Birdwatchers, at least in Britain, tend to think of ducks as nesting in the open and on the ground, but cavity-nesting is actually normal, if not obligatory, in almost one-third of the 162 members of the wildfowl family (Anatidae). Geffen & Yom-Tov (2001) suggested that hole-nesting has evolved independently at least three times within the group. I think that it is more likely to have arisen five or six times; indeed, hole-nesting could be the primitive condition. In any event, the habit occurs among whistling-ducks (Dendrocygnini), shelducks (Tadornini), in two or three different groups of surface-feeding ducks (Anatini), including those which we used to call ‘perching ducks’, and in the seaducks (Mergini).

Because ducks are incapable of making holes for themselves, however, they must rely on natural agents for the construction of nest cavities, and this dependence has profound implications for their lifestyles, breeding productivity and conservation. As Eberhard (2002) pointed out, because they are not excavators, cavity-adopting ducks have limited control over the location of their nests, and rarely nest colonially. The skills of a variety of other animals

**ABSTRACT** This paper poses a number of related questions and suggests some answers. Why were there no resident tree-hole-nesting ducks in Britain until recently? Why is the Black Woodpecker *Dryocopus martius* not found in Britain? Could the supply of invertebrate food items, especially in winter, be responsible for the distribution of woodpeckers in western Europe? It is concluded that, in Europe, only the Black Woodpecker can construct holes large enough for ducks to nest in, and that this woodpecker does not occur in Britain & Ireland because of the absence of carpenter ants *Campanotus*. A plea is made for the global conservation of dead and dying timber, since it is vital for the biodiversity of plants, insects, woodpeckers and ducks.
are employed, but the bird family which contributes most to the process of hole-making, as ‘primary cavity excavators’ (Aitken et al. 2002), is the woodpeckers (Picidae), of which there are just over 200 species (Winkler et al. 1995).

To give a few examples: Audubon (1835) observed the North American Wood Duck *Aix sponsa* laying for three successive years in holes made and abandoned by the large, and probably now extinct, Ivory-billed Woodpecker *Campephilus principalis*. Indeed, all early American explorer-naturalists (who were mostly Europeans) noted with interest that the Wood Duck nested in woodpecker holes. Bellrose & Holm (1994) actually speculated that the duck evolved its particular size and slim shape in order to take advantage of cavities created by a woodpecker which is slightly smaller than Ivory-billed but much commoner – the Pileated Woodpecker *Dryocopus pileatus*. They made the point that the range of the Wood Duck fits completely within that of the Pileated Woodpecker.

The Wood Duck’s nearest relative, the Mandarin Duck *Aix galericulata*, breeds in temperate forests similar to those inhabited by the Wood Duck, but on the opposite side of the Pacific Ocean. The males of these two beautiful ducks differ substantially in plumage and a little in size – the Wood Duck being stouter – but the females, which alone incubate the eggs, are extremely similar in appearance and body proportions (Madge & Burn 1988). Since it has been suggested, quite convincingly, that the size and shape of the American bird evolved to enable it to sit in a woodpecker hole, it seemed sensible to look for an Asian woodpecker, about the same size as the Pileated, which may have had a similar influence on the Mandarin. While it is not as rare as used to be assumed, the Mandarin is still uncommon. The forests of Manchuria, where it formerly bred, have been almost totally destroyed, and its breeding biology is little studied (Shurtleff & Savage 1996). The only woodpecker which occurs in Japan in sufficient numbers, and can produce cavities large enough for the Mandarin, is the Black Woodpecker *D. martius*. As a breeder, the woodpecker is more or less confined to Hokkaido and northern Honshu – and so is the nesting Mandarin. Black Woodpeckers are plentiful among the steep mountains of eastern Hokkaido, where Mandarins and Goosanders *Mergus merganser* also occur in the nesting season. As the female Goosander uses Black Woodpecker holes in Europe (and Pileated Woodpecker holes in America; Mallory & Metz 1999), it is likely that the Goosander and the Mandarin adopt such cavities in Japan as well. Perhaps at one time, the Mandarin nested in...
Cavity-nesting ducks: why woodpeckers matter

Male and female Mandarin Ducks *Aix galericulata*, Virginia Water, Surrey. In Japan, the current breeding range of the Mandarin closely matches that of the Black Woodpecker *Dryocopus martius* (plate 156), which is found chiefly in Hokkaido and northern Honshu.

