Distribution and range expansion of deer in Ireland

Ruth F. CARDEN* National Museum of Ireland – Natural History, Merrion Street, Dublin 2, Ireland. E-mail: rcarden@museum.ie
Caitríona M. CARLIN Applied Ecology Unit, Centre for Environmental Science, Environmental Change Institute, National University of Ireland Galway, Ireland. E-mail: caitriona.carlin@nuigalway.ie
Ferdia MARNELL National Parks and Wildlife Service, Department of the Environment, Heritage & Local Government, 7 Ely Place, Dublin 2, Ireland. E-mail: ferdia_marnell@environ.ie
Damian MCELHOLM The British Deer Society, Northern Ireland Branch, c/o The British Deer Society, The Walled Garden, Burgate Manor, Fordingbridge, Hampshire SP6 1EF, Britain. E-mail: info@damianmcelholm.com
John HETHERINGTON The British Deer Society, Northern Ireland Branch, c/o The British Deer Society, The Walled Garden, Burgate Manor, Fordingbridge, Hampshire SP6 1EF, Britain. E-mail: hetherington@utvinternet.com
Martin P. GAMMELL Department of Life and Physical Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland. E-mail: martin.gammell@gmit.ie

ABSTRACT
1. Throughout Europe, the range of many deer species is expanding. We provide current distribution maps for red deer *Cervus elaphus*, sika *Cervus nippon*, fallow deer *Dama dama* and muntjac deer *Muntiacus* sp. in Ireland, and estimates of range expansion rates for red deer, sika and fallow deer.
2. There was a considerable expansion in the ranges of red deer, sika and fallow deer between 1978 and 2008. The compound annual rate of expansion was 7% for red deer, 5% for sika and 3% for fallow deer. The total range increase was 565% for red deer, 353% for sika and 174% for fallow deer. The potential implications of these expansions are discussed.
3. There are unknown numbers of red-sika hybrid deer in some parts of Ireland. Range expansion is likely to lead to further hybridizations with implications for the genetic integrity of deer stocks.
4. Sightings of free-roaming muntjac deer were first recorded in 2007. The distribution of confirmed sightings of single and multiple animals in the eastern region of Ireland suggests multiple releases.
5. Deer are already impacting on both the economic and biodiversity values of habitats in Ireland, where, at present, no sustainable deer management policy exists.

*Keywords*: deer densities, dispersal, invasive species, non-native species, translocations

*Correspondence author.
INTRODUCTION
Throughout Europe, the range of many deer species is expanding (Apollonio et al. 2010). In many countries, deer densities are also increasing with many negative implications such as (i) detrimental impacts on ecosystems, habitats and vegetation; (ii) damage to protected environments; (iii) conflict with commercial land use objectives; (iv) increased risk of deer being involved in motor vehicle collisions with potential for both deer and human fatalities or severe injuries; and (v) increased risk of disease transmission (Johnson et al. 2003, Gortazar et al. 2005, Böhm et al. 2006, Linden et al. 2010). Some of these negative impacts are already apparent on the island of Ireland (hereafter referred to as Ireland) due to increasing and expanding populations of deer species (Purser et al. 2010).

There are four species of wild-ranging deer in Ireland. Three species have certainly been introduced by humans: fallow deer *Dama dama*, sika *Cervus nippon* and muntjac deer *Muntiacus* sp. Red deer (*Cervus elaphus*) may be native or introduced; the debate is ongoing (for further detail see Whitehead 1964, Woodman et al. 1997, McCormick 1999, Staines et al. 2008, McDevitt et al. 2009, Pérez-Espona et al. 2009). Whitehead (1960, 1964) provided a detailed review of the origins of Irish populations of sika, fallow deer and red deer.

Hybridization between red deer and sika has been documented in both Britain and Ireland (Harrington 1973, Lowe & Gardiner 1975, Harrington 1982, Ratcliffe et al. 1992, Goodman et al. 1999, Diaz et al. 2006, Pemberton et al. 2006, McDevitt et al. 2009, Pérez-Espona et al. 2009) and in the Czech Republic (Bartoš et al. 1981, Bartoš & Žirovnický 1981, Zima et al. 1990, Bartoš 2009), and there is concern about the potential for hybridization elsewhere (e.g. Germany: Wotchikowsky 2010). Hybridization of red deer and sika first occurred in eastern Ireland soon after sika were introduced to the country, and as a result of escapees to the wild and subsequent interbreeding, a substantial proportion of wild red- and sika-like deer in the east and north of the country are now thought to be hybrid animals (Harrington 1973, 1982, Hayden & Harrington 2000). As yet, there is no direct evidence that the sympatric red deer and sika are hybridizing in the south-west region (McDevitt et al. 2009). Recent molecular analyses indicate that hybridization in the eastern region of Ireland may not be as extensive as was previously thought (McDevitt et al. 2009) although further investigations are warranted as species purity is difficult to prove.

