1980	823	605	566	446	434	398	44.28
32	Zevenbergen W.	1980	1265	1028	249	266	1619	1603	48.04
33	Zevenbergen E.	1980	502	454	418	450	514	696	52.74
38	Tilburg	1980	1184	1522	385	553	461	736	58.07
25	Oude-Tonge	1981	2609	824	1727	722	109	45	26.36
32	Zevenbergen W.	1981	1821	1516	461	474	31	35	46.68
33	Zevenbergen E.	1981	169	187	297	310	45	57	52.02
4	Delft	1978	229	3	60	2	26	1	1.87
10	Utrecht C.	1978	191	38	1469	287	470	77	15.88
4	Delft	1979	61	1	215	8	53	4	3.80
7	Harmelen	1979	47	9	118	26	—	—	17.50
10	Utrecht C.	1979	245	62	377	89	106	32	20.09
64	Zierekzee	1979	217	32	78	14	—	—	13.49
25	Oude-Tonge	1980	326	68	1133	503	3750	1483	28.28
31	Oudenbosch	1980	770	798	38	46	121	133	51.26
52	Antwerp	1980	257	225	383	380	432	506	50.89
10	Utrecht C.	1981	109	25	4472	1048	—	—	18.98
11	Utrecht E.	1981	219	42	1007	272	—	—	20.39
12	De Uithof	1981	261	64	2125	724	—	—	24.83
28	Willemstad	1981	230	156	787	719	130	81	45.46
38	Tilburg	1981	984	1137	45	56	8	12	53.75

# Differential winter mortality and seasonal selection in the polymorphic ladybird *Adalia bipunctata* (L) in the Netherlands

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Seasonal selection acting on the melanic polymorphism in the two-spot ladybird *Adalia bipunctata* was investigated in The Netherlands. An increase in melanic frequency over the spring–summer reproductive period was quantified. The selective advantage gained by melanics averaged 9%, but significant heterogeneity occurred between populations. Adult hibernation behaviour is described. The beetles when outdoors show a highly clumped distribution both between and within trees. The distribution of the morph classes between aggregations is random. Survivorship in a hibernating cohort (initial  $n = 1898$ ) on a grid of 70 lime trees near Utrecht was monitored by making three counts over the winter of 1981–1982. Intense selection favouring each melanic morph occurred during December and January. The relative fitness of non-melanics was 0.55 (melanics = 1). The discovery of dead beetles in late January (about 5% of total losses) and the absence of spatially density-dependent mortality were consistent with a climatic stress rather than selective predation. The period of selection was associated with very cold temperatures averaging up to 4°C below normal and an overall mortality of nearly 75%. There was no change in morph frequency, near normal temperatures and a lower mortality from February to early April. Examination of groups of nearby trees in late January strongly suggested that similar differential mortality had occurred except on some willows. This difference was probably due to the more protected hibernation sites available on these trees. Samples of hibernating cohorts at three other sites showed no evidence of differential mortality. Laboratory experiments with hibernating beetles found no difference in survivorship or rate of weight loss between starved non-melanics and melanics in temperature regimes with and without periods of adult activity. It is concluded that the intense winter selection on the study limes is probably exceptional. Examination of changes in morph frequency through the annual cycle suggests that at some sites the selection favouring melanics during reproduction is counterbalanced by selection against melanics in late summer or early autumn. The results are discussed in relation to mathematical models of cyclical selection and to other field studies including that of Timofëeff-Ressovsky (1940), who found large decreases in melanic frequency during hibernation in Berlin.

KEY WORDS:—Coccinellidae – *Adalia bipunctata* – melanism – polymorphism – seasonal selection – cyclical selection – reproduction – selective advantage – hibernation – differential mortality.

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## INTRODUCTION

Timoféeff-Ressovsky (1940) found that the frequency of the melanic forms of the two-spot ladybird *Adalia bipunctata* declined substantially over the period of winter hibernation in Berlin (see also Timoféeff-Ressovsky & Svirezhev, 1966). His study provides one of the most striking examples of the operation of seasonal selection. Such cyclical patterns of selection are of considerable interest because theoretical work has shown that they can maintain polymorphism or at least delay the time to fixation (e.g. Haldane & Jayakar, 1963; Hedrick, 1974; Hoekstra, 1975). However, the conditions necessary for protected polymorphism are usually very restricted but are much less so when gene frequencies are intermediate and selection coefficients large. These conditions prevailed in the population studied by Timoféeff-Ressovsky.

The polymorphism in *A. bipunctata* is controlled by a number of alleles at a single gene locus with melanics dominant to non-melanics (Lus, 1928, 1932). Timoféeff-Ressovsky (1940) sampled a population at the beginning and end of the winter at hibernacula in crevices between the stone blocks of a ruined church. He obtained large samples in each of the 12 consecutive years, 1929–1940, with a single gap in spring, 1932. The consistent decrease in melanic frequency during hibernation averaged about 20%. In each of three years Timoféeff-Ressovsky collected all the *A. bipunctata* from an area of wall prior to the end of hibernation. Comparison of living and dead beetles demonstrated that the change in melanic frequency was due to differential mortality. Some other workers have obtained considerably fewer data for hibernating populations of *A. bipunctata*, which have not indicated a difference in winter survivorship between the morph classes (Bengtson & Hagen, 1975; Honek, 1975; Zakharov & Sergievsky, 1980).

My study of *A. bipunctata* in The Netherlands was designed to examine the dynamics of the polymorphism in more detail than previous workers (Brakefield, 1984a, b, c). Comparisons of mating and non-mating *A. bipunctata* at sites along clines have shown that melanics gain a mating advantage in post-hibernation populations (Brakefield, 1984c). Analysis of frequency data for sites where large numbers of mating animals were found strongly suggested that this mating advantage resulted in an increase in melanic frequency in the next generation. More extensive data sets are analysed in this study which confirm that such an increase occurs over the reproductive period in The Netherlands. The survivorship of cohorts of hibernating *A. bipunctata* is then examined to determine whether differential winter mortality counterbalances this increase. Finally, the changes in melanic frequency which occur through the whole annual cycle of the species are followed.