Black Woodpecker holes in other parts of the latter’s extensive range, so that the Wood Duck/Pileated Woodpecker association in North America was mirrored by one involving Mandarins and Black Woodpeckers in Asia.

A number of holarctic seaducks are cavity-nesters, and many likewise depend on woodpeckers. Nearly 100% of Buffleheads *Bucephala albeola* use holes made by a smaller woodpecker, the Northern Flicker *Colaptes auratus*. Smeew *Mergellus albellus*, Hooded Merganser *Lophodytes cucullatus* and Common Goldeneye *B. clangula* also use cavities made by large woodpeckers, as does Barrow’s Goldeneye *B. islandica* in North America (Evans *et al.* 2002). The population of about 2,000 Barrow’s Goldeneyes in Iceland uses crevices in the lava rock, however, since neither trees nor woodpeckers are available (Kear in press).

The requirement for a degree of adaptability and accommodation by cavity-nesting ducks is obvious. The Goosander will occasionally nest among boulders, in a hole in the ground or a cavity in the bank, so treeless areas are sometimes used (Sharrock 1976; Mallory & Metz 1999). Wood Ducks and Mandarin Ducks, on the other hand, are obligate tree hole-nesters, not laying at all unless an elevated cavity can be found. By no means all will use woodpecker holes, but many prefer them if they are available. In North America, Pileated Woodpecker nests constituted only 5% of cavities deemed ‘suitable’ by researchers in one study of over 300 such holes; nonetheless, 20% of cavities actually used by Wood Ducks were old woodpecker nests (Soulliere 1990). Why should they seek out a woodpecker hole rather than one which has merely rotted? By choosing a site in which to excavate their nest, woodpeckers are maximising their chances of being free of interference from their own kind, free from last year’s nest parasites (20-50% of Black Woodpeckers may reuse last year’s hole if it was successful, but Pileated Woodpeckers seldom do; Bull & Meslow 1977; Winkler *et al.* 1995), and, most of all, free from egg-eaters such as climbing snakes and mammals. In Europe and Asia, mammalian predators include Pine Martens *Martes martes*,
Japanese Martens *M. melampus*, Stone Martens *M. foina* and Raccoon Dogs *Nyctereutes procyonoides*, while in North America, Common Raccoons *Procyon lotor* and the large Fox Squirrel *Sciurus niger* are potential predators. Woodpeckers intend their nests to be, so far as possible, out of the reach of predators, with few perches or ledges to give a foothold, and with a small entrance, so that an enemy has difficulty gaining access. Since woodpeckers are usually territorial, their holes are dispersed through the forest, and often concealed under dense canopy cover (Evans *et al.* 2002). This may not be the case with natural cavities; so, from the duck’s point of view, old woodpecker holes are more likely to be cryptic and impregnable, and to produce live ducklings at the end of 30 days of incubation.

Cavity capacity may seem a tight fit for a duck and her eggs, as most female ducks are twice as large as a woodpecker. The size of the cavity excavated by the woodpecker, however, as opposed to that of the entry hole, is determined by the size of four or five full-grown fledglings because, unlike ducks, young woodpeckers grow up within the cavity. Nest-hole capacity will, therefore, be greater than that needed for an adult woodpecker plus eggs. The Pileated Woodpecker nest has a rounder entrance than that of the Black Woodpecker: 10.8 cm × 8.7 cm was the average of 13 entrances (Haramis 1990), and the Wood Duck seems quite capable of getting through a hole of that size. Black Woodpecker entrance holes, at 13 cm × 8.5 cm, are more oval (Winkler *et al.* 1995), and a female Smew or Mandarin must turn through 90° to enter. Cavity depth and width are less easy to measure, but the average of 13 Pileated Woodpecker nests was 56 cm deep by 23 cm wide (Bull & Meslow 1977) – long enough to make it hard for a Raccoon to reach the bottom with its arm, and quite wide.

Even those few birds, including woodpeckers, which make burrows in the ground, can be useful to ducks. In South America, for instance, ground-burrowing woodpeckers (probably Campo Flicker *Colaptes campestris*) sometimes provide a home for the Speckled Teal *Anas flavi-*
rostris (Nores & Yzurieta 1980). In Africa, the African Pygmy-goose Nettapus auritus, at 250 g the smallest of all ducks, nests in the disused holes of barbets Megalaima spp. as well as those of woodpeckers. The female Ruddy-headed Goose Chlorophaga rubidiceps sometimes nests in penguin burrows, as does the Falkland Steamerduck Tachyeres brachypterus, and the Torrent Duck Merganetta armata may use the abandoned burrow of the Ringed Kingfisher Megaceryle torquata (Kear in press).

