

A REMARKABLE SAPROXYLIC INSECT FAUNA FROM A TRADITIONAL ORCHARD IN WORCESTERSHIRE – BUT ARE THE SPECIES RESIDENT OR TRANSITORY?

K. N. A. ALEXANDER¹, L. BOWER² & G. H. GREEN³

¹*59 Sweetbrier Lane, Heavitree, Exeter EX1 3AQ*

²*PTES, 15 Cloisters House, 8 Battersea Park Road, London SW8 4BG*

³*Windy Ridge, Pershore Road, Little Comberton, Pershore, Wores WR10 3EW*

ABSTRACT

Two flight interception traps were operated within a traditional orchard nature reserve across the 2013 field season. The resulting catch included four species with British Red Data Book status and 16 with Nationally Scarce status, with the emphasis very much on saproxylic species and especially those regarded as characteristic of ancient wood pasture situations. The same site has been surveyed on two occasions previously, although by direct investigation using standard collecting techniques. The three datasets show remarkably low levels of consistency, raising the question of whether, on the one hand, this is an extraordinarily rich site which has yet to come close to being fully documented or, alternatively, the site is subject to considerable interchange of species with the surrounding landscape. While a traditional orchard may provide habitat for typical wood pasture species, it cannot be considered ancient wood pasture habitat as its history as suitable habitat may be relatively short – an isolated traditional orchard such as this may therefore be acting as an important stepping stone habitat, offering scope for species operating meta-population dynamics.

INTRODUCTION

The insect fauna of traditional orchards has been subject to very little interest from entomologists historically. The development of the UK Biodiversity Action Plan process has however stimulated considerable survey work, initially by the addition of Noble Chafer *Gnorimus nobilis* (L.) to the list of Priority Species. The People's Trust for Endangered Species (PTES) quickly adopted Noble Chafer as a focus for research work and has been at the forefront of conservation action on traditional orchards ever since. Other key studies in Britain include English Nature's (now Natural England) biodiversity studies of six traditional orchards (Lush *et al.*, 2009) and the Wyre Forest Study Group's survey of three traditional orchards within the Wyre Forest SSSI (Smart & Winnall, 2006). Inventory studies such as these have inspired scientific studies in the Czech Republic (Horak *et al.*, 2013).

The PTES purchased a traditional orchard in Worcestershire in 2003 in order to conserve it as an example of a traditional orchard within the British range of Noble Chafer. The orchard has been subject to a series of specialist invertebrate surveys in order to maintain an overview of site quality and condition, and this article reports on the results of the latest survey, carried out over summer 2013, and discusses some of the implications.

THE STUDY SITE

Rough Hill Orchard occupies a steep escarpment slope above a meander of the River Avon at Birlingham, Worcestershire (SO929442). The escarpment is cut by the

south-westerly-flowing river and deflects the river eastwards for a short section before it swings back around south of Birlingham. The orchard is therefore east-facing and sheltered from the prevailing south-westerly weather systems by the plateau behind on the west side and to the south. The orchard enclosure is about 10ha in extent.

At the time of acquisition the orchard contained about 82 veteran apple trees. These were concentrated in the southern half of the enclosure, the northern half being dominated by mature hawthorn trees. Many of the veteran apple trees had already collapsed and others have continued to do so. The total of standing trees is now probably closer to 30. The veteran apple trees have been individually tagged and GPS mapped. New plantings of both apple and plum have been carried out – there are a few veteran plum trees along the upper boundary fence, demonstrating previous use of the site as a plum orchard, at least in part. The orchard had formerly been managed by grazing but this had long since ceased and the herb-rich grasslands have suffered from very extensive bramble encroachment. A limited cattle grazing regime has recently been re-established as part of a programme of bramble control and restoration of the grassland.

The orchard lies in an area rich in saproxylic invertebrates. It is situated between the important sites of Bredon Hill (Whitehead, 1996) and Croome Park (Lott *et al.*, 1999), respectively at about 3km to the south-east and to north-west. The Worcestershire Wildlife Trust (WWT) reserve of Tiddesley Wood is closely adjacent to the north and includes a traditional plum orchard on its far, north side. The area historically held a large concentration of fruit orchards but most have subsequently been grubbed out.