## MATERIALS AND METHODS

*Sampling in the summer*

The study sites were on four transects which traversed an area between a region of low, and one of high melanic frequency. Details of the sites, methods of sampling, geographical variation of melanism and population biology are given in Brakefield (1984a, b). Sequences of samples from each summer generation were obtained from a number of sites with differing frequencies. Their analysis examines the combined data for the two melanic morphs, *quadrimaculata* and *sexpustulata*, and those for the non-melanic *typica*.

*Sampling in the winter*

The main study site for hibernating *A. bipunctata* was Utrecht E. (site 11, Brakefield, 1984a) in the central region of The Netherlands. This is a recreation area of roads, grass and planted trees just outside the city boundary. In the winter of 1981–1982 three separate counts of hibernating beetles were made on grid L<sub>1</sub> of 70 lime trees (*Tilia* sp.) planted in two, or sometimes three, rows (Fig. 1A). The trees were about 40 years old. Since beetles were rarely completely hidden (Fig. 1B & C) a thorough search of the bole and main branches of each tree revealed most, if not all, of them. The beetles were not disturbed. During the mid-winter visit collections of all beetles were made from surrounding groups of trees.

A similar series of counts were made of a smaller cohort on a grid of 48 poplar trees (*Populus abeele*) at the nearby site of De Uithof (no. 12). Some samples of hibernating beetles were collected from an eight-storey building and surrounding walls and trees at this site.

*Laboratory studies of survivorship*

Some hibernating *A. bipunctata* were used to investigate survivorship of the morph classes in the laboratory. Beetles were assigned at random to cohorts of at least 90 individuals of each morph class. They were weighed and placed in stoppered 9 ml glass vials. Survivorship and loss of weight (in two cohorts) were then examined at regular intervals. Cohorts of each morph class were kept without feeding in three controlled environment rooms.

## RESULTS

*Selection during summer reproduction*

The combined frequency data for 26 post-hibernation adult populations and for their offspring collected as pupae or adults are given in the Appendix. In some years and at some sites the later samples include members of a second summer generation (Brakefield, 1984a). Some of the samples of adults collected after emergence from pupae began, included surviving adults of the parental generation. This source of error is excluded when the 'second' generation samples are made up of pupae only. Figure 2 shows that there is a trend of increasing melanic frequency over the reproductive period. The changes in



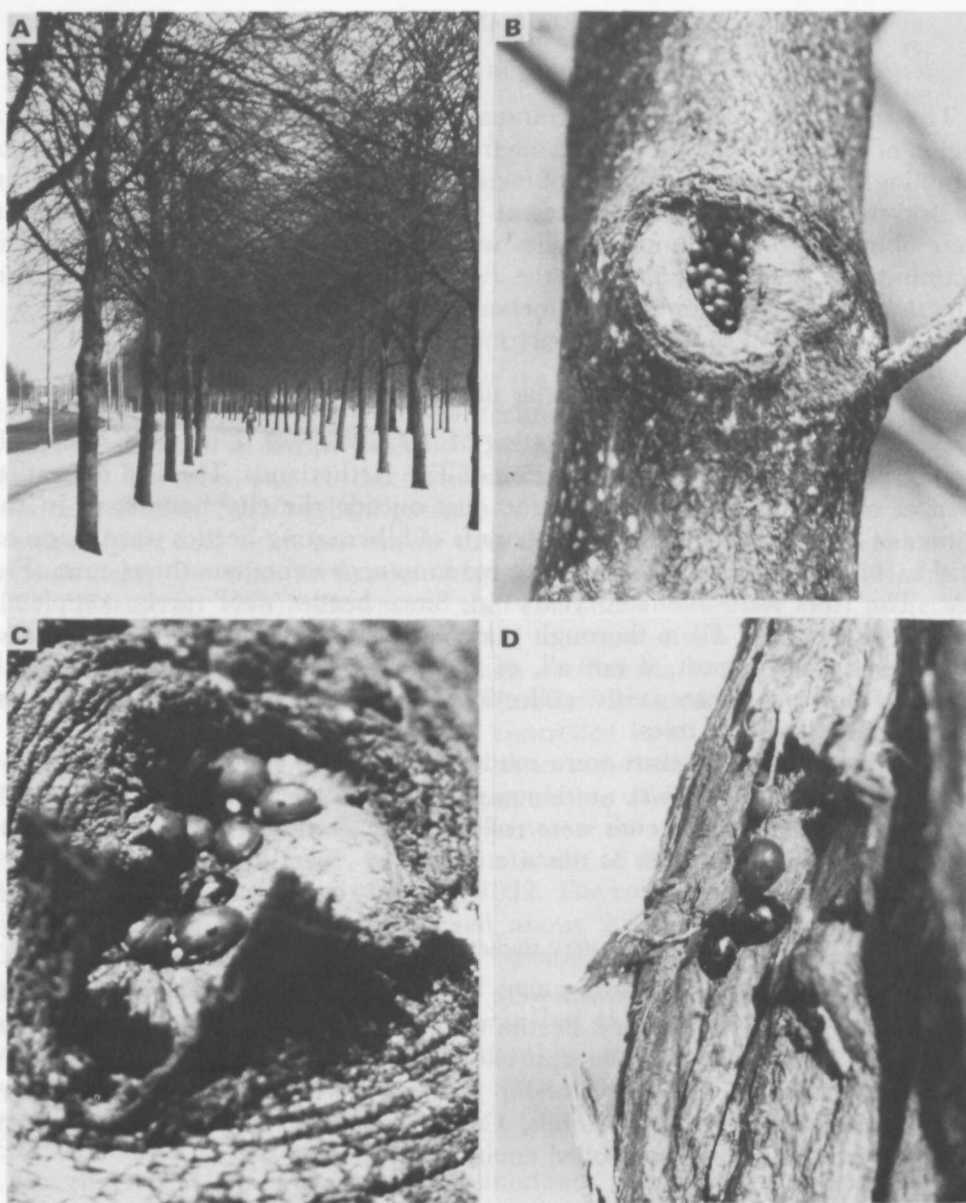


Figure 1. A, Lime trees on grid L, at Utrecht E in December 1981 (looking NE); B and C, examples of hibernating aggregations of polymorphic *Adalia bipunctata* on the limes; D, a group of beetles on *Salix alba* exposed after removal of bark.

melanic frequency are quite small, averaging 3.2% for all data. The magnitudes of these changes are not strictly comparable since overall melanic frequencies ranged from 3 to 58% (see Appendix). Figure 2 includes frequency distributions of estimates of the selective advantage gained by melanics over the reproductive period. For all data this advantage averages 9%.