In Argentina, Speckled Teals choose abandoned chambers in the crowded compound nests of Monk Parakeets Myiopsitta monachus, and may nest colonially – a rare phenomenon among ducks; the large, enclosed stick nests are 5-20 m high in the tree canopy. At the beginning of the twentieth century, parakeet nests were built only in Tala Celtis tala trees but, since then, exotic and much taller Eucalyptus gums have been introduced. These are selected almost exclusively by parakeets and ducks as providing higher and better security from terrestrial predators (Gibson 1920; Hudson 1920; Weller 1967; Port 1998a,b). Absolute height is not a problem, since young wildfowl of hole-nesting species hatch without a fear of heights (Kear 1967) and, being small and light in weight, jump without harm to join their parent on the ground beneath.

In Australia and Madagascar, there are no woodpeckers; nevertheless, many ducks are cavity-nesters, and so storms, fire, moisture, fungus, ants (Formicidae) and termites (Isoptera) must be relied upon to provide holes, mostly in trees but in other structures as well (Simpson & Wilson 2001). The Radjah Shelduck Tadorna radjah in Australia adopts cavities made by termites and fungal infections (Frith 1982). The grey teal group, including Chestnut Teal Anas castanea, Sunda Teal A. gibberifrons, Andaman Teal A. (gibberifrons) albogularis and Bernier’s Teal A. bernieri, are essentially birds of the Grey Mangrove Avicennia marina ocean fringe of a tropical and semi-tropical range which stretches from Madagascar to Australia, and all are cavity-nesters (Young et al. 2001; Young 2002; plate 157). Cavities in mangrove trees are caused by the fall of side branches, and then by rot and termite action. Once rot sets into the crown, the tree will not live for long, so a cycle of maturing and dying swamps is essential for successful duck reproduction.

The endangered White-winged Duck Cairina scutulata of the tropical wet forests of southeast Asia is yet another obligate cavity-nester; its continued presence in largely cleared areas of southeast Sumatra has been attributed to its habit of nesting in rot-created holes in rengas trees Gluta spp. These trees are frequently left uncut in former swamp forest on account of their irritant sap, which is poisonous to humans (although apparently not to monkeys and squirrels which eat the fruit), and so are rejected by tree-cutters and the timber trade (Green 1992). Thus, the duck can sometimes survive in places which are otherwise cleared of trees. While the Egyptian Goose Alopochen aegyptiacus in South Africa is not an obligate hole-nester – about two-thirds of the population nests on the ground – it will nest in elevated positions up to 60 m high and many of these are in holes (Milstein 1993); Brown et al. (1982), Maclean (1993) and Milstein (1993) noted sites which included old Hamerkop Scopus umbretta, crow Corvus spp. and African Fish-Eagle Haliaeetus vocifer nests, cliff ledges, tree holes, burrows, church steeples, caves and buildings.

Most shelducks use mammal burrows, rather than tree holes, except for the Paradise Shelduck Tadorna variegata of New Zealand, which, until recently, lived where there were no mammals.
(the females of this species, like Barrow’s Gold-eyes in Iceland, use rock crevices instead). The Common Shelduck *T. tadorna* must have been far less numerous in Britain before the Normans introduced the burrowing Rabbit *Oryctolagus cuniculus*. Rabbits were initially kept by monks as a source of food, and housed in special warrens which were bordered by high banks and gorse hedges. The Dissolution of the Monasteries in the first half of the sixteenth century meant that the warrens were sold into private hands and, eventually, the rabbits escaped to populate the countryside, and their burrows provided underground nesting sites for shelducks. The Australian Shelduck *T. tadornoides* has likewise adopted the burrows of introduced rabbits; formerly, they must have used holes provided by ground-burrowing marsupials, some of which are now extinct. The South African Shelduck *T. cana* almost always selects burrows made by Aardvarks *Orycteropus afer*.