Prior to purchase, the PTES commissioned J. & P. Whitehead, Landscape Consultants, to carry out a day's field survey to assess site quality for arboreal insects, with particular regard to the potential for Noble Chafer. None was detected but the orchard proved to be notably rich in other saproxylic insects (Whitehead, 2001). KNAA was subsequently commissioned to carry out baseline surveys of the saproxylic invertebrates in order to maintain knowledge of the fauna and the conservation management implications (Alexander, 2006 & 2013). The results of the 2013 survey are reported here and compared with those of the earlier surveys.

SURVEY TECHNIQUES

The two previous surveys had been based on standard entomological hand survey techniques, i.e. searching the trees and associated decaying wood, supplemented by use of a beating tray and sweep net. With the continuing decline in the health and stability of the veteran apple trees, and – in particular – due to the volume and height of bramble scrub amongst the trees, it was decided to focus on trapping for the 2013 survey. Some supplementary hand survey was also carried out on the more accessible trees while on site.

Flight interception trapping is becoming a very popular way of extending the sampling periods so that sampling continues uninterrupted between each visit by the surveyor. It is especially valuable in wet climates such as ours as continuous trapping enables sampling to take place during any dry periods between the visits. Two flight interception traps were accordingly placed in the orchard on 30 May 2013, emptied and re-set 15 July, and finally emptied and removed 30 October. The aim of sampling was qualitative rather than quantitative.

The flight interception trap used in this study is based on a standardised construction (see Fig. 1). The basic collecting containers are four 2l plastic drinks



Fig 1. A small flight interception trap, of four bottle design, tied above a rot-hole on an old apple tree in Rough Hill Orchard.

bottles with large windows cut into their sides. The bases of the bottles are screwed into a square wooden base, and the four windows positioned facing outwards. The wooden base is then suspended – from the base of a branch or just tied around a tree trunk – using baler twine, with the bottles hanging upside-down beneath. The lower parts of the upside-down bottles are filled with a preservative solution (50% commercial antifreeze solution in tap-water, plus a little washing up liquid to reduce surface tension). The solution and catch are later drained through the neck of the bottle by removing the plastic cap and draining the contents into a collecting pot for sorting under a microscope later. The basic design is derived from a trap devised by Carrel (2002) for sampling field layer invertebrates.

A flight trap of this construction was chosen in preference to a Malaise trap as the latter trap design has a reputation for killing large volumes of flying insects which then become a logistical problem to sort and identify. The position of Malaise traps also has a major influence on catch size and composition. The bottle flight traps are multidirectional and so do not suffer from this complication; sample size is much

more manageable; they are also small and flexible for targeted positioning. No studies comparing the two types of traps have been carried out but it appears that Malaise traps may be better at intercepting large strongly-flying insects such as hoverflies.

The two selected trapping sites were as follows:

- Inside the hollow trunk cavity of a veteran apple tree, the trap suspended in the void above a large accumulation of wood mould;
- Below a medium-sized branch-scar rot-hole in the upper trunk of another veteran apple tree; although there was no sign of any bracket fungi at the time, fresh growth of Dryad's Saddle *Polyporus squamosus* Huds. ex Fr. had developed by the time of the July visit.

RESULTS

Eighty-nine saproxylic (wood-decay) species of invertebrates were found during 2013. These include four British Red Data Book (RDB) species, all new to the site list: the False click beetle *Eucnemis capucina* Ahrens (Eucnemidae), the beetle *Scaptia testacea* Allen (Scaptiidae), the freeloader fly *Madiza britannica* Hennig (Milichiidae) and the crane fly *Rhipidia uniseriata* Schiner (Limoniidae). There were additionally nineteen species of Nationally Scarce (NS) status – not all saproxylic – as well as many local and generally uncommon species. The RDB and NS species are listed in Table 1 together with species of equivalent status found during the previous surveys.

Additionally a Nationally Scarce spider, *Nigma walckenaeri* (Roewer) (Dictynidae) was knocked from *Clematis* growth over scrub. This is best known in Britain around the lower Thames basin but there is also a small population known along the Severn/Avon valley; it has apparently been found much more widely in recent years and its status merits downgrading. The spider spins a small web and retreat on the upper surface of leaves of bushes growing in parks, gardens, and other suitable situations.