The data presented in Fig. 2 involve the factors: site (*S*), generation (*G*) and frequency (*F*). The statistical significance of the changes in melanic frequency is

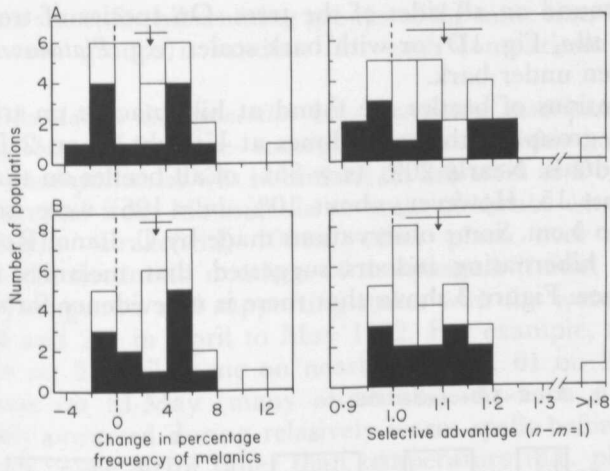


Figure 2. Frequency distributions for the change in frequency of melanic *Adalia bipunctata*, and the selective advantage of melanics (non-melanics = 1) over the period from post-hibernation adults to their progeny collected either as A pupae or B pupae and adults, at individual sites. Shaded histograms show sites for which sequential samples were obtained in each generation. Mean  $\pm$  95% C.L. are shown for each total distribution.

examined using a 3-way  $G$  test (Sokal & Rohlf, 1981) to analyse: (a) the full data set; and (b) those data for sites at which sequential samples were obtained in each generation and including only pupae in generation 2. These analyses show that the change in melanic frequency between generations is significant but that it is not independent of site ((a)  $G_{(S)GF} = 145.2$ ,  $df = 26$ ,  $P < 0.001$ ;  $G_{SGF} = 47.21$ ,  $df = 25$ ,  $P < 0.01$  and (b)  $G_{(S)GF} = 56.30$ ,  $df = 12$ ,  $P < 0.001$ ;  $G_{SGF} = 30.40$ ,  $df = 11$ ,  $P < 0.01$ ). Thus there are differences between sites in the selective advantage gained by melanics over the reproductive period. Nevertheless, the increase in melanic frequency over this period is consistent with the occurrence of seasonal selection in The Netherlands similar to that in Berlin (Timoféeff-Ressovsky, 1940) but involving considerably smaller changes in frequency.

### Hibernation behaviour

Adult *Adalia bipunctata* in The Netherlands hibernate from late October or early November until April or early May. In many built-up urban areas they usually hibernate inside buildings. At De Uithof where modern multistorey buildings are surrounded by large planted areas, some beetles enter the buildings while others remain on trees or are found in crevices on the concrete blocks of the buildings' walls. In villages and smaller towns a similar diversity of hibernation sites occurs. In more rural areas with few buildings most beetles hibernate on trees; particularly species of lime (*Tilia*), willow (*Salix*), poplar (*Populus*) and plane (*Platanus*), but also others including hawthorn (*Crataegus*), ash (*Fraxinus*) and oak (*Quercus*).

*Adalia bipunctata* hibernating on young lime trees (Fig. 1A) are usually more or less exposed in small crevices or cavities on the bole or beneath large branches (Fig. 1B and C). They are found from about 60 cm up to several

metres above ground on all sides of the trees. On species of tree with fissured bark (e.g. *Salix alba*, Fig. 1D) or with bark scales (e.g. *Platanus X hispanica*) the beetles are hidden under bark.

Small aggregations of beetles are found at hibernacula on trees (Fig. 1B to D). The largest group on the study limes at Utrecht E. on 2 December 1981 was of 59 individuals. Nearly 20% ( $n = 351$ ) of all beetles on that date were in groups of at least 15. However, about 10% ( $n = 196$ ) were isolated with no neighbour within 5 cm. Some observations made by C. Lane (Rothschild, 1962) on *A. bipunctata* hibernating indoors suggested that melanics might tend to aggregate together. Figure 3 shows that there is no evidence for such behaviour

