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Localized breeding of the *Anopheles gambiae* complex (Diptera: Culicidae) along the River Gambia, West Africa

C. Bøgh1*, S.E. Clarke1, M. Jawara2, C.J. Thomas3 and S.W. Lindsay3

1Danish Bilharziasis Laboratory, Jaegersborg Allé 1D, DK-2920 Charlottenlund, Denmark: 2Medical Research Councils Laboratories, PO Box 273, Fajara, The Gambia: 3School of Biological and Biomedical Sciences, University of Durham, South Road, Durham, DH1 3LE, UK

**Abstract**

A study was undertaken to identify the major larval habitats of the *Anopheles gambiae* (Giles) complex in rural Gambia. Mosquito larvae and pupae were sampled along transects and in specific habitats in the central region of the country during the rainy seasons of 1996 and 1997. The sampling showed that the major breeding sites were located on the flooded alluvial soils bordering the river. The largest numbers of larvae were found during September, one month after the peak rains. Polymerase chain reaction analysis of specimens showed that *Anopheles melas* (Theobald) was the dominant species in the flooded areas (81.5%), followed by *A. gambiae* s.s. (18.0%) and *A. arabiensis* (Patton) (0.5%). By sampling in specific habitats it was evident that *A. arabiensis* was mainly breeding in rain-fed rice fields along the edge of the alluvial soils. *Anopheles melas* and *A. gambiae* s.s. often coexisted but whereas *A. melas* were found in water with a salinity of up to 72% sea water (25.2 g NaCl 1̊), *A. gambiae* s.s. only occurred in water with up to 30% sea water (10.5 g NaCl 1̊). *Anopheles melas* larvae were found in association with plant communities dominated by sedges and grasses (*Eleocharis* sp., *Paspalum* sp., *Sporobolus* sp.) and sea-purslane (*Sesuvium portulacastrum* (L.) and the presence of cattle hoof prints, whereas *A. gambiae* s.s. larvae mainly occurred in association with *Paspalum* sp. and *Eleocharis* sp. The study showed that even during the peak rainy season, breeding of the *A. gambiae* complex is almost entirely restricted to the extensive alluvial areas along the river.

**Introduction**

Malaria transmission in the Sahel region of Africa is characterized by often intense seasonal transmission because of the brief, but often heavy rainfall. Large geographical differences are seen in the epidemiology of malaria in the region and even between villages a few kilometres apart (Vercruyssse, 1985; Julvez et al., 1992, 1997; Alonso et al., 1993; Touré et al., 1996; Thomson et al., 1996; Thomas & Lindsay, 2000, Clarke et al., 2002). To understand the reasons behind these geographical variations in transmission dynamics, it is essential to determine where and when the vector mosquitoes are breeding and describe the characteristics of their breeding habitats.

The Gambia lies in the Sahel region of West Africa, where the climate is characterized by a short rainy season from...
June to October, with an annual rainfall of ~600–800 mm. The most important malaria vectors are *Anopheles gambiae* sensu stricto (Giles) *Anopheles melas* (Theobald) and *Anopheles arabiensis* (Patton) (Diptera: Culicidae) (Bryan, 1983; Lindsay et al., 1993), all members of the *A. gambiae* complex (Gilles & Coetzee, 1987). A considerable amount of research has been carried out on adult mosquitoes in this country but only two studies have investigated the breeding of mosquito larvae. Bertram et al. (1958), working on the coast, found freshwater *A. gambiae* sensu late breeding near a small stream and in puddles formed by car tracks. *Anopheles melas* was found breeding in saline flooded areas with sea-purslane *Sesuvium portulacastrum* L. (Aizoaceae) and beneath or near white mangrove *Avicennia* sp. (Avicenniaceae). A later study by Thomas and Lindsay (2000) found that the highest density of larvae was found on the landward edge of the extensive areas of pooled sediment bordering the River Gambia. However, in this study collections were carried out at one point in time during the rainy season (August, 1995) and the *A. gambiae* larvae collected were not identified to sibling species level.