To summarise, many wildfowl use cavities for
nesting, although not all are obligate hole-nesters. A variety of agents create the holes, and some of the most important of these are woodpeckers. Both wildfowl and woodpeckers are thought to have evolved at much the same time in the Cretaceous period (approximately 144 to 66.4 million years ago), quite early in the evolution of the birds. So, wildfowl have been around for a long time – long enough to get used to, and make use of, the woodpeckers.

The missing ducks

Until a pair of Goosanders produced young in Perthshire in 1871, no tree-hole-nesting duck had bred in Britain. There are now two more: the human-introduced Mandarin Duck, which has been breeding successfully in the region of Virginia Water, Berkshire, since 1930 (Shurtleff & Savage 1996), and the self-introduced Common Goldeneye which first nested in the Scottish Highlands of Strathspey in 1970 (Dennis & Dow 1984). All three have spread since their initial hatch (fig. 1). The Goosander, despite being culled by fishermen concerned for salmon Salmo salar stocks, is now breeding throughout Scotland, Wales and England as far south as Devon. The Mandarin is still commonest in the Thames Valley, where, 15 years ago, it was thought to have reached a population size of at least 7,000 individuals (Davis 1988). More than 100 pairs of Common Goldeneyes now produce young every year in Scotland. In 1999, a pair bred in the Borders region,
which may suggest a slow spread southwards, and individuals are seen increasingly during the summer in England (Ogilvie et al. 2001).

Why did tree-hole-nesting ducks take so long to reach Britain? Providing the answer to that question is one of the purposes of this paper—and while I cannot be certain, I am going to suggest some explanations.

**Distribution of woodpeckers**

Leaving aside ducks for a moment, what dictates the distribution of woodpeckers, especially the larger ones, to whose ranges our northern tree-nesting ducks seem so tied? In particular, why are there no Black Woodpeckers in Britain despite a thriving population just across the channel in France and Belgium, at the edge of a huge range stretching across Europe and Asia to Japan?

Let me also pose a related query: why are there no woodpeckers of any size in Ireland? They occur on the Isle of Wight, Anglesey, and Jersey, but not on the Isle of Man nor in Ireland. Are woodpeckers such poor flyers that they cannot negotiate the Irish Sea? Hutchinson (1989) thought that the absence of woodpeckers, along with other forest birds such as Tawny Owl *Strix aluco*, European Nuthatch *Sitta europaea*, and Marsh Parus palustris and Willow Tits *P. montanus*, was due to their inability to reach Ireland at all, and their absence does support the hypothesis that immi-
Migration rates are dependent on distance from the source pool (MacArthur & Wilson 1967). Fossils of the Great Spotted Woodpecker *Dendrocopos major* have been found in Co. Clare from the time of the last glaciation, when Ireland was joined to Britain, but only the Green *Picus viridis* and Great Spotted Woodpeckers have been recorded as recent vagrants, and according to Hutchinson (1989) most of the Great Spotted Woodpecker records are of irruptive Continental birds. Lack (1969), on the other hand, thought that the difficulty of dispersal across the Irish Sea could not be the factor responsible for the lack of woodpeckers, nuthatches etc. in Ireland. The fact that the Continental Great Spotted Woodpecker is occasionally irruptive suggests that it is quite capable of reaching Ireland and the Isle of Man – it just does not thrive once it gets there. Some explanation other than their inability to fly there is necessary for the missing Irish woodpeckers.

Woodpeckers do have a curious worldwide distribution (Winkler *et al.* 1995). Although occurring in the Bahamas, the Canaries and the Philippines, they are not found on some other conspicuous islands and continents, such as New Zealand, Australia, New Guinea, Madagascar (where the Aye-Aye *Daubentonia madagascariensis* is said to fill their niche by eating insects from rotting wood with a hugely elongated third finger – Young 2002) or on the Galapagos, where the Woodpecker Finch *Camarhynchus pallidus* classically performs that role (Lack 1947). There seems to be no evidence that Black Woodpeckers have been wiped out from Britain – the species has not been present since the last Ice Age (10,000-12,000 years ago) at least. Similarly, Ireland seems to have had no recent resident woodpeckers. Fungal decay of trees large enough for cavity excavation is a priority requirement. In Belgium, 40% of Black Woodpeckers make their nests in Beech *Fagus sylvatica* wood, often in the avenues of Beeches which line busy roads, and only 20% in pines *Pinus*. The Beech is a hardwood tree which is subject to heart rot and so becomes easy for the birds to excavate. Historically, it is a native of only the southeast corner of Britain, but Black Woodpeckers also excavate the decaying wood of pine and spruce *Picea*, so that the comparative rarity of Beech until recently does not seem sufficient reason for the absence of Black Woodpeckers.