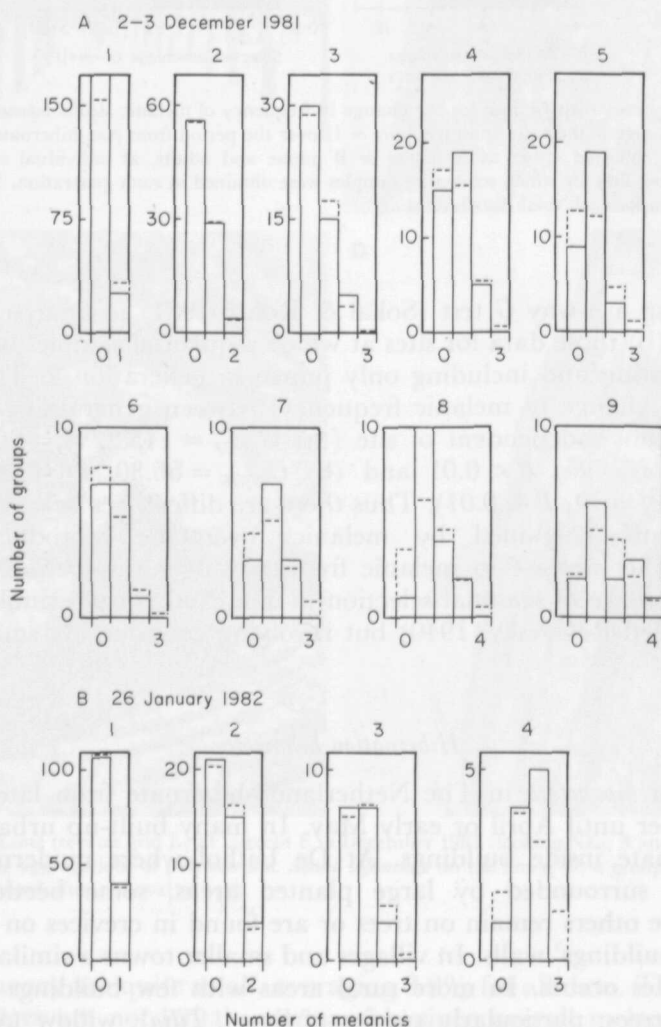


Figure 3. Comparison by group size of frequency distributions of aggregations of hibernating *Adalia bipunctata* with differing numbers of melanics. Group size is given above each histogram. Solid histograms show observed frequencies and broken ones expected frequencies calculated for single beetles from overall melanic frequency and for groups from a binomial distribution (where necessary expecteds are combined for higher numbers of melanics). Data are for grid L<sub>1</sub> of lime trees at Utrecht E. on the dates indicated for all group sizes with at least ten aggregations.



on the study limes since, for hibernating groups of the same size, the distribution of melanics between groups is random (for each comparison by chi-square,  $P > 0.05$ ).

The coccinellids *Adalia decempunctata* (L.), *Exochomus quadripustulatus* (L.) and *Synharmonia conglobata* (L.) were sometimes found within aggregations of *A. bipunctata*. *E. quadripustulatus* was abundant on ash trees at De Uithof.

The spring dispersal from hibernacula to areas of shrubs where feeding and reproduction begins (Brakefield, 1984a) takes place over several weeks. Observations on the decline in numbers of *A. bipunctata* (initial total = 634) at hibernacula on young trees and supporting stakes with ties were made at three sites (nos 12, 23 and 25) in April to May 1982. For example, at site 25 there were 121 beetles on 3 April (none on nearby shrubs), 61 on 23 April, 54 on 10 May and none on 13 May (many on shrubs). At each site most of the dispersal probably occurred during relatively warm spells before 23 April and 13 May. However, some factor other than temperature (e.g. photoperiod, see Hodek, 1973) appears to be involved in initiating dispersal since there was no emigration on warm days in late March. There was no evidence at any of the sites that the timing of dispersal differed between the morph classes (heterogeneity chi-square tests,  $P > 0.1$ ). Movement to hibernacula in the autumn was not closely monitored (one marked melanic released on lime trees at De Uithof on 15 September 1980 was found on a concrete wall about 75 m away on 8 April 1981, see Brakefield, 1984a).

#### *Selection during winter hibernation*

*Survivorship of a cohort:* Table 1 gives the frequency data for the three winter counts of *A. bipunctata* on the study limes at Utrecht E. There was a highly significant increase in the proportion of each melanic morph between early December and late January. During this period nearly 75% of all beetles died. The following period of similar length extending nearly to the commencement of dispersal from hibernacula was associated with much lower mortality (33%) and no further change in morph frequency.

The number of beetles per tree in December varied widely (range = 0–76, mean = 27.1) with an extremely clumped distribution ( $s^2/\bar{x} = 15.51$ ). Because of this variability and the presence of many trees with few or no beetles, the effects of selection are analysed further by dividing the linear grid of trees into eight

Table 1. Changes in the frequency of the non-melanic and melanic morphs of *Adalia bipunctata* in a hibernating cohort on grid L<sub>1</sub> of limes at Utrecht E

Date	Number of non-melanics	Number of melanics <sup>a</sup> quad.	semp.	Total (n)	% melanic	Chi-sq. (df = 2)
2–3 Dec. 1981	1581	224	93	1898	16.70	26.39***
26 Jan. 1982	362	89	42	493	26.57	2.60
1 April 1982	237	47	36	320	25.94	

<sup>a</sup>, quad. = *quadrimaculata*; semp. = *sempustulata*.

\*\*\* $P < 0.001$ .

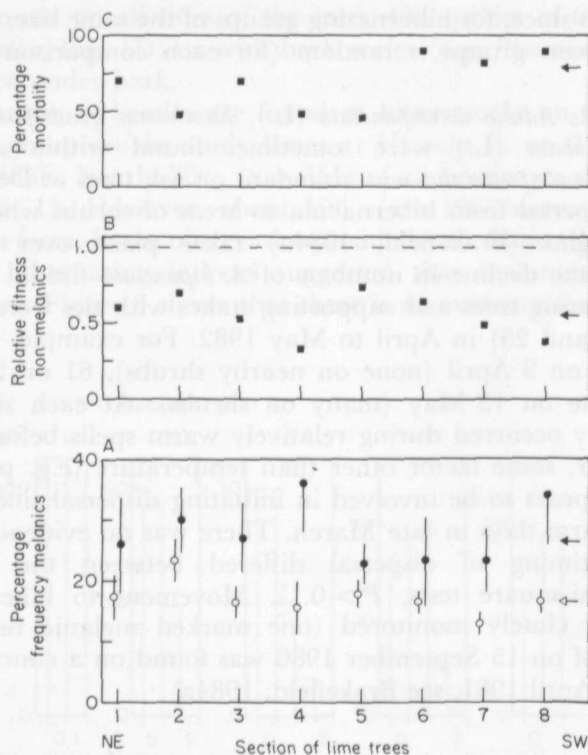


Figure 4. Analysis of counts of *Adalia bipunctata* made on 2-3 December 1981 (○) and on 26 January 1982 (●) in sections of grid  $L_1$  of lime trees at Utrecht E. A, frequency of melanics on each data; B, relative fitness of non-melanics (melanics = 1) over the study period; and C, percentage mortality over the study period. Vertical ranges show standard errors and arrows indicate mean values.

sections of roughly equal length and of six to ten trees. Figure 4 shows that the change in melanic frequency between early December and late January occurred in each of these sections. Application of a 3-way  $G$  test shows that this change was significant ( $G_8 = 23.17$ ,  $P < 0.01$ ) and independent of selection (3-way  $G_7 = 4.34$ ,  $P > 0.1$ ). The mean relative fitness ( $\pm$  S.E.) of non-melanics is  $0.554 \pm 0.052$  (melanics = 1) which is equal to the overall mean.