More extensive studies of the breeding of the *A. gambiae* complex have been carried out in other West African countries, including Sierra Leone (Ribbands, 1944b; Thomson-Muirhead, 1945; Ford Tredre, 1946), Liberia (Gelfand, 1955) and Nigeria (Barber et al., 1951; Chwatt, 1949). The ecology of these study sites resembles The Gambia in having riverine ecosystems affected by saltwater intrusion but they are all located outside the Sahel region and have much higher annual rainfall. These accounts describe the larval ecology of *A. melas* and fresh water breeding *A. gambiae* s.l. The fresh water breeding *A. gambiae* s.l. were found on the landward edge of floodplains whereas the salt-tolerant species *A. melas* was most commonly associated with saline grass covered floodplains and extensive orchards of white mangrove *Avicennia* sp. (Barber et al., 1951; Ribbands, 1944b; Thomson-Muirhead, 1945; Gelfand, 1955). None of the larval studies from West Africa separated the freshwater breeding *A. gambiae* sibling species into *A. gambiae* s.s. and *A. arabiensis*. However, both are known to breed in open sunlit freshwater pools (Gilles & Coetzee, 1987).

The malaria transmission season in The Gambia is brief but intense from July to the beginning of December, when the mosquito populations decline rapidly (Lindsay et al., 1993; Hemingway et al. 1995). The entomological inoculation rate per transmission season varies enormously within the study area and ranges from less than one to more than 165 infective bites (Bow et al., 1999), with the highest transmission rates being found nearest the river (Bow et al., 1999; Thomas & Lindsay, 2000).

This study aimed to describe the geographical and seasonal variation in the breeding of different members of the *Anopheles gambiae* complex in The Gambia. It is part of a larger study describing the ecology of malaria in the central part of the country (Bow, 1999; Bow et al., 2001; Clarke, 2001).

**Materials and methods**

**Study area**

The country is dominated by the River Gambia, which is characterized by saltwater intrusions in its lower reaches caused by tidal differences. The flow of the river is highly seasonal and depends largely on the precipitation in the Futa Jallon highlands in Guinea. During the dry season, the salt front can travel 200 km up river, creating large areas of salt marsh and mangrove forests near the river. Only during the rainy season is the outflow of fresh water so high that river and adjacent flooded areas become completely or partly non-saline (Sylla et al., 1995). The soil structure of The Gambia is characterized by two main types: sandstone inlands where most of the villages and farms are located; and alluvial deposits along the river (Trolldalen, 1991). Descriptions of the physical and chemical composition of the swamp soils have been made by Giglioli & Thornton (1965).

The study area covered approximately 2500 km² and was located in the central part of the country, extending from 50 km east to 50 km west of Farafenni town (1500200N, 435500E). Co-ordinates are given in Universal Transverse Mercator (UTM) grid metres from UTM zone 28. Figure 1 illustrates the study area which was bounded by the northern and southern border to Senegal and the UTM meridians (410000E) and (480000E). To identify the major mosquito breeding sites, transects were established at four different sites along the river (see fig. 1). Two sites were chosen in the west to describe the breeding in more saline habitats and two sites in the east to cover the habitats less dominated by seawater. Each transect started at the periphery of a village near the floodplains. The selected villages were Jumansari Koto (UTM: 1493300N, 420500E) and Samba Soto (UTM: 1503500N, 456500E) on the north bank and Toniataba (UTM: 1486000N, 437200E) and Sowe Kunda (UTM: 1497300N, 466600E) on the south bank. Each transect began from the house nearest the river or major tributary and continued directly towards the nearest waterway. Compass bearings for the transects were taken from survey maps (DOS, 1974) and used in the field with a hand-held compass. The distance from the starting point was measured with a manual odometer but during the peak of the rainy season the mud became so sticky that it was impossible to use. During this period the distance was estimated by counting the number of paces between collection points. The precise location of each transect was determined during 1997 with the use of a hand-held, differential Global Positioning System (GPS) receiver (Geosexplorer II™, Trimble Navigation Limited, California, USA) which had an accuracy of about 5 m.