**Woodpecker food supply**

I believe that the clue to woodpecker distribution in Britain & Ireland lies in their food supply, and in the availability of two kinds of wood-living insects – beetles (Coleoptera) and ants. The birds collect these insects with the aid of a long tongue and sticky saliva. The variety and size of insects becomes fewer and smaller respectively as one goes west from the Continent to England and then across the Irish Sea. Sixty-two species of longhorn or woodboring beetle (Cerambycidae) occur in Britain, particularly on oaks *Quercus* spp., willows *Salix* sp., poplars *Populus* spp. and pines, but this is only a quarter of the 250 species occurring in central Europe, and the Continental ones are typically larger in body size (McLean & Speight 1993). A Black Woodpecker may consume 900 bark beetle larvae or 1,000 ants in a single meal, and the largest beetle larva recorded as being taken was over 6 cm long (Cramp & Simmons 1977) – there is nothing of this size in Britain. Why have the larger longhorn beetles not spread more widely? Presumably because they do not fly powerfully, as there is no strong selection in

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**Fig. 2.** The number of ant species per British vice-county and the zones where daily sunlight in May averages 5-6 hours. Black: over 30 species; dense dots: over 20; light dots: over 10; blank: 1-10. Reproduced from the New Naturalist *Ants* (Brian 1977) with kind permission of HarperCollins.
favour of long-distance dispersal – the next dead tree in an unmanaged forest is usually not far away (McLean & Speight 1993). As adults, they are dependent on the pollen of flowers, and are often to be seen feeding in the sunshine, or on warm evenings. Possibly our summers are not warm enough nor, especially, dry enough for them, or perhaps our winters are not sufficiently cold.

All European woodpeckers take ants, notably, of course, our own Green Woodpecker, which takes about 2,000 daily, mostly collected from lawns and meadows. Pileated and Black Woodpeckers are especially fond of carpenter ants of the genus *Campanotus*, which, although extremely widespread, do not occur in Britain & Ireland. Unlike the longhorns, ants live in, rather than feed on, dead wood. Their distribution again seems to be determined mainly by temperature, and a map of ant abundance (fig. 2) closely mirrors one showing abundance of British breeding woodpeckers (fig. 3). A bias to the south is obvious: of the 42 species of ant found in Britain & Ireland, 33 occur in Dorset, 31 in Hampshire, 29 in Surrey, 18 in North Wales, 14 in the northern Highlands of Scotland, 18 in Leinster and nine in Ulster (Brian 1977). I believe that it is the availability of longhorn beetles and ants, especially in winter, that determines woodpecker success in Britain.

Nevertheless, British woodpeckers obviously do eat other things besides beetle larvae and ants. The Great Spotted Woodpecker seems particularly adaptable; since the 1960s, it has come onto bird tables, where it consumes fat, and seeds such as peanuts. Indeed, the fact that it eats spruce and pine seeds on the Continent, and that these fail in some years, is probably the cause of its occasional irruptive behaviour. It also takes nestling birds and moths. The two larger British woodpeckers have spread and increased in the last 100 years as the climate has...
ameliorated, and they are presumably helped by increasing forestation, which has assisted the spread of the wood ants *Formica* spp. The Green Woodpecker has invaded Scotland, the Great Spotted Woodpecker has moved north, and both are thought to have benefited, temporarily, from Dutch Elm disease (Sharrock 1976). The Lesser Spotted Woodpecker *Dendrocopos minor* eats moths (Lepidoptera) and greenfly (Aphididae) in Britain (but seems to feed its nestlings on tree-climbing ants), and its numbers are currently declining for reasons which are not obvious.

Ants and beetles may have multiplied and spread in Britain during the last half-century, but they are not counted so regularly nor completely as birds, and few distribution maps have been compiled.