The mortality of *A. bipunctata* over the first period was considerably higher in three sections of trees at one end of the grid (overall  $\chi^2_1 = 141.1$ ). There is no evidence of a relationship between mortality and intensity of selection for the eight sections (Fig. 4;  $r = +0.28$ ,  $P > 0.1$ ). A comparison of melanic frequency between the two groups of sections with differing mortality showed no significant differences before or after selection ( $\chi^2_1 = 2.71$  and  $0.01$  respectively).

Although *A. bipunctata* is distasteful and warningly-coloured some predation by birds occurs (refs in Muggleton, 1978; Brakefield, 1984a). Furthermore, Betts (1955) showed by gut analysis that the closely related *A. decempunctata* can form a substantial component of the winter diet of great tits *Parus major* in oak woodland. Titmice and other insectivorous birds were present at Utrecht E. I have no direct data on the involvement of bird predators in the differential mortality in the hibernating cohort of *A. bipunctata*. However, there is no relationship between the number of beetles on a tree in early December and the

percentage mortality up to late January (minimum five beetles and arcsin transformation:  $b = -0.014$ ,  $F_{(1,61)} = 0.02$ ,  $P > 0.1$ ). This argues against a major rôle of predation by birds since they would be expected to act in a density-dependent manner. Thus, studies of predation by titmice have found strong spatially density-dependent mortality of overwintering larvae of the moths *Ernarmonia conicolana* in pine cones (Gibb, 1958), and *Cydia pomonella* under the bark of apple logs placed within trees (Solomon & Glen, 1979; and see other refs therein). The range in density and mortality in Solomon and Glen's experiments was similar to that at Utrecht E.

The presence of some dead *A. bipunctata* lodged in cavities on trees within the study area in late January was consistent with mortality associated with a climatic stress. The 59 dead beetles on the study limes represented less than 5% of those disappearing since early December. The total dead beetles ( $n = 185$ ) showed no difference in melanic frequency to the counts of all living beetles made in December or January ( $\chi^2_1 = 0.47$  and 1.59 respectively). A sample collected on 11 March 1982 inside a building at De Uithof similarly showed no differences between living and dead beetles ( $\chi^2_1 = 0.01$ , with  $n = 366$  and 244 respectively), although in this case there was also no evidence of a change in melanic frequency over the winter.

Lusis (1961) suggested that greater changes of body temperature in melanics than non-melanics, as recently demonstrated by Brakefield & Willmer (1984) for *A. bipunctata* under illumination, is involved in winter selection on the polymorphism. Differential activity is one expected consequence of the differing thermal properties. Some slow locomotory activity was observed on the study limes on sunny winter days. This will lead to turnover in the hibernating aggregation in addition to losses due to death. If differential activity occurs, changes in the distribution of melanics between aggregations of different sizes may be expected (for example, an accumulation of melanics as isolated individuals or within small groups). Figure 5 shows no indication of such changes. There is no significant heterogeneity in melanic frequency between the size classes shown in Fig. 5 (Dec.:  $\chi^2_{14} = 9.87$ ; Jan.:  $\chi^2_7 = 3.35$ ).

*Winter climate:* Some climatic data for the period of hibernation are summarized in Table 2 for De Bilt 4 km north-east of Utrecht E. Extreme cold conditions occurred in December 1981 and January 1982 with temperatures averaging up to 4°C below normal. Temperatures of below -12°C were recorded in each of these months. Continuous periods of days with a frost occurred from 7-28 December and 5-24 January. Thus the period of intense selection and high mortality of *A. bipunctata* at Utrecht E. coincided with a time of extreme cold. In other months, including February and March 1982, when no selection and lower mortality occurred, temperatures were similar to normal.

*Survivorship of laboratory cohorts:* Details of the conditions used in the laboratory experiments are given in Fig. 6. The three regimes represent one in which no beetle activity occurred (A), one in which periods of days with activity alternated with those without (B), and one with constantly high temperatures and high illumination during the hours of light (C). The survivorship curves of the cohorts of non-melanic and melanic *A. bipunctata* were closely similar in each regime (Fig. 6). Furthermore, the loss of body weight in cohorts A and B was

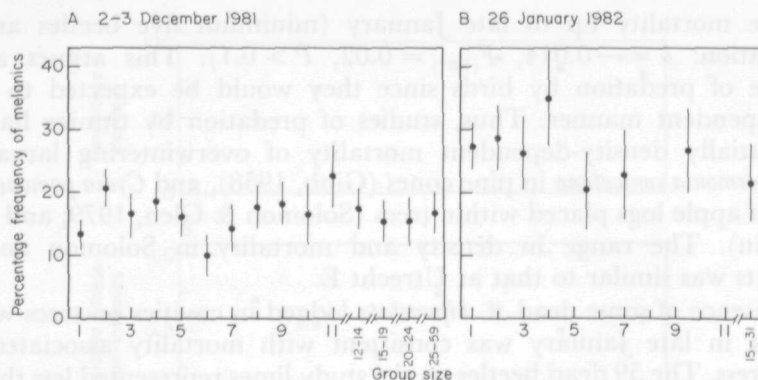


Figure 5. Frequency of melanic *Adalia bipunctata* in combined counts for hibernating aggregations of different sizes on grid  $L_1$  of lime trees at Utrecht E. on the dates indicated. Vertical ranges show standard errors.

similar for each morph class (see Fig. 6). Comparisons of the initial weights of beetles dying up to the last date when mortality was  $< 25\%$  (see Fig. 6) with those surviving, show that smaller beetles tend to die earlier (A:  $t_{183} = 8.46$ ; B:  $t_{182} = 6.88$ , with  $P < 0.001$ ). The percentage of initial weight lost over this period by surviving beetles decreases with size, although the relationship is only significant for cohort B (A:  $b = -0.439$ ,  $F_{1,139} = 4.02$ ,  $P \cong 0.1$ ; B:  $b = -0.445$ ,  $F_{1,149} = 7.30$ ,  $P < 0.05$ ). A general increase in mortality rate with higher temperatures is evident in Fig. 6.