**Larval collections along transects**

During 1996, transects were surveyed in July, September and October, except for transect 3 and 4 where surveys were not carried out in July. During 1997 all four transects were surveyed in August, October and November. Measurements were made every 100 m along the transects and additionally at the edges of any water collections or streams crossing the transect. Sampling continued along the transects towards the river until further progress was impossible due to deep water or dense mangrove forest. At each collection site, dipping was delayed for 3 min to let the mosquito larvae surface after the disturbance of the water. A total of ten dips were taken within a 5 m radius using a 350 ml WHO standard dipper. Sampling was done by sampling purposely among plants and roots to catch the maximum number of larvae at any site. All instars and pupae of anopheline larvae were carefully collected from each scoop, counted and then transferred to a small plastic container for later species identification.
Larval collection in specific habitats

To confirm that the transects were representative of the study area, larval sampling was also carried out in a variety of aquatic habitats in different parts of the study area during the rainy seasons of 1996 and 1997. Sampling was focused in the floodplains and in the natural depressions on the periphery or outside areas with alluvial deposits. If a water body was located, sampling was purposely carried out with up to 20 dips at each site. At each site the presence or absence of anophelines and vegetation characteristics were recorded. All instars of anopheline larvae were collected from each scoop, counted and then transferred to a small plastic container for later species identification (see below).

Environmental measurements

At all sites where dipping took place, the depth of water, salinity and surface characteristics were recorded. Salinity was measured using a salinity meter (M30/10 FT, YSI Inc. Ohio, USA). The land surface types were classified into the following main categories:
1. Upland agriculture
2. Forest
3. Upland grassland
4. Barren mudflat
5. Barren mudflat with hoof prints
6. Mudflat dominated by spike-rush *Eleocharis* sp. (Cyperaceae)
7. Mudflat dominated by paspalum *Paspalum* sp. (Poaceae)
8. Mudflat dominated by sea grass *Sporobolus* sp. (Poaceae)
9. Mudflat dominated by swamp rice *Oryza sativa* (L.) (Poaceae)

Specimens were taken of predominant plant species and preserved for later identification at the Botanical Museum and Library, University of Copenhagen, Denmark.

Species identification

In the laboratory, larvae were transferred to 96% ethanol for later identification. Since nearly all malaria in The Gambia is transmitted by members of the *A. gambiae* complex (Bryan, 1983; Lindsay *et al*., 1989, 1993), species identification was performed using a polymerase chain reaction (PCR) technique specific for this group of mosquitoes (Scott *et al*., 1993). The primers used were for *A. gambiae* s.s., *A. melas* and *A. arabiensis*, which are the only known members of the complex present in The Gambia (Bryan *et al*., 1982). DNA was extracted from first instar larvae through to pupae and analysed twice for presence of *A. gambiae* complex DNA. If a specimen was negative in both PCR tests it was classified as a non-member of the *A. gambiae* complex. When more than 30 larvae were caught at one sampling location only the first 30 randomly selected larvae were identified by PCR and the total number of larvae of a given species calculated from the proportion of analysed specimens and the total number of caught larvae. Fourteen larval containers from 1996 were spoilt during transport and could not be identified to species level. These samples were only included in the part of the analysis presenting the total annual catches along the four transects.
Geographical information system

A geographical information system (GIS) was constructed on the basis of 1:50,000 survey maps (DOS, 1974). These maps were originally developed from aerial photography and include the outline of the main types of land cover along the river. Maps were digitized using ArcInfo® (ESRI, California, USA) and measurements of distances from the floodplain edge done using Arcview® (ESRI, California, USA).

Statistical analysis

Data entry was done in DBASE IV® (Borland International, California, USA) software and statistical analysis using SPSS® software (version 9.0, SPSS Inc., Chicago, USA). The total number of each species caught in ten dips was recorded and recalculated as geometric means (GM) to adjust for the skewed distribution of mosquito larvae. Discriminant analysis was used to identify associations between land surface classes and the presence or absence of the different species of mosquito larvae. The analysis was based on the presence or absence of larvae in a given habitat using the combined transect data sets from 1996 and 1997.

Results

Larval catches along transects

The major habitats near the River Gambia are shown schematically in fig. 2. The general profile of the transects walked from a village was first an area of farmland followed by a narrow strip of forest. This led to an open area of alluvial deposits of which the first part normally consisted of barren dry mud flats followed by flooded mud flats with alluvial deposits of which the first part normally consisted of barren dry mud flats followed by flooded mud flats with large areas of sea grass (Sporobolus sp.), spike-rush (Eleocharis sp.) and sea-purslane (Sesuvium portulacastrum). Finally, there were white and red mangrove trees (Avicennia sp. and Rhizophora sp. (Rhizophoraceae)) bordering saline sections of the River Gambia and its major tributaries.