So I may not be entirely correct in suggesting that the comparative lack of ant and beetle diversity in Ireland accounts for the lack of woodpeckers there. Clive Hutchinson wrote in 1989 that ‘the only certainty at this stage is that much more remains to be said on the subject’. I do, however, feel that food supply, especially in winter, is likely to be the critical factor. Moreover, I suspect that the reason why there is no thriving population of Black Woodpeckers in Britain is the absence of carpenter ants, which are such an important element of their winter food across a range that extends from France to Japan. The closest carpenter ant to these islands in Europe is the tree-dwelling *Campanotus herculeanus*, which, as its name suggests, is large. It lives in rotten wood and in big colonies; it therefore needs large old trees (Holldobler & Wilson 1990). Maybe our trees are generally too small for it. It also likes warm dry summers and cold winters. It has ‘anti-freeze’ arrangements in its physiology so that it is able to hibernate, stationary, within the wood, unless it is dug out by a probing woodpecker. Apparently, *C. herculeanus* occurred in Britain during the last interglacial period, but died out; today, it would probably find our climate too warm and our winters too unpredictable.

Food supply, in particular the comparative lack of ant and beetle diversity, may be a critical factor in explaining why this species is absent from Ireland.
To return to the missing tree-hole-nesting ducks, I suggest that Britain historically had no such birds because of the absence of Black Woodpeckers – the only creature large enough to excavate safe, sizeable cavities in wood. Why, then, do we now have three? Three changes may have influenced this situation, to varying degrees. One is that predator-proof cavities have become available from another source – from humans, in the form of nestboxes. Another factor has been a drastic decrease in our largest tree-climbing and egg-eating predator, the Pine Marten, brought almost to extinction during the last two centuries by gamekeepers who treated it as vermin (Corbet & Southern 1977). A third factor might be climate change – we entered another warming period in the 1880s, and our springs have become milder. Warmer springs are likely to have been relevant to both Common Goldeneye and Goosander as they are early nesters and lay on shorter daylengths than other species in the seaduck group (Murton & Kear 1978). I am inclined to believe that the Mandarin Duck is also affected by early spring temperatures (Kear 1990), and would not have survived its release into Britain if the climate had been that of the pre-1850s when the River Thames regularly froze in winter.

Nestboxes
Secure nesting sites are a priority requirement of cavity-nesting ducks, and boxes which can be rendered predator-proof can be an excellent tool for increasing the local productivity (Zicus 1990; Ludwichowski et al. 2002). In the case of Black-bellied Whistling-duck *Dendrocygna autumnalis* in Texas, hatching success was 44% in cavity nests but 77% in nesting boxes protected with predator guards (Bolen 1967).

Almost all Scottish Common Goldeneyes use nestboxes, but it took 14 years for the first bird to lay in one of the boxes supplied (Dennis & Dow 1984) – perhaps the individual was a female that had herself hatched in a box on the Continent. The small British breeding population is still largely dependent on boxes rather than on natural holes, and I doubt that the Common Goldeneye would be nesting so successfully were it not for those nestboxes. An absence of large tree-climbing predators probably contributed to that initial success – though a gradual increase in Pine Martens since the 1920s (Corbet & Southern 1977), owing to a reduction in keepers and the growth of new conifer plantations, has meant that martens now take Common Goldeneye eggs in the Highlands occasionally (Dennis & Dow 1984).

Obviously, Mandarin Ducks would not be
breeding in Britain if someone had not intro-
duced them. The initial breeding of a sizeable
population of flying Mandarins was in boxes
placed around a waterfowl collection at
Foxwarren Park in Surrey (Kear 1990; Shurtleff
& Savage 1996). Their successful escape and
spread, into a relatively predator-free environ-
ment (domestic cats *Felis silvestris catus* and
Grey Squirrels *Sciurus carolinensis* do not, on
the whole, take eggs as large as those of ducks),
was aided by the boxes which were put up
around Windsor Great Park, in Berkshire. For
instance, in the six seasons before 1985, an
average of 56 ducklings annually left the
Windsor boxes (Davis & Baggott 1989a,b).

The Goosander arrived by its own means,
and its colonisation seems to be part of the
species’ natural increase and spread through
western Europe. Its initial success was not due
to boxes, although its spread, in Northumbria
for instance, may have been, and some birds in
Strathspey certainly make use of boxes put up
for Common Goldeneyes. Perhaps the most
important factor here was the comparative
scarcity of a tree-climbing egg-eater; if the Pine
Marten, which also nests in hollow trees, had
been present when Goosanders started to
colonise and breed in the 1870s, I believe that
they would have had greater difficulty in
becoming established.