*Survivorship in other natural cohorts:* The spatial variation in melanic frequency in late January on surrounding trees to the main grid of study limes ( $L_1$ ) at Utrecht E. is shown in Fig. 7. The three areas of limes have homogeneous frequencies ( $\chi^2_2 = 3.06$ , overall =  $24.9\%$  mel.). However, those for all the areas of trees are heterogeneous ( $\chi^2_9 = 22.84$ ,  $P < 0.01$ ). Examination of Fig. 7 suggests

Table 2. The winter climate at De Bilt. Mean monthly figures for daily maximum and minimum temperature and relative humidity are given for 1981-1982 together with differences to the 30-year means for 1951-1980 in parentheses. The number of days with maximum and minimum temperatures below  $0^\circ\text{C}$  are included

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Maximum $^\circ\text{C}$	11.9 (-2.4)	9.8 (+1.1)	1.7 (-4.0)	4.3 (-0.1)	6.1 (+0.7)	9.6 (+0.8)	12.6 (+0.1)
Minimum $^\circ\text{C}$	4.8 (-1.6)	3.2 (+0.3)	-3.4 (-3.9)	-2.4 (-1.7)	-0.5 (+0.2)	1.2 (+0.1)	2.6 (-0.7)
Days with max. $< 0^\circ\text{C}$	0 (0)	0 (-1)	10 (+7)	7 (+3)	1 (+3)	0 (-1)	0 (0)
Days with min. $< 0^\circ\text{C}$	2 (0)	8 (0)	23 (+10)	21 (+6)	16 (+1)	11 (-3)	3 (-2)
R.H. %	87 (+1)	85 (-3)	93 (+4)	87 (-2)	82 (-4)	80 (-1)	74 (-4)

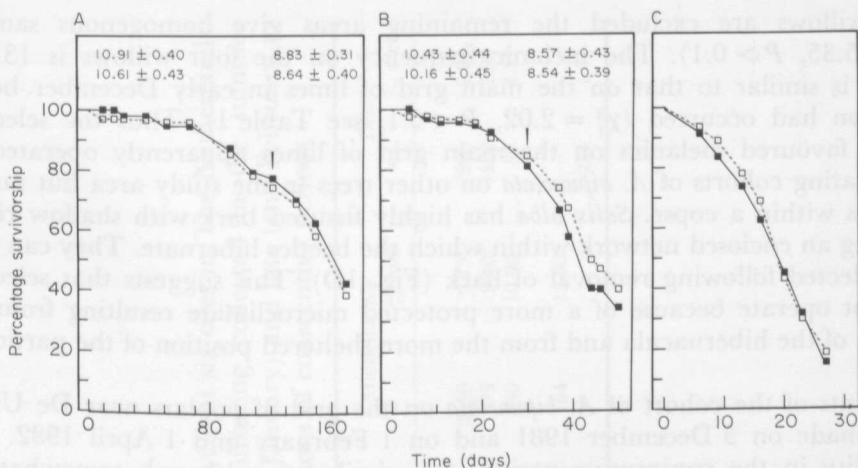


Figure 6. Survivorship of cohorts of non-melanic (□) and melanic (■) *Adalia bipunctata* in controlled environment rooms. A, 4°C with 12:12 h light: dark; B, 2 days at 18°C: 5 d at 4°C, 12 L: 12 D; C, 16 h L at 25°C and 60% R.H.: 8 h D at 16°C and 90% R.H. Initial fresh weights in mg (mean ± 95% C.L.) and those on the latest dates when mortality was < 25% (see arrows) are shown for non-melanics (above) and melanics in cohorts A and B. Note that the time axes are not directly comparable.

that there is a lower frequency on each of four large willows, *Salix alba*, within a copse of trees with few or no coccinellids. These four trees give homogeneous frequencies ( $\chi^2_3 = 0.14$ ), but the combined sample is different from those for all other areas ( $\chi^2_1 = 16.64$ ,  $P < 0.001$ ) and for the three other willows which are isolated and alongside a canal ( $\chi^2_1 = 11.69$ ,  $P < 0.001$ , see Fig. 7). When the

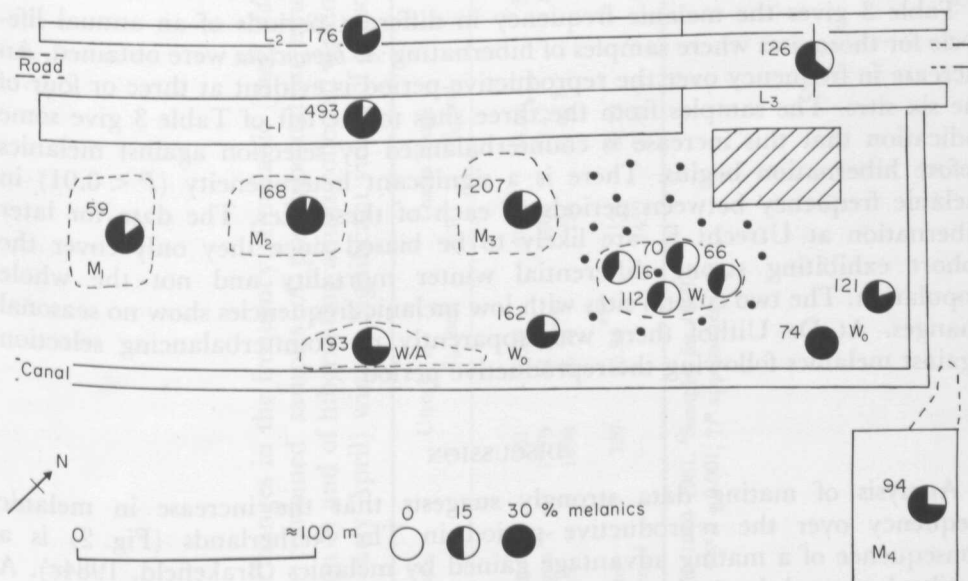


Figure 7. Sketch map of the study area at Utrecht E. showing the frequency of melanic *Adalia bipunctata* with sample sizes, for different habitats on 20–27 January 1982. L, grid of lime trees; M, group of mixed trees including ash and oak; W/A, group of willow and ash; W<sub>0</sub>, isolated willows and W<sub>1</sub>, four willows within other trees with no hibernacula (●).



four willows are excluded the remaining areas give homogenous samples ( $\chi^2_8 = 5.35$ ,  $P > 0.1$ ). The melanic frequency on the four willows is 13.3%, which is similar to that on the main grid of limes in early December before selection had occurred ( $\chi^2_1 = 2.02$ ,  $P < 0.1$ , see Table 1). Thus the selection which favoured melanics on the main grid of limes apparently operated on hibernating cohorts of *A. bipunctata* on other trees in the study area but not on willows within a copse. *Salix alba* has highly fissured bark with shallow ridges forming an enclosed network within which the beetles hibernate. They can only be collected following removal of bark (Fig. 1D). This suggests that selection did not operate because of a more protected microclimate resulting from the nature of the hibernacula and from the more sheltered position of the particular trees.