There have recently been several substantiated reports of muntjac deer in the east of Ireland: almost certainly *M. reevesi* as this is the species that is now well established in Britain (Chapman 2008). There have also been unsubstantiated reports from the north-west of Ireland and anecdotal reports in various locations in Northern Ireland (see Dick et al. 2009). This suggests that there have been recent multiple deliberate releases of this species, although the source or sources of these releases are unknown at present. Under the Irish Wildlife Acts (1976, 2000) and the 1985 Wildlife Order to Northern Ireland (presently under review), it is illegal to introduce new faunal species to Ireland.

Ní Lamhna (1979) produced 10km distribution maps for deer in Ireland. More recently, Hayden and Harrington (2000) produced distribution maps for wild deer in Ireland, based on their presence in 20km squares. In this later survey, however, the
authors did not attempt to assess rates of range expansion. Ward (2005) and Ward et al. (2008) recently produced distribution maps and estimates of rates of range expansion for wild deer in Britain, based on their presence in 10km squares. The aim of this study is to offer a parallel analysis by providing updated distribution maps for red deer, sika and fallow deer in Ireland, based on their presence in 10km squares, and to provide estimates of rates of range expansion in the 30-year period since the publication of the 1978 distribution atlas (Ni Lamhna 1979). In addition, the current distribution of confirmed sightings and reports from Ireland of muntjac deer is presented for the first time.

METHODS
Information on deer distribution in 1978 was taken from maps compiled by the Irish Biological Records Centre (Ni Lamhna 1979). These maps provided records of all 10km squares occupied by each species up to 1978. The data originated mainly from professional biologists, although some records from the public were included subject to critical review by experts (Ni Lamhna 1979).

Republic of Ireland (ROI)
Information on the distribution of all red deer, sika and fallow deer in 2008 was obtained from a variety of sources. Firstly, data were collated from distribution maps received from the local branches of the Irish Deer Society, on which the branch secretaries had collated the knowledge of the Society members and local contacts. Data were also collected by regional staff of the National Parks and Wildlife Service: each ranger completed a deer record sheet for his or her geographical area in the ROI. Additionally, various ‘users’ of the countryside (consultant ecologists, mammal surveyors, recreational users, etc.) were consulted directly. To reduce the likelihood of misidentification of deer species, all recorders contacted were provided with species recognition profiles. All recorders demonstrated an ability to identify all deer species correctly in all seasons. Similarly, confirmed sightings and all unsubstantiated reports of muntjac deer were collated during 2008 and 2009; only confirmed sightings were used to estimate distribution of muntjac deer. In addition, supplementary records were validated by one of the authors (RFC) in the ROI by direct visual observations in the field and from digital images. This methodology is comparable to the methods used in the 1978 survey (see Ni Lamhna 1979).

Northern Ireland (NI)
In 2005, The British Deer Society (BDS) carried out a specific deer survey in Great Britain and Northern Ireland; for each 10km square, the presence of sika, fallow deer and red deer was recorded. To our knowledge, this was the first time that the whole of Northern Ireland was surveyed for deer. BDS-NI members sent their field observation reports to the BDS-NI Deer Recorder (J Hetherington), who used this information in conjunction with his local knowledge to compile distribution maps for Northern Ireland. Where it was possible, records were verified by the Deer Recorder who either personally checked reports or consulted with local experts.

Distribution and range expansion
Distribution maps were plotted for red deer, sika, fallow deer and muntjac deer using MapMate Version 2.2.1 (MapMate® software version 2.2.1. MapMate Ltd,
Exeter, UK, http://www.mapmate.co.uk). We did not attempt to compile distribution maps for red-sika hybrids, as their exact range can only be clarified through a large-scale molecular study (McDevitt et al. 2009). In those areas of the country where hybrid deer are thought to exist, we classed all red-like deer as red deer and all sika-like deer as sika based on external morphological appearance.