**Competition for holes**

Sizeable cavities, suitable for ducks, are desir-
able if not essential for a wide range of other
vertebrates and invertebrates, and competition
for their possession can be considerable
(Conner *et al*. 2001; Semel & Sherman 2001;
Aitken *et al*. 2002). In Madagascar, for example,
many parrots (Psittacidae), Comb Ducks
*Sarkidiornis melanotos*, African Pygmy-geese
and nocturnal lemurs (*Lepilemur* and
*Cheirolemur*) spend time in holes (Young
2002), and compete with the Bernier’s Teal for
nest sites. Wood Ducks rival Black-bellied
Whistling-ducks for cavities in the south of
their range in Texas (Bolen & Cain 1968), and
Hooded Mergansers, Buffleheads, goldeneyes,
owls (Strigiformes), and mammals such as
martens, squirrels and bats (Chiroptera) farther
north (Bellrose & Holm 1994). Wood Ducks
have been seen trying to usurp Pileated Wood-
pecker nests while they were still in use by
the owner and excavator (Conner *et al*. 2001).

Introduced European Honeybees *Apis mellifera*
and Common Starlings *Sturnus vulgaris*
(Kerpez & Smith 1990) provide further prob-
lems for the ducks.

Tree-hole-nesting ducks in continental
Europe clash with Eurasian Jackdaws *Corvus
monedula*, European Rollers *Coracias garrulus*,
Stock Doves *Columba oenas*, owls and starlings,
hornets (*Vespidae*) and bats (*Winkler *et al*.1995*), among others. In Brazil, the critically
dangerous Brazilian Merganser *Mergus octose-
taceus* has to share a limited tree-hole resource
with Muscovy Ducks *Cairina moschata*, toucans
*Ramphastos* spp., parrots and mammals such as
White-eared Opossums *Didelphis albiventer* (*Silveira & Bartmann 2001*). Parrots, cockatoos,
owls, tree kingfishers (Halcyonidae), opossums
(*Didelphidae*), bats, reptiles, bees (*Hymenoptera*) and introduced Common Star-
lings and Common Mynas *Acridotheres tristis*
compete with ducks for cavity nests in Australia
(Simpson & Wilson 2001). It is unusual for
there to be enough large cavities present to
satisfy local demand.

**Conservation implications**

The biodiversity of whole habitats needs pre-
serving in order to maintain successful breeding
populations of cavity-living animals, including
ducks. Many primary cavity excavators can play a positive role; an increase in the number of North American Beavers *Castor canadensis* has been suggested as a factor in the North American Wood Duck’s comeback since the 1920s and 1930s, as natural cavities in ‘snags’ standing in water tend to hatch more ducklings (Beard 1953; Haramis 1990). The ant-eating Aardvark is listed as Endangered by IUCN; its conservation is vital if the South African Shelduck is to find sufficient nesting opportunities.

In Poland, Mikusinski et al. (2001) found a positive relationship between woodpecker species richness and the numbers of other forest birds. They suggested that the woodpecker group is a good indicator for assessing avian diversity, and that in regions of Europe where data on forest bird numbers are not readily available, woodpecker surveys provide an excellent assessment tool. Sadly, many species of woodpecker are in decline because of habitat loss, and nestboxes do not work well for them (Winkler et al. 1995). It was the destruction and fragmentation of the old pine and hardwood forests of southeastern USA, as well as overhunting, that eliminated the Ivory-billed Woodpecker (Jackson 1996); the same was probably true of the extinct Imperial Woodpecker *Campephilus imperialis* of Mexico, which, at 563 g, was the largest of the woodpeckers. The Brazilian gallery forests contain few old, large holed trees because most have been removed by humans and, perhaps as a consequence, the hole-nesting Brazilian Merganser is reduced to just 250 individuals (Silveira & Bartmann 2001). Mangroves, the home of many of the grey teal group, and of great value as fish nurseries, are being destroyed at an alarming rate to provide farmed prawns for western markets. In Australia, governments are encouraging the planting of vast numbers of new trees while continuing to allow the clearing and logging of old-growth forest and woodland (Simpson & Wilson 2001), and this goes on elsewhere.

Where a shortage of safe nesting sites for ducks is limiting productivity, artificial ones need to imitate a range of features. The North Americans, in an environment still full of predators, make great efforts to create boxes for Wood Ducks which resemble tree trunks and woodpecker holes – because those are the ones which the ducks prefer. Maybe the Japanese, in trying to increase the numbers of Mandarin Ducks, should do the same. If no woodpecker holes are available for the ducks to make a comparison with the site in which they were hatched (as in Britain), then all sorts of boxes seem to be acceptable. In the tropics, artificial nest sites will need to be examined frequently as they themselves may decay, or be swept away in hurricanes.