Counts of the cohort of *A. bipunctata* on the grid of poplars near De Uithof were made on 3 December 1981 and on 1 February and 1 April 1982. The mortality in the consecutive periods was similar to, although somewhat less intense than on, the study limes at Utrecht E. (49.5 and 22.1%). There was no heterogeneity in melanic frequency between counts ( $\chi^2_2 = 0.09$ ; with consecutive melanic frequencies of 24.27% ( $n = 206$ ), 25.00% (104) and 25.93% (81)). Thus although this cohort was hibernating in similarly exposed positions on trees close to the limes at the main study site, there is no corresponding differential mortality.

Table 3 includes some details of counts of *A. bipunctata* made on trees at Middelharnis and Oude-Tonge near the coast in early January and early April. At neither site was there a change in melanic frequency.

#### *Overall seasonal changes in melanic frequency*

Table 3 gives the melanic frequency in different periods of an annual life-cycle for those sites where samples of hibernating *A. bipunctata* were obtained. An increase in frequency over the reproductive period is evident at three or four of the six sites. The samples from the three sites to the left of Table 3 give some indication that this increase is counterbalanced by selection against melanics before hibernation begins. There is a significant heterogeneity ( $P < 0.01$ ) in melanic frequency between periods at each of these sites. The data for later hibernation at Utrecht E. are likely to be biased since they only cover the cohort exhibiting strong differential winter mortality and not the whole population. The two coastal sites with low melanic frequencies show no seasonal changes. At De Uithof there was apparently no counterbalancing selection against melanics following the reproductive period.

#### DISCUSSION

Analysis of mating data strongly suggests that the increase in melanic frequency over the reproductive period in The Netherlands (Fig. 2) is a consequence of a mating advantage gained by melanics (Brakefield, 1984c). A similar but much larger increase presumably occurs in Berlin to counterbalance the higher winter mortality of melanics (Timoféeff-Ressovsky, 1940 and see Lusi, 1961). There are apparently three annual generations in Berlin as against one or two in The Netherlands (Timoféeff-Ressovsky & Svirezhev, 1966;

Table 3. Changes in the frequency of melanic (mel) *Adalia bipunctata* over the annual cycle at six sites in The Netherlands. Data are combined samples of post-hibernation adults (generation 1) and their offspring collected in the summer (generation 2) and of hibernating adults collected outdoors in mid- (December to early January) and late (end February to early April) winter. Significant values of chi-square are indicated for comparisons of consecutive periods

Period	Utrecht E.		Oude-Tonge		Zevenbergen W.		De Uithof		Middelharnis		Delft <sup>a</sup>	
	<i>n</i>	% mel	<i>n</i>	% mel	<i>n</i>	% mel	<i>n</i>	% mel	<i>n</i>	% mel	<i>n</i>	% mel
1981:												
Spring gen. 1	261	16.09	3433	24.00***	3337	45.43**	325	19.69*	3650	9.15 <sup>b</sup>	906	2.98
Summer gen. 2	1279	21.27**	2603	29.47	1001	50.85	2849	25.41	979	9.40 <sup>b</sup>	1488	2.90
Mid-winter	1898	16.70	221	23.98†	141	44.68	206	24.27	390	10.00	96	4.17
1982:												
Late winter	320	25.94***	121	32.23	—	—	577	22.18	164	12.80	—	—
Spring gen. 1	—	—	1452	27.41	1122	43.05	2293	24.25	—	—	234	1.71

<sup>a</sup>Sequence for 1980-1981. <sup>b</sup>Samples for 1980. <sup>\*\*</sup> $P < 0.01$ ; <sup>\*\*\*</sup> $P < 0.001$ ; <sup>†</sup> $P$  approaches 0.05.



Brakefield, 1984a). Samples collected at different times in the summer period of adult activity by other workers in various regions of Europe have provided little evidence of changes in melanic frequency (Meissner, 1907a, b, 1909, 1910; Creed, 1966, 1975; Lusi, 1973; Bengtson & Hagen, 1975; Honek, 1975; Muggleton, 1978; Zakharov & Sergievsky, 1980; Klausnitzer & Schummer, 1983). However, many samples are small and comparisons often involve single sampling occasions or grouped data for 'early' and 'late' periods which cover only part of the whole reproductive period. The occurrence of overlapping generations and of spatial and temporal heterogeneity in morph frequency within generations (Brakefield, 1984a, b) means that care is necessary in interpreting such data.

My observations in The Netherlands indicate a similar diversity of hibernation sites to those found in Britain (Benham & Muggleton, 1978). The aggregative behaviour is characteristic of the species (see Hodek, 1973).

This study shows that differences in survivorship between non-melanic and melanic *A. bipunctata* may occur in hibernating cohorts in The Netherlands, but that they are probably exceptional. The only cohorts which exhibited such a difference were associated with exposed hibernacula at a single study site and experienced particularly harsh climatic conditions. The subpopulation with differential mortality showed an increase in melanic frequency from about 17 to 27% over the mid-winter period of powerful selection and heavy mortality. This selective advantage contrasts with the intense winter selection against melanics in Berlin observed by Timoféeff-Ressovsky (1940). Some samples of hibernating *A. bipunctata* obtained by other workers have provided no examples of differential winter mortality (Zakharov & Sergievsky, 1980; see also Bengtson & Hagen, 1975; Honek, 1975). Thus, although differences in winter survivorship of the morphs may occur in some populations of *A. bipunctata*, there is no indication that they are a general phenomenon. Evidence of changes in the frequency of melanic forms during hibernation has been obtained in two other species of coccinellids (Tan, 1948; Parry & Peddie, 1981).