The species composition of the saproxylic Coleoptera and Diptera appears to be exceptional – even for a traditional orchard – but this partly reflects lack of understanding of the potential of such sites: the more research that goes into the saproxylic invertebrates of old orchards the more surprises emerge. It is becoming increasingly clear that our traditional orchard landscapes may be as important for saproxylic invertebrates as the historic parklands and wood pasture systems. The main differences appear to be that the latter may include larger trees, with larger volumes of heartwood decay and wood mould, but that traditional orchards tend to have higher densities of veteran and hollowing trees. It is generally assumed that larger volumes of decay and wood mould are required by some of our rarest and most threatened species, and so these species cannot live in traditional orchards because the trees have too small girths. Increasingly, however, the list of saproxylic species which have never been found in traditional orchards is being eroded away.

KEY BEETLE SPECIES

The discovery in 2013 of the beetle *S. testacea* is an excellent example of an old growth species which might not be expected in a traditional orchard, as this species is best known from sites with concentrations of ancient oaks. This appears to be the first British record from a traditional orchard as well as from a hollow apple tree. However, the species has been reared out of old nest material from a hollow grey poplar (Mendel, 1989) and found in association with rotten alder wood (Collier,

Table 1 British Red Data Book and Nationally Scarce insects recorded in Rough Hill Orchard, with dates of capture (Falk, 1991; Hyman, 1992; Falk & Chandler, 2005; Falk & Crossley 2005).

Species	Status	2001	2006	2013
Coleoptera				
<i>Plegaderus dissectus</i> Erichson	Nationally Scarce	+		
<i>Euplectus mutator</i> Fauvel	Nationally Scarce			+
<i>Gyrophana jovi</i> Wendeler	Nationally Scarce	+		
<i>Gyrophana manca</i> Erichson	Nationally Scarce	+		
<i>Quedius maurus</i> (C. R. Sahlberg)	Nationally Scarce			+
<i>Quedius truncicola</i> Fairmaire & Laboulbène	Nationally Scarce			+
<i>Eucnemis capucina</i> Ahrens	RDB1 (Endangered)			+
<i>Ampedus rufipennis</i> (Stephens)	RDB2 (Vulnerable)	+		
<i>Megatoma undata</i> (L.)	Nationally Scarce			+
<i>Hedobia imperialis</i> (L.)	Nationally Scarce	+		
<i>Hadrobregmus denticollis</i> (Creutzer)	Nationally Scarce			+
<i>Tillus elongatus</i> (L.)	Nationally Scarce			+
<i>Opilo mollis</i> (L.)	Nationally Scarce		+	
<i>Pseudotriphyllus suturalis</i> (F.)	Nationally Scarce			+
<i>Mycetophagus piceus</i> (F.)	Nationally Scarce			+
<i>Hallomenus binotatus</i> (Quensel)	Nationally Scarce			+
<i>Orchesia micans</i> (Panzer)	Nationally Scarce		+	
<i>Abdera flexuosa</i> (Paykull)	Nationally Scarce	+		
<i>Osphya bipunctata</i> (F.)	RDB3 (Rare)		+	
<i>Prionychus ater</i> (F.)	Nationally Scarce	+		
<i>Prionychus melanarius</i> (Germar)	RDB2 (Vulnerable)		+	
<i>Ishnomena sanguinicollis</i> (F.)	Nationally Scarce			+
<i>Scraptia testacea</i> Allen	RDB3 (Rare)			+
<i>Scolytus mali</i> (Bechstein & Scharfenberg)	Nationally Scarce	+	+	+
Diptera				
<i>Ctenophora pectinicornis</i> (L.)	Nationally Scarce			+
<i>Rhipidia uniseriata</i> Schiner	RDB3 (Rare)			+
<i>Exechiopsis membranacea</i> (Lundström)	Nationally Scarce			+
<i>Eupachygaster tarsalis</i> (Zetterstedt)	Nationally Scarce			+
<i>Tachypeza fuscipennis</i> (Fallén)	Nationally Scarce			+
<i>Lasiambia brevivucca</i> (Duda)	Nationally Scarce			+
<i>Madiza britannica</i> Hennig	RDB2 (Vulnerable)			+

1994), and so it is known to be capable of breeding in smaller girth trunks. It is known from both Bredon Hill (Whitehead, 1996) and Croome Park (Lott *et al.*, 1999).

