Committee on the Status of Endangered Wildlife in Canada

Comité sur le statut des espèces menacées de disparition au Canada

Ottawa, Ont. K1A 0H3
(819) 997-4991

STATUS REPORT ON THE PASSENGER PIGEON

ECTOPISTES MIGRATORIOUS

IN CANADA

BY

DAVID A. KIRK

STATUS ASSIGNED IN 1985
EXTINCT*

REASON: THE PASSENGER PIGEON BECAME EXTINCT IN 1914, WHEN THE LAST INDIVIDUAL DIED IN CAPTIVITY IN THE CINCINNATI ZOO.

OCCURRENCE: N/A

*THIS SPECIES WAS DESIGNATED EXTINCT BY COSEWIC IN 1985 BASED ON HISTORICAL FACT. DUE TO THE LARGE NUMBER OF REQUESTS FOR INFORMATION ON THIS EXTINCT BIRD THE COSEWIC BIRD'S SUBCOMMITTEE HAD THIS REPORT PREPARED AND APPROVED BY COSEWIC MEMBERS IN 1994.

COSEWIC — A committee of representatives from federal, provincial and private agencies which assigns national status to species at risk in Canada.

CSEMDC — Un comité de représentants d'organismes fédéraux, provinciaux et privés qui attribue un statut national aux espèces menacées de disparition au Canada.

STATUS REPORT ON THE PASSENGER PIGEON

ECTOPISTES MIGRATORIOUS

IN CANADA

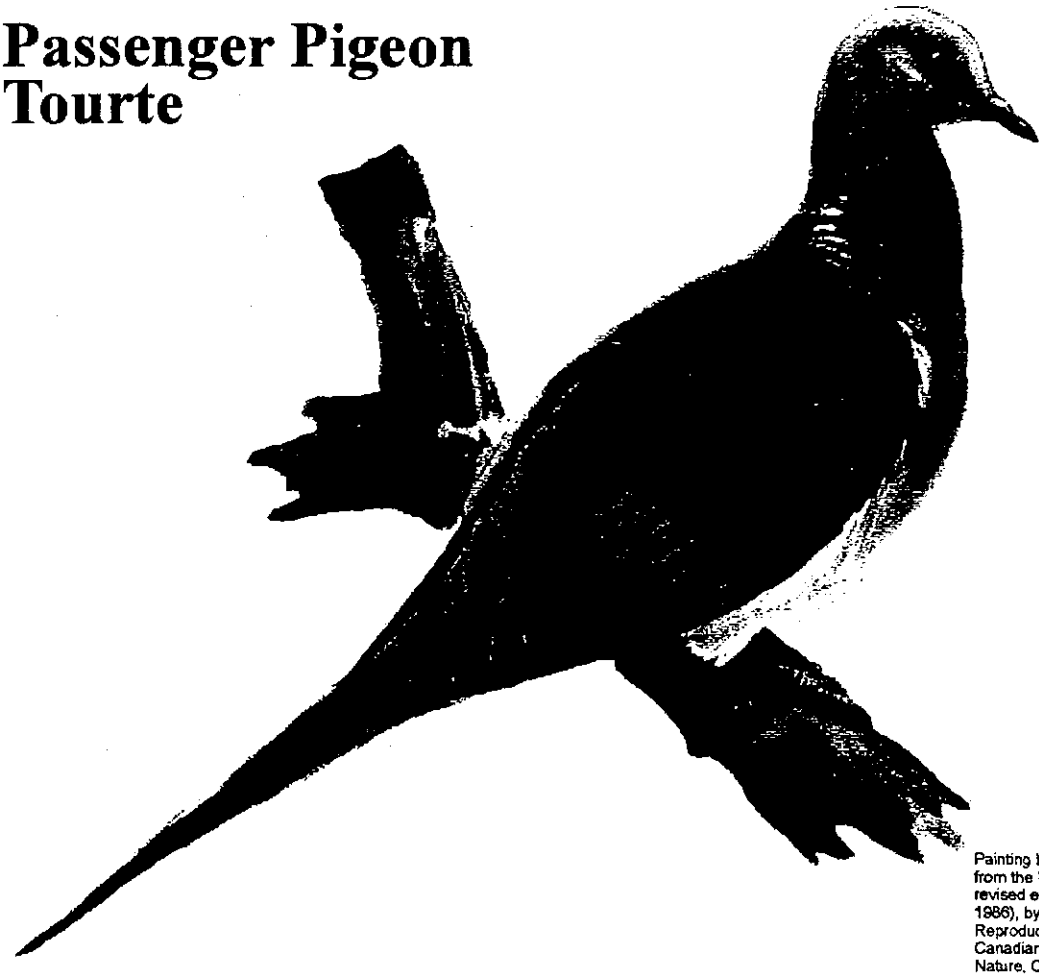
BY

DAVID A. KIRK
C/O CANADIAN WILDLIFE SERVICE
ENVIRONMENT CANADA
351 ST. JOSEPH BOULEVARD
HULL, QUEBEC
K1A 0H3

STATUS ASSIGNED IN 1985
EXTINCT

STATUS REPORT ON ENDANGERED WILDIFE IN CANADA

Passenger Pigeon
Tourte



Painting by John Crosby from the Birds of Canada revised edition (Ottawa, 1986), by W. Earl Godfrey. Reproduced courtesy of the Canadian Museum of Nature, Ottawa Canada.

COSEWIC

COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA

Committee on the Status of Endangered Wildlife in Canada

Comité sur le statut des espèces menacées de disparition au Canada

JUNE 1990

OH3 (819)
Ottawa, Ont. K1A [illegible] (613) 997-4991

NOTES

1. This report is a working document used by COSEWIC in assigning status according to criteria listed below. It is released in its original form in the interest of making scientific information available to the public.

2. Reports are the property of COSEWIC and the author. They may not be presented as the work of any other person or agency. Anyone wishing to quote or cite information contained in status reports may do so provided that both the author and COSEWIC are credited. Reports may be cited as in the following example:

   Bredin, E. J. 1989. Status report on the Northern Prairie Skink, Eumeces septentrionalis, in