Following Ward (2005), we calculated the compound annual rate of range expansion, expressed as a percentage, and quantified the total percentage range expansion between 1978 and 2008, for all three species.

RESULTS
There was a considerable expansion in the ranges of all three species of deer in Ireland between 1978 and 2008 (Fig. 1; Table 1). The compound annual rate of expansion ranged from 3% per annum (p.a.; fallow) to 7% p.a. (red). Total range increase at the end of the 30-year period ranged from 174% (fallow) to 565% (red).

Red deer increased their range at the greatest rate (7% annually over the 30-year period). In the 1978 survey, red deer were found in four separate populations; two in the east of the country, one in the south-west and one in the north-west (see Fig. 1). These areas were still strongholds for the species in 2008. The populations in each area expanded during the last 30 years (total range increase 565%) but red deer remained the least widely distributed species in 2008 (they occupied the lowest number of grid squares).

Most sika records in 2008 were in the same general areas of the country that this species occupied in 1978. However, there were also several outlying records (see Fig. 1). Sika expanded their total range by 353% (or 5% p.a.) during the 30-year period.

Fallow deer were the most widely distributed species although their total range increase was the lowest (174%). In 2008, fallow deer occupied a total of 268 grid squares (out of a possible total of 1168); although they were not recorded in 30 of the grid squares that they occupied in 1978 (see Fig. 1). Over the 30-year period covered by this study, fallow deer expanded at a slower rate (3% compound annual rate of expansion) than the other two species, and were largely absent from the areas occupied by red deer and sika.

Muntjac deer were observed in eight 10km squares within two counties in the east of Ireland (Wicklow and Kildare). Further anecdotal sightings which to date remain unsubstantiated were reported from Counties Wexford, Longford, Leitrim, Sligo, Roscommon and Donegal. Neither these nor the anecdotal sightings from Northern Ireland (Dick et al. 2009) were included in the distribution map (Fig. 1) as they have not been independently verified.

DISCUSSION
The total ranges of three species of deer in Ireland expanded considerably over the 30-year period from 1978 to 2008: red deer expanded their total range by the greatest percentage, followed by sika and then fallow deer. In two recent studies, researchers estimated range expansion in deer species in Britain. Ward (2005) calculated annual rates of range expansion over a 30-year period, between 1972 and 2002 (0.3% for red deer, 5% for sika and 2% for fallow deer). Ward et al. (2008) calculated
annual rates of range expansion between 2003 and 2007 (7% for red deer, 7% for sika and 13% for fallow deer). It is difficult to make direct comparisons between expansion rates calculated in each study due to varying time periods, potential differences in methodologies and recording efforts, and differences in land mass and

Fig. 1. Distribution maps of (a) red deer, (b) sika, (c) fallow deer and (d) muntjac deer in 10km squares in Ireland in 1978 (squares indicate positive records) and 2008 (2009 for muntjac deer; dots indicate positive records).
habitat cover. Ward et al. (2008) noted that the differences in the expansion rates between both of the British studies (Ward 2005, Ward et al. 2008) may be real or may be due to better coverage or reporting in the later study, or due to habitat cover or topography differences between the studies.

The methodology used in our study may have had a bearing on the rates of range expansion that we calculated. Our distribution maps are based on recorded presence data only, and do not show absence. The absence of a species from any area is impossible to prove due to numerous factors that include species’ ecologies, mobility, environmental and habitat variables (Greenwood & Robinson 2006, Krebs 2006). However, it is reasonable to assume that the absence of records from 10km squares is broadly indicative of the actual pattern of absence.

To facilitate our analyses, we had to assume that the deer were correctly identified (as did Ward 2005), but it is possible that some deer may have been misidentified. However, we minimized the possibility of this occurrence through the provision of species recognition profiles and validation of records by experts, either in the field or from digital images. Our results could also be affected by differences in methodology and/or recording effort in 1978 and 2008. We minimized these differences by taking a broadly similar approach to that followed in 1978.