The water depth and species composition of the larvae collected along the four transects in 1996 and 1997 is presented in fig. 3. Transects 1, 2 and 4 were little affected by daily tides but transect 3 was affected substantially by the tide due to its proximity to the river. The average water level along transect 3 was higher in 1996 compared to 1997 tide due to its proximity to the river. The average water level along transect 3 was higher in 1996 compared to 1997 because sampling by chance was carried out during high tides in 1996. There were also large differences in salinity along the transects. Transect 1 had the highest level with an average of 27.6% (95% CI: 24.8–30.3%) sea water compared to only 3.4% (1.7–5.0%) along transect 2, 9.2% (6.6–11.8%) along transect 3 and 13.5% (10.3–16.6%) along transect 4. These differences in salinity did not reflect the distance from the ocean (i.e. salt front) but rather the combined result of freshwater out-flux, distance from river, evaporation and soil salt saturation. There was considerable variation in mosquito breeding among transects and between years. However, larval breeding generally took place at the same sites along the transects each year and the species composition of the larvae was also generally consistent between years.

Larval breeding over the rainy season

The seasonal variation in larval density along the transects in 1996 and 1997 is shown in figure 4. This shows that most breeding took place in September, about a month after the peak rainy season, and continued after the rains stopped in October. These findings also suggest that A. melas breeding started earlier than A. gambiae s.s. and continued for a longer period after the rains had stopped. However, this apparent difference may be an artefact of differential detection rates for the different sibling species caused by the limitations of sampling low densities of larvae.

Location of the species-specific breeding sites

Figure 5 illustrates the total geometric mean (GM) number of A. gambiae s.s. and A. melas larvae collected along all four transects in both 1996 and 1997 in relation to the edge of the alluvial deposits. This also shows how open surface water was confined to the alluvial deposits. The GM number of A. gambiae s.s. per ten dips was 0.09 (95% CI: 0.01–0.16) larvae and 0.55 (0.099–1.00) per ten dips for A. melas. The highest larval densities of both sibling species were seen close to the edge of the floodplains although high larval densities continued to be recorded more than a kilometre into the alluvial flood plains. Along the transects A. arabiensis was only found on one occasion in 1997 about 400 m into the flooded areas on transect 4.

Larval breeding and salinity

Figure 6 illustrates the range of salinity where A. gambiae s.s. and A. melas larvae were found. Anopheles gambiae s.s. and A. melas were often found co-existing in the habitats but whereas A. gambiae s.s. larvae only occurred in up to 30% sea water (10.5 g NaCl l⁻¹), A. melas were caught at salinities as high as 72% sea water (25.2 g NaCl l⁻¹). On the one occasion where A. arabiensis larvae were found along the transects, this was in 12% sea water (4.2 g NaCl l⁻¹).

Plant species markers for larval breeding

The relationships between dominant plant species and land surface types and the presence of either A. gambiae s.s. or A. melas are shown in table 1. A total of 365 sampling sites was included in the discriminant analysis using ten land surface classes for both mosquito species. There were too few A. arabiensis caught for this type of analysis. The presence of Eleocharis sp. and Paspalum sp. were both key indicators for the breeding of A. gambiae s.s. and A. melas. In

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**Fig. 2.** A cross-sectional view of the floodplains in the central part of The Gambia.
addition, *A. melas* was also found associated with *Sporobolus* sp., *Sesuvium portulacastrum* and hoof prints in the mud flats. Anopheline larvae were never found on the farmland and grasslands around the villages or in the forests near the alluvial deposits.

Results of larval collections outside the transects

Results of larval catches outside the transects during 1996 and 1997 are presented in table 2. Collections from flooded grass and sedge habitats inside the floodplains were
dominated by *A. melas* and *A. gambiae* s.s. with a few *A. arabiensis* confirming the findings from the transects. Rain-fed rice fields, common in alluvial creeks far from the river, were dominated by anopheline species not belonging to the *A. gambiae* complex. However, these rain-fed rice fields did have the highest density of *A. arabiensis* compared to any other aquatic habitat.

**Discussion**

The findings on the breeding of *A. gambiae* s.s., *A. melas* and *A. arabiensis* in the central part of The Gambia both support and expand the knowledge from previous work on the breeding behaviour of these species. Most larvae were caught in September, just after the peak rainy season, when the alluvial soils were flooded with relatively fresh water. This is consistent with the results from adult collections, which show a similar seasonal pattern (Bøgh et al., 1999). Most breeding took place within the first kilometre of the floodplains but high densities of larvae were found as far as 1400 m from the edge of the alluvial soils. This is most likely the result of active flight and oviposition by female mosquitoes. Eggs or larvae are unlikely to be transported this far by water flow since in transect 3, which was most affected by tides, the larvae were no greater dispersed than in the other transects. It is possible that breeding occurs even further into the floodplains, provided a suitable habitat is present. The highest density of anopheline mosquito larvae was found amongst dense vegetation, and only rarely in the free water surface. This could indicate that the adult females may use the plant species for guidance when laying their eggs. Laboratory studies further indicate that predation by fish is less frequent when the larvae lie close to grass shoots emerging from the water (S.W. Lindsay, unpublished data).

*Anopheles melas* was the most abundant species breeding in the flooded alluvium, comprising 81.5% of the *A. gambiae* complex larvae sampled, followed by 18% *A. gambiae* s.s. and 0.5% *A. arabiensis* (Bøgh et al., 2001). This apparent contradiction reflects the more zoophilic and exophilic behaviour of *A. melas* and the highly endophilic and anthropophilic habits of *A. gambiae* s.s. (Gillies & DeMeillon, 1968). Thus although *A. melas* predominates in the riparian breeding sites, *A. gambiae* s.s. is the principal vector of malaria in the area (Lindsay et al., 1993; Hemingway et al., 1995). The main breeding habitats of *A. melas* were found in flooded areas with vegetation dominated by *Sporobolus* sp., *Eleocharis* sp., and *Sesuvium* sp. resembling findings from Liberia (Gelfand, 1955) and Nigeria (Barber et al., 1931; Chwatt, 1945). The only exception to this finding was in Sierra Leone, where *A. melas* was found breeding under large stands of white mangrove (*Avicennia* sp.) (Thomson-Muirhead, 1945). Breeding in cattle hoof prints occurred where the salty mud flats became
Breeding of Anopheles gambiae along the River Gambia

Table 1. Results of discriminant analysis showing the vegetation and land surface types that are associated with the breeding of Anopheles gambiae s.s and Anopheles melas and the strength of the derived models in predicting presence of larvae based on the surface types.

<table>
<thead>
<tr>
<th>Anopheles gambiae s.s.</th>
<th>Variable</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Paspalum sp.</td>
<td>0.811</td>
</tr>
<tr>
<td></td>
<td>Eleocharis sp.</td>
<td>0.791</td>
</tr>
</tbody>
</table>

Correct classification: 80.5% (canonical correlation 0.25, Wilks’ lambda 0.94, P < 0.001)

<table>
<thead>
<tr>
<th>Anopheles melas</th>
<th>Variable</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Eleocharis sp.</td>
<td>0.700</td>
</tr>
<tr>
<td></td>
<td>Paspalum sp.</td>
<td>0.633</td>
</tr>
<tr>
<td></td>
<td>Sesuvium sp.</td>
<td>0.374</td>
</tr>
<tr>
<td></td>
<td>Sporobolus sp.</td>
<td>0.210</td>
</tr>
<tr>
<td></td>
<td>Hoof prints</td>
<td>0.204</td>
</tr>
</tbody>
</table>

Correct classification: 82.7% (canonical correlation 0.47, Wilks’ lambda 0.78, P < 0.001)

Partly flooded, creating thousands of small isolated breeding sites protected from aquatic predators. That A. melas larvae were found in association with several vegetation and surface types illustrates their less restricted choice of breeding habitat within the floodplains. Anopheles melas is a well known saltwater breeding mosquito, and was found in salinities up to 72% sea water, although it can develop successfully in 200% sea water (Rribbands, 1944a). Collections of A. melas larvae in water with less than 5% sea water, show that A. melas breeds in a wide spectrum of salinities in nature. Since Gelfand (1955) found that adult A. melas are unable to distinguish between different salinities, the association with specific plant types suggests that the mosquitoes may use these for guidance for ovipositioning sites.

The highest densities of A. gambiae s.s. larvae were found near the edge of the floodplain area. This supports the findings of Muirhead-Thomson (1945) in Sierra Leone who described freshwater A. gambiae s.l. breeding near the landward edges of the floodplains. Anopheles gambiae s.s. larvae were, however, also found at high densities up to 1300 m into the flooded alluvial soils illustrating that they breed in most of the flooded areas as long as a suitable habitat is present. Although A. gambiae s.s. larvae are typically associated with freshwater, larvae were found in water up to 30% sea water, which is close to the upper limit of tolerance of 37.5% found under laboratory conditions for freshwater A. gambiae s.l. (probably A. gambiae s.s.) (Ribbands, 1944a). To our knowledge this is the first time A. gambiae s.s. has been described at such high salinities in nature, showing that A. gambiae s.s. do breed in mildly brackish waters. The highest number of A. gambiae s.s. larvae were, however, found just after the peak rainy season when water salinity was at its lowest. Anopheles gambiae s.s. were found breeding in association with the grass Paspalum sp. and the spike rush Eleocharis sp. Sporobolus sp. is abundant along the edges of the floodplains, whereas Eleocharis sp. is found in more constantly flooded areas further into the floodplains. A. gambiae s.s. and A. melas often coexisted in the same sites. This phenomenon may have been enhanced by the water movements and changing salinity caused by the rains and tidal changes. Whilst some inter-species competition may occur it is clearly not enough to exclude coexistence of the two species. Presumably A. gambiae s.s. and A. melas have overlapping larval habitats and the immediate saltwater concentration defines which of the two species will be the most successful competitor.

Collections from outside the transects confirmed that the larval habitats on the flooded alluvium are dominated by A. melas and A. gambiae s.s., with occasional breeding of A. arabiensis. It was expected that the rain-fed rice fields on the edge or just outside the alluvium would be an important breeding sites not covered by the transect collections. The catches from these sites, however, suggest that they are of only minor importance for A. gambiae s.s. and A. melas, but are the main habitat for A. arabiensis, since this species was found in relatively high numbers in this habitat. These findings suggest that the main breeding habitat for A. arabiensis is not in the large flooded areas but in the more temporary rain-fed pools on the periphery of the alluvial deposits. High densities of adult A. arabiensis have previously been described near irrigated rice fields in The Gambia during the dry season (Lindsay et al., 1991).

In conclusion, this study demonstrates that almost all breeding of the A. gambiae complex takes place within the flooded alluvial soils illustrating that they breed in most of the flooded areas as long as a suitable habitat is present. Although A. gambiae s.s. larvae are typically associated with freshwater, larvae were found in...
done in an area affected by salt-water intrusion, it is likely that similar breeding patterns exist along other flood-prone river systems in the Sahel region of Africa. Despite these areas covering only a small proportion of the landmass of Sahelian Africa, they account for a disproportionately large part of the malaria transmission in the region.

Acknowledgements

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A Dictionary of Entomology

G Gordh, University of Queensland, Australia, and
D H Headrick, California Polytechnic State
University, USA

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Readership
All professionals and students of entomology and related disciplines.

Description
This book is a comprehensive, fully cross-referenced collection of over 28,000 terms, names and phrases used in entomology, incorporating an estimated 43,000 definitions. It is the only listing which covers insect anatomy, behaviour, biology, ecology, histology, molecular biology, morphology, pest management, taxonomy and systematics. The origin, etymology, part of speech and definition of each term and phrase are all provided, including the language, meaning or root of each term and constituent parts. Where meanings have changed, or terms have been borrowed from other disciplines, the most current usage is indicated.

The common names of insects, their scientific binomen and taxonomic classification are provided, with diagnoses of pest species in many cases. All insect order, suborder, superfamily, family and subfamily names are given, together with the diagnostic features of orders and families. Names of deceased entomologists, or scientists from other fields who have contributed to entomology are included, with the citation for their biography or obituary. This book is an essential reference source for all professionals and students of entomology and related disciplines.