The click beetle *Ampedus rufipennis* (Stephens) might also be a great surprise to find breeding in a traditional apple orchard, although knowledge of its ecology is actually consistent with this situation. Whitehead (2005) published his discovery of larvae in a fallen apple tree in this orchard in 2001. While it has not been detected here subsequently it may still be present. Larvae and elytra of this species have also been found by KNAA in the WWT's traditional plum orchard at Tiddesley Wood Reserve in 2013, when surveying as part of a Field Studies Council course. The apple trees at Rough Hill Orchard are being hollowed by the bracket fungus *Inonotus hispidus* (Bull.) P. Karst., the typical heartwood-decay fungus of both apple and ash trees, while the Tiddesley plum trees are being white-rotted by *Phellinus pomaceus* (Pers.) Maire. At Bredon Hill, this click beetle is particularly associated with ash

pollards hollowed by *I. hispidus*. It appears to be associated with white-rotten heartwood, irrespective of the decay fungus involved. Smaller girth trees can clearly provide suitable habitat. This beetle is not known from nearby Croome Park.

The third beetle species which merits special mention is *E. capucina* as it currently has ‘Endangered’ status (Hyman, 1992). For many years this was only known from the New Forest, but was later discovered in Windsor Forest, and then on Bredon Hill (Whitehead, 1996). The New Forest and Windsor host trees were all beech, with the exception of a single report from ash at the latter site. At Bredon Hill it was found in a field maple, and it has subsequently been found at other sites in the Herefordshire and Worcestershire area, most recently from a cherry orchard (Alexander, 2010). Most reports which specify the details associate the species with rot-holes, and rot-holes may form on a wide variety of trees – both large girth and relatively small – in response to loss of lateral branches. It has not been found in Croome Park. A total of 18 beetles were taken by the rot-hole trap and just one from the hollow tree trap. Trapping is often said to be less damaging than hand-searching but clearly trapping has the capability of killing large numbers of emerging adults, and this should be a consideration when designing a survey programme.

KEY FLY SPECIES

The most notable dipteran found at Rough Hill Orchard is the freeloader fly *M. britannica*, another rot-hole species. The distribution and ecology of this species has recently been described elsewhere (Alexander & Perry, 2013), although Rough Hill Orchard provides the first records from: i) an apple tree as host, ii) a traditional orchard, and iii) the first record from Worcestershire. Rot-holes formed by *Polyporus squamosus* seem to be the most common factor in its presence at sites, and so its presence here is entirely consistent with its known ecology.

Amongst the nationally scarce fly species are three particularly interesting finds: *Eupachygaster tarsalis* (Zetterstedt) (Stratiomyiidae), *Lastambia brevibuca* (Duda) (Chloropidae) and *Tachypeza fuscipennis* (Fallén) (Hybotidae). These records are discussed elsewhere (Alexander, in press).

ASSESSMENT OF SITE QUALITY

Two schemes have been developed for site assessment for nature conservation importance of saproxylic beetles: Site Quality Index (Fowles, Alexander & Key, 1999) and Index of Ecological Continuity (Fowles, Alexander & Key, 1999; Alexander, 2004). The SQI uses the national rarity statuses of the beetles to calculate an index. The IEC attempts to assess the old growth aspect of the site. Both have their own strengths and shortcomings and are best used alongside each other. A shortcoming of the SQI is that the index may increase or decrease with further recording and so, while it may provide a snapshot of site quality/condition at any point in time, it does not provide a reliable minimum assessment of the level of the value of a site in the way provided by the IEC.

The IEC is intended to provide a minimum assessment of the degree of ecological continuity on a particular site – the extent of continuity of old growth conditions over time. The index can only increase with further recording effort, it cannot decrease. The number of qualifying species known from Rough Hill Orchard has now increased to 19 and these generate an IEC of 33. The threshold for assessing national significance is 25 and the current figure of 33 therefore suggests the reserve now achieves national conservation importance for saproxylic beetles. It is the first individual orchard to do so. Attingham Park in Shropshire was designated as an

Table 2 Site Quality Index calculations for Rough Hill Orchard

Year of survey	2001	2006	2013
Site Quality Score	112	100	201
Number of qualifying species	28	23	44
Site Quality Index	400	435	457

SSSI primarily for its saproxylic beetle fauna which also had an IEC of 33 at the time.