A different benefit of nestbox schemes is that the construction and erection of boxes can involve the public and hunters’ organisations,
such as ‘Ducks Unlimited’ in North America and in New Zealand (www.ducks.org). As well as providing local employment, the construction of nestboxes can help to demonstrate practical conservation techniques (Fredrickson et al. 1990). Their use was pioneered long ago in captivity by aviculturists who wanted their tame ducks to breed; the development of structures which are predator-proof has been in the hands of biologists working with wild populations. The Orinoco Goose Neochen jubata of the Amazon and the rare Scaly-sided Merganser Mergus squamatus in far-eastern Russia are among species which have benefited recently, and taken successfully to artificial sites (Kear in press). The installation of boxes is suggested for the even rarer Brazilian Merganser in order to test whether the availability of good-quality nest sites is limiting breeding success (Silveira & Bartmann 2001).

Boxes may seem to be the answer to many problems of nesting-site shortage, but should not be employed to the detriment of an interest in conserving natural sites (Aitken et al. 2002; Evans et al. 2002). Bellrose (1990) thought that nestboxes made only a small contribution (4-5%) to the juvenile component of the Wood Duck’s autumn population, despite some 100,000 boxes being available – more than for any other cavity-nesting duck. Extra boxes may not ensure extra young. As Poysa & Poysa (2002) pointed out, following a 12-year study of box-nesting Common Goldeneyes, density-dependent features such as competition, predation and food supply also limit reproductive success. The tendency for females to dump eggs can increase in boxes which appear identical (Bolen 1967; Semel et al. 1988; Evans et al. 2002). Semel & Sherman (2001) investigated the situation in a colour-marked, box-nesting population of Wood Ducks over seven breeding seasons. They concluded that a scarcity of preferred nesting sites was probably the key factor behind four characteristics of cavity-nesting ducks, including Wood Duck: natal philopatry, nest-site fidelity, aggressive competition for nest sites and high levels of intraspecific parasitism. Evans et al. (2002) found larger clutch sizes, lower nesting success and different major predators of Barrow’s Goldeneyes nesting in boxes compared with those laying in natural cavities. They concluded that studies of Barrow’s Goldeneye which use nestboxes may not be representative of a population that uses natural holes. On the other hand, Buffleheads nesting in boxes were found to behave more like birds nesting in natural sites. Ideally, a thorough investigation of population ecology should be undertaken before any management measure, such as the provision of nestboxes, is put in place. In the real world, such perfection is seldom achieved – time always seems far too short.

Woodland, especially moist and flooded woodland, needs protection worldwide. In order to ensure that woods and forests contain healthy populations of primary excavators, such as woodpeckers, dead and dying timber is needed. Ironically, even the predators may suffer if no old wood is available: Brainerd et al. (1995) thought that woodland management reduced the number of natural den sites for martens in Scandinavian forests, and made them dependent upon the Black Woodpecker for the provision of breeding cavities. In Britain, veteran trees and dead timber are required for the conservation of numerous rare lichens, fungi and spiders (McLean & Speight 1993), and 20% of British insects are dependent on dead wood. Woods must be mature (over-mature from the forester’s point of view) and not ‘tidy’ and disease-free. Old, rot-prone trees tend to be removed by foresters during the thinning process, so that the cavity-bearing, dead-wood component is now largely missing from managed forest. ‘Limbs with decay should not automatically be cut back to sound wood, cavities should not be drained, filled and sealed, and damage to bark should not automatically be regarded as in need of remedial treatment. Outright felling of an ancient tree should be regarded as unacceptable’ (Key & Ball 1993). Generally, fungi and insects which rot dead wood do not attack healthy trees (Winter 1993), although there are exceptions.

Dead wood matters – it turns to gold. Almost all agents responsible for cavity construction need moribund timber in order to start the process. In a natural, unmanaged forest, 50% of the wood will be dead or dying, and the slow process of decomposition is necessary to return nutrients to the soil. Attitudes must be changed; heart rot and rot holes in deteriorating woodland should be welcomed and not deplored, not just for the sake of hole-nesting ducks, but for a huge range of other organisms whose lives depend on wood that is rotten.
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