The winter climate in Berlin is usually colder than in The Netherlands (Table 4). However, the difference was considerably less during the mid-winter period of selection at Utrecht E. (cf. Table 2). Thus general differences in climate are unlikely to account for the difference in direction of selection at Utrecht E. and Berlin or for the absence of selection in other cohorts in The Netherlands.

Hibernating coccinellids, including *A. bipunctata*, characteristically have high levels of stored fat and glycogen, inactive ovaries and reduced respiration rates. They can have very low supercooling points which may change with time (see,

Table 4. Comparison of the mid-winter climates at De Bilt and Berlin. Figures are 30-year means for 1931–1960

	Maximum daily temperature (°C)			Minimum daily temperature (°C)			Relative humidity (%)		
	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.
De Bilt	5.4	4.3	5.3	0.6	−0.8	−0.8	88	86	83
Berlin	3.1	1.7	2.9	−1.4	−3.5	−3.1	88	84	82

e.g. Hariri, 1966; Hodek, 1973; Parry, 1980). Factors other than temperature and energy reserves are likely to influence overwintering survivorship in *A. bipunctata*. One such factor is moisture in the air, since insects freeze internally at higher temperatures when their surfaces are wet than when they are dry (Salt, 1936). The extreme period of cold in December 1981 in The Netherlands coincided with relative humidities which were higher than normal in the study area or Berlin (Tables 2 and 4). This may then have contributed to the climatic stress experienced by *A. bipunctata* at some exposed sites. Further laboratory experiments on winter survivorship using very low temperatures would be valuable. However, the significance of the results would be difficult to interpret without more understanding of the microclimates at hibernacula.

The data collected for some sites in The Netherlands (Table 3) suggest that the increase in melanic frequency over the reproductive period is counterbalanced by selection against melanics before hibernation commences. More data sets which include large samples taken in early hibernation are necessary to establish how general this pattern of selection is. Brakefield & Willmer (1984) found that the temperature excess over ambient air reached by larger melanic *A. bipunctata* under illumination similar to bright sunlight can be  $> 10^{\circ}\text{C}$  (compared to  $7^{\circ}\text{C}$  for non-melanics). Thus a possible causal mechanism for the selection against melanics is the occurrence of greater heat stress in conditions of prolonged sunshine and very high ambient temperatures. Unfortunately the late summer and early autumn period of the life-cycle is the least well understood (see Brakefield, 1984a). Field observations in The Netherlands suggest that the species becomes less active and more widely dispersed during this period. They may tend to aestivate in diapause (see Ipert, 1966).

The relevance of mathematical models of cyclical selection (e.g. Haldane & Jayakar, 1963; Hedrick, 1974; Hoekstra, 1975) to the dynamics of melanism in *A. bipunctata* in populations in The Netherlands is unclear, since a second annual generation probably does not always occur and, in such cases, the period of selection in opposing directions must operate within single generations (see Goux, 1978; Pasteur, 1977). In regions with more than one annual generation adults from each one probably overwinter and are subject to opposing selection pressures when these occur. The moderate nature of the selection coefficients involved in seasonal selection in The Netherlands (Fig. 2) and their variability between populations (see also Brakefield, 1984c) suggests that in any case they are unlikely to provide a unitary explanation for the polymorphism. Seasonal selection may, however, contribute in some regions to maintaining the polymorphism by interacting with other factors such as a balance between migration and selection or frequency-dependent effects introduced by forms of sexual selection or differential timing of reproduction (see Brakefield, 1984b; O'Donald *et al.*, 1984).

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## APPENDIX

Numbers of non-melanic (n-m) and melanic (mel) *Adalia bipunctata* in the combined samples for each generation in the summer period of reproductive activity for sites in The Netherlands. The twelve sites at which sequential samples were obtained in each generation are given above (see text for details)

no.	Site name	Year	Generation 1		Generation 2 pupae		Generation 2 adults		Overall % mel
			n-m	mel	n-m	mel	n-m	mel	
23	Middelharnis	1979	901	76	689	58	569	60	8.24
4	Delft	1980	879	27	1052	31	394	11	2.88
10	Utrecht C.	1980	902	223	1786	357	966	249	18.49
12	De Uithof	1980	1367	407	373	148	1814	727	26.51
23	Middelharnis	1980	3316	334	521	47	366	45	9.20
28	Willemstad	1980	823	605	566	446	434	398	44.28
32	Zevenbergen W.	1980	1265	1028	249	266	1619	1603	48.04
33	Zevenbergen E.	1980	502	454	418	450	514	696	52.74
38	Tilburg	1980	1184	1522	385	553	461	736	58.07
25	Oude-Tonge	1981	2609	824	1727	722	109	45	26.36
32	Zevenbergen W.	1981	1821	1516	461	474	31	35	46.68
33	Zevenbergen E.	1981	169	187	297	310	45	57	52.02
4	Delft	1978	229	3	60	2	26	1	1.87
10	Utrecht C.	1978	191	38	1469	287	470	77	15.88
4	Delft	1979	61	1	215	8	53	4	3.80
7	Harmelen	1979	47	9	118	26	—	—	17.50
10	Utrecht C.	1979	245	62	377	89	106	32	20.09
64	Zierekzee	1979	217	32	78	14	—	—	13.49
25	Oude-Tonge	1980	326	68	1133	503	3750	1483	28.28
31	Oudenbosch	1980	770	798	38	46	121	133	51.26
52	Antwerp	1980	257	225	383	380	432	506	50.89
10	Utrecht C.	1981	109	25	4472	1048	—	—	18.98
11	Utrecht E.	1981	219	42	1007	272	—	—	20.39
12	De Uithof	1981	261	64	2125	724	—	—	24.83
28	Willemstad	1981	230	156	787	719	130	81	45.46
38	Tilburg	1981	984	1137	45	56	8	12	53.75