A particular feature of the SQI is that it enables comparisons between datasets for a particular site and so can be used as part of long-term monitoring of site condition – an SQI approach underlies Natural England’s invertebrate site condition monitoring for SSSIs. Rough Hill Orchard has now been surveyed on three separate occasions and the three datasets are analysed and compared in Table 2. It should be noted however that Fowles, Alexander & Key (1999) suggest that assessment may be unreliable below a threshold of 40 qualifying species and that the two previous surveys are below this threshold.

Interestingly, the three data sets show a gradual increase in SQI between surveys. This most probably reflects the site coming under conservation management, with all dead and decaying wood now being left in situ.

Fowles, Alexander & Key (1999) suggest a threshold of 500 for national importance, and so Rough Hill Orchard falls not far short of this level. That threshold is however believed by the present authors to be set far too high, and examination of the site data in Fowles, Alexander & Key (1999) suggests that Rough Hill’s SQI of 457 is comparable with some of the richest sites in Britain for saproxylic beetles.

The conclusions from this analysis are that ecological continuity at Rough Hill Orchard is relatively high and of national significance, and that site condition for saproxylic beetles appears to be increasing. Unfortunately no system has been developed for similar analyses of saproxylic Diptera assemblages.

ARE THE SPECIES RESIDENT OR TRANSITORY?

The three datasets however show remarkably low levels of consistency. Of the 31 species listed in the table, just one has been found during each survey episode, *Scolytus mali* (Bechstein & Scharfenberg). No other species has been detected more than once; the rest have been detected just once from the three surveys. No individual survey can be considered to have been exhaustive and so some variation would be expected, but the level of consistency does seem remarkably low. One option might be that this is an extraordinarily rich site which has yet to come close to being fully documented, that subsequent surveys will continue to detect additional species while the consistency level will gradually increase as the results tend towards completeness. Alternatively – and perhaps more likely for such a small site within a landscape relatively rich in veteran trees – the site may be acting as a stepping stone for species moving around this rich landscape; it may be part of a complex meta-population structure, with species continually colonising from neighbouring areas while others die out at the site level. Of course, both explanations may be partially correct.

Two of the beetle species recorded in 2013 suggest that some species at least are passing through. Single specimens of *Mycetophagus piceus* (F.) and *Cis fagi* Waltl

were taken in the rot-hole flight trap. Both are believed to exclusively develop in the mycelial sheets of *Laetiporus sulphureus* (Bull.) ex Fr.) Murr. deep within the red-rotting heartwood of trees. Neither the fungus nor red-rot have been seen in the veteran apple trees present in this particular orchard, although apple trees are occasionally colonised by this fungus. Adults of *M. piceus* are known to be attracted to the brackets of other fungi species, presumably feeding on the spores, and the fruiting of *Polyporus squamosus* may explain the presence of this species here.

The fauna found in Rough Hill Orchard bears closest resemblance to that of Bredon Hill (see Whitehead, 1996), although about 3km distant. Could there be interchange of species between these two sites? The prevailing winds are south-westerly of course, but southerly and south-easterly winds might aid dispersal from Bredon Hill to Rough Hill on occasion. The rarest beetle species so far known from Rough Hill Orchard, the False click beetle *E. capucina*, is known from a number of sites across the Worcestershire and Herefordshire area, and meta-population dynamics may help to explain its presence in relatively small concentrations of suitable veteran trees. The sites may be acting as short-term holding areas for breeding populations, but this would require greater mobility than currently credited for the species.

CONCLUSIONS

The survey has demonstrated that Rough Hill Orchard continues to support a relatively high quality saproxylic invertebrate fauna. Analysis of the species data demonstrates that ecological continuity of old growth habitat at Rough Hill Orchard is relatively high and of national significance, and that site condition for saproxylic beetles appears to be increasing.

This single orchard has now produced records for five Coleoptera and two Diptera which currently have RDB status in Britain, and 19 and 5 respectively with Nationally Scarce status. This is a remarkable assemblage for a group of so few veteran apple trees.

What is clear is that Rough Hill Orchard and the landscape in which it sits has the potential to form a very interesting research site for the investigation of the population dynamics of some of our rarest saproxylic insects, and especially research of their dynamics at landscape scale.