Ward (2005) and Ward et al. (2008) found that the extent of overlap between sika and red deer ranges increased in Britain, in particular between 1972 and 2007 in Scotland and north England, thereby providing more opportunities for inter-breeding between the species. Even with such opportunities, interbreeding does not seem to be a common occurrence. In Britain, hybridization is an uncommon event even where substantial populations of both red deer and sika occur in the wild (Goodman et al. 1999, Diaz et al. 2006, Senn & Pemberton 2009, Senn et al. 2010). Hybridization of red deer and sika does not seem to have occurred in the Kerry region in the south-west of Ireland (McDevitt et al. 2009), despite their sympatric occurrence in that region for nearly 150 years (sika were introduced to Killarney, County Kerry in 1865; Whitehead 1960, 1964). The population of red deer in County Kerry may be the remnants of an ancient late Pleistocene or early Holocene population, although it is equally plausible that it is descended from stock introduced at some stage during the early Mesolithic or Neolithic periods and/or later by humans (Woodman et al. 1997, McCormick 1999, McCormick & Murray 2007). The eastern deer population is known to contain red-like hybrids (McDevitt et al. 2009). If range expansion continues, it is likely that the eastern and south-western deer populations will meet. The genetic integrity of the Kerry red deer and sika populations may then be threatened by hybridization with the red-like hybrids. It is difficult to predict when these separate populations will meet,

Table 1. Deer distributions (10km squares) in Ireland in 1978 and 2008, rates of range expansion over 30 years and total increase in range by the end of the 30-year period covered by this study

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of squares occupied in 1978</th>
<th>Number of squares occupied in 2008</th>
<th>Compound annual rate of range expansion</th>
<th>Total increase in range 1978–2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red deer</td>
<td>31</td>
<td>206</td>
<td>6.5%</td>
<td>564.5%</td>
</tr>
<tr>
<td>Sika</td>
<td>47</td>
<td>213</td>
<td>5.2%</td>
<td>353.2%</td>
</tr>
<tr>
<td>Fallow deer</td>
<td>98</td>
<td>268</td>
<td>3.4%</td>
<td>173.5%</td>
</tr>
</tbody>
</table>

318 R. F. Carden et al.

as numerous factors could have an impact on the continued rate of range expansion of both populations. For example, landscape features have been shown to be a barrier for dispersal (gene flow) for red deer in mainland Scotland (see Pérez-Espona et al. 2008). Swanson and Putman (2009) remarked that populations of sika found in England and parts of Scotland are expanding at different rates; some populations show rapid increases but others do not. They suggest that these different rates reflect availability of suitable habitat for colonization, and to a lesser extent, that landscape features such as roads, railways and urban settlements impede dispersal of this species. Lone young individual sika males disperse first and can appear in areas with no established sika, and join red deer populations (Bartoš 2009, Swanson & Putman 2009). As proposed in Britain (Pérez-Espona et al. 2009), selective culling of these ‘pioneering’ sika males should be encouraged if there is a threat to the genetic purity of red deer populations, and this has been the recommended management strategy for County Kerry (McDevitt et al. 2009).

There are other, probably more immediate, threats to the genetic integrity of the south-west populations of red deer and sika in Ireland. There are populations of red deer in Ireland in addition to those that occur in their original strongholds (see Whitehead 1960, 1964), partly as a result of planned translocations, but also probably due to accidental and deliberate releases. At least one of the outlying records of sika between the south-west and eastern populations (Fig. 1, closest single record immediately north-east of the south-west sika population) is strongly suspected to be due to a deliberate release, currently of unknown origin and pedigree. Moreover, the genetic integrity of both species is threatened by the potential for interbreeding with populations of red deer and sika derived from multiple stocks (British, Scandinavian, various other European locations) that have been introduced to privately owned estates, parks (some of which are not enclosed), deer farms and other locations in Ireland (Whitehead 1960, 1964, Carden 2007). For example, the subpopulation of Kerry red deer that was translocated to Connemara National Park, County Galway in 1982, has been infiltrated by deer of unknown provenance (Nolan & Walsh 2005). In Ireland, a targeted survey of the area between the south-west and eastern populations of red deer and sika (wild populations and those enclosed on deer farms and in deer parks) may be timely, along with further genetic studies that can clarify the history of each population.

The increase in the number of grid squares occupied by sika between 1978 and 2008 appears to have been primarily due to natural range expansion, as most sika records in 2008 were in the same general areas of the country that this species occupied in 1978 (Ni Lamhna 1979). However, there were also several outlying records of sika, suggesting some anthropogenic influences on their range expansion between 1978 and 2008. As discussed above, at least one of these outlying records is thought to be due to a deliberate release. There are, of course, other possible explanations for the outlying records. They may represent populations that have been established for some time but were overlooked in the 1978 survey, although we consider this unlikely because, based on the changes to other populations over the 30-year period, there is no evidence of the expansion expected if there had been a population present in 1978. It is also possible that some were a result of misidentifications in the current (2008) study, although we made efforts to minimize the potential impact of misidentifications on our data (see Methods section).
Fallow deer can now be found in most counties of Ireland, compared to less than half of the 32 counties of Ireland in which Whitehead (1964) and Ni Lamhna (1979) reported them. An obvious feature of the distribution maps in Fig. 1 is that, in Ireland, fallow deer appear, in general, to occupy different areas of the country than red deer and sika. Sika seem to be associated with acidic soils in Britain (Putman 2008), whereas fallow deer appear to favour a mosaic of open woodland and pasture – a landscape typical of the largely limestone-based Irish lowlands. Such distribution differences between deer species may be due to competitive exclusion, differing habitat preferences, the locations of the original founder populations or a combination of these factors (Putman 1988). A similar general pattern was presented by Ward (2005) and Ward et al. (2008). Fallow deer, in Ireland at least, seem to expand their range very slowly; they can build up to high densities, but tend to remain in the area of the original release or escape (Chapman & Chapman 1975, Macdonald & Tattersall 2001).

The muntjac is a recent arrival in Ireland. The exact range of the Irish population is not known with certainty. Unknown numbers of muntjac are held in captivity in privately owned collections throughout the island; it is possible that some of these may have escaped or were deliberately released into the wild. It is also possible that Britain, as the closest landmass with wild-ranging muntjac, is a source of illegal introductions to Ireland. It is probable that Irish sightings are of Chinese muntjac *M. reevesi* as this is the only widespread muntjac species in Britain (Chapman 2008). The muntjac is classified as an invasive species in Ireland; at high densities, there is a potential for serious impact on woodlands (ground flora and coppice) and they may become a nuisance in gardens. Previous studies on the negative impacts of muntjac on vegetation in Britain have focused on extreme situations where population densities are high, and therefore, these studies are not necessarily more widely representative of the potential impact of this species at lower densities (e.g. Tabor 1993, Cooke & Farrell 1995, Díaz & Burton 1996, Tabor 1999, Cooke & Farrell 2001, Cooke 2006).

Confirmed sightings of muntjac, comprising one or more deer, appear to be concentrated in parts of Counties Wicklow and Kildare. There have also been reports of muntjac from Counties Wexford, Leitrim, Sligo, Roscommon, Donegal and Longford, although these are not, as yet, validated. Dispersed sightings suggest multiple original release sites. Populations in some areas may have been established for a number of years, since this species is only now coming to general attention. The National Parks and Wildlife Service (NPWS) in the ROI have declared a 12-month open season on this species in recognition of its threat to biodiversity and in an attempt to control its spread in Ireland. However, there is a real danger that this species will become established in the country.

Our study shows that the ranges of the three established deer species in Ireland have increased significantly in the past 30 years, suggesting that population sizes have also increased. Irish deer-hunting returns indicate increasing numbers of deer are being shot each year nationally – from 6173 in 1997/1998 to 24513 in the 2007/2008 season (source: NPWS). Additionally, the number of deer-hunting licences issued in Ireland is increasing every year. In 1977, 231 licences were issued; in 2008, 3444 licences were issued, primarily to non-commercial or recreational hunters (source: NPWS). However, these licences are not issued based on the number of deer present in any given area and therefore, the numbers of deer shot could be a reflection of the number of issued licences rather than of increases in population.
sizes. As range expansion of the various deer species present in Ireland (including the recent introductions) continues, it is likely that local biodiversity will be impacted, unless there is sufficient deer management effort to maintain deer densities at levels that limit negative impacts on the ecosystems and landscape units. Of particular concern is the potential negative impact on woodland habitats protected under the European Union’s Habitats Directive, and on timber production in commercial forests (both broadleaved and conifer plantations; Purser et al. 2010).

There is no national deer management policy in Ireland and no single authority with responsibility for managing deer (Purser et al. 2010). The time has come for integration between State agencies (e.g. Department of Agriculture, the Forest Service, Coillte Teoranta, NPWS), other bodies (e.g. Woodlands of Ireland, Irish Farmers’ Association, non-governmental organizations such as the Irish Wildlife Trust, Pro Silva and all deer societies) and independent experts, and for the allocation of dedicated staff and funding towards the management of deer in Ireland. Purser et al. (2010) recommend the establishment of a dedicated independent all-Ireland deer management unit, with adequate statutory powers and budgets to effect necessary changes resulting in a deer management system, which is fully integrated with forest management and other land use and related policies. We propose a similar approach, although a national management plan (specific for each species) suited to Ireland would, ideally, combine different aspects and approaches drawn from deer management policies and plans already successfully established in other European countries, such as those from Britain (e.g. the Deer Initiative and the Deer Commission for Scotland; Putman 2010) and Scandinavia (Andersen & Holthe 2010, Andersen et al. 2010, Liberg et al. 2010, Ruusila & Kojola 2010). All species need to be managed to and at levels that minimize negative impacts on land-use objectives and that take the potentially conflicting requirements of various interested parties, such as commercial foresters, recreational hunters and conservation biologists, into account. This will necessitate the coordination of actions in Northern Ireland and the Republic of Ireland. Full enforcement of the Wildlife Acts (ROI) and the Wildlife Order (NI) and the European Communities (Trade in Animals and Animal Products) Regulations 1994 (S.I. no. 289 /1994; S.I. no. 269/2004) is certainly required, in particular with relation to the importation of live deer at various first points of entry to Ireland. The introduction of additional legislation may also be necessary; for example, an ear tagging system for importing and holding deer, particularly species at high risk of escape and establishment in the wild. Equally beneficial would be statutory monitoring of captive deer populations by suitably qualified personnel from within the Departments of the Environment, Heritage & Local Government and Agriculture, Fisheries & Food (ROI) and the Department of Agriculture & Rural Development and Northern Ireland Environment Agency (NI).

Educational initiatives are also required to provide information on various aspects of deer ecology, management issues and the potential impacts of illegal releases of deer species. The general public should be made aware of both the negative and the positive impacts of deer as well as the most humane, cost-effective and efficient options for managing deer populations, which are primarily likely to involve sustained culling practices, along with the judicious use of other methods, such as tree guards to reduce browse damage (Ward & Mervosh 2008), and signs, fences and road-crossing structures to reduce vehicle collisions (Putman 1997, Mata et al. 2008).
The expansion observed in Irish deer stocks during the last three decades may be explained by a variety of factors. Possible explanations include the introduction of protection under the 1976 Wildlife Act (ROI) and the 1985 Wildlife Order (NI), the significant spread of forest cover in recent decades (in particular the establishment of commercial plantations nationwide) and some illegal translocations, deliberate releases, and/or escapees from captive holdings that may account for unexpected records of deer in certain areas. Expanding deer populations are likely to have a variety of negative impacts, particularly on biodiversity and commercial forestry, and especially if populations reach unacceptable densities in relation to local land-use objectives. The development of an integrated all-Ireland management strategy for each of the three established species of deer therefore seems overdue. Such a strategy should also consider options, such as enhanced legislative powers, for reducing the likelihood of exotic species (such as muntjac) becoming established in the wild.

ACKNOWLEDGEMENTS
We thank the members of the various deer societies in the Republic of Ireland (Wicklow Deer Society, Wild Deer Association of Ireland and Irish Deer Society) and to the British Deer Society-Northern Ireland members who helped with the 2005 NI survey and additional records, Mr John Maguire and the regional staff of the National Parks and Wildlife Service, Conor Kelleher, Bruce Banwell, Hugh Rose, Daniel Buckley and all those who provided information on the distribution of deer in Ireland. We thank Rory Putman, Nigel Monaghan, Allan McDevitt and David O’Brien who kindly provided invaluable comments on earlier versions of the manuscript. We also thank Klaus Hackländer and two anonymous reviewers for the suggestions and comments, which helped refine the paper. RFC gratefully acknowledges the facilities provided by Mr Nigel T. Monaghan, Keeper of Natural History, National Museum of Ireland.

REFERENCES


Submitted 4 February 2010; returned for revision 4 March 2010; revision accepted 2 July 2010
Editor: KH