ACKNOWLEDGEMENTS

Thanks to Peter Chandler for identifying the Diptera from the flight trap samples; also to Pete Boardman of the Field Studies Council for organising the Biodiversity in Traditional Orchards course under their Biodiversity Fellows programme.

REFERENCES

- Alexander, K. N. A. 2004. Revision of the Index of Ecological Continuity as used for saproxylic beetles. *English Nature Research Report No. 574*.
- Alexander, K. N. A. 2006. *Rough Hill Orchard, Birlingham, Worcestershire. Baseline Survey of Saproxylic Invertebrates*. Unpublished contract report to People's Trust for Endangered Species.
- Alexander, K. N. A. 2010. A remarkable wood-decay beetle fauna from a group of traditional orchards at Colwall, Herefordshire. *The Coleopterist* **19**: 11–14.

- Alexander, K. N. A. 2013. *Rough Hill Orchard, Birlingham, Worcestershire. Baseline Survey of Saproxyllic Invertebrates*. Unpublished contract report to People's Trust for Endangered Species.
- Alexander, K. N. A. in press. A remarkable Diptera fauna found by flight trapping in a Worcestershire traditional apple orchard. *Dipterists Digest*.
- Alexander, K. N. A. & Perry, I. 2013. The distribution and ecology of the freeloader fly *Madiza britannica* Hennig (Diptera, Milichiidae). *Dipterists Digest* **20**: 202–204.
- Carrel, J. E. 2002. A novel aerial-interception trap for arthropod sampling. *Florida Entomologist* **85**: 656–657.
- Collier, M. 1994. Some notable Norfolk Coleoptera, including four new county records. *British Journal of Entomology & Natural History* **7**: 168.
- Falk, S. J. 1991. A review of the scarce and threatened flies of Great Britain (Part 1). No. 39. Nature Conservancy Council.
- Falk, S. J. & Chandler, P. J. 2005. A review of the scarce and threatened flies of Great Britain. Part 3: Empidoidea. Species Status No. **3**. Peterborough: Joint Nature Conservation Committee.
- Falk, S. J. & Crossley, R. 2005. A review of the scarce and threatened flies of Great Britain. Part 2: Nematocera and Aschiza. Species Status No. **2**. Peterborough: Joint Nature Conservation Committee.
- Fowles, A. P., Alexander, K. N. A. & Key, R. S. 1999. The Saproxyllic Quality Index: evaluating wooded habitats for the conservation of dead-wood Coleoptera. *The Coleopterist* **8**: 121–141.
- Horak, J., Peltanova, A., Podavkova, A., Safarova, L., Bogusch, P., Romportl, D. & Zasadil, P. 2013. Biodiversity responses to land use in traditional fruit orchards of a rural agricultural landscape. *Agriculture, Ecosystems & Environment* **178**: 71–77.
- Hyman, P. S. (revised Parsons, M. S.). 1992. A review of the scarce and threatened Coleoptera of Great Britain. Part 1. *UK Nature Conservation No. 3*. Peterborough: Joint Nature Conservation Committee.
- Lott, D. A., Alexander, K. N. A., Drane, A. B. & Foster, A. P. 1999. The dead-wood beetles of Croome Park, Worcestershire. *The Coleopterist* **8**: 79–87.
- Lush, M., Robertson, H. J., Alexander, K. N. A., Giavarini, V., Hewins, E., Mellings, J., Stevenson, C. R., Storey, M. & Whitehead, P. F. 2009. Biodiversity studies of six traditional orchards in England. *Natural England Research Report NERR025*.
- Mendel, H. 1989. *Transactions of the Suffolk Natural History Society* **25**: 26.
- Smart, M. J. & Winnall, R. A. (eds.) 2006. The biodiversity of three traditional orchards within the Wyre Forest SSSI in Worcestershire: a survey by the Wyre Forest Study Group. *English Nature Research Report No. 707*.
- Whitehead, P.F. 1996. The notable arboreal Coleoptera of Bredon Hill, Worcestershire, England. *The Coleopterist* **5**: 45–53.
- Whitehead, J. & P., 2001. *Rough Hill Orchard, Birlingham, Worcestershire, VC37, SO929442. Synopsis of bio-assessment undertaken on 14.6.2001*. Unpublished contract report to People's Trust for Endangered Species.
- Whitehead, P. F. 2005. Notable Coleoptera records 5. *Entomologist's Gazette* **56**: 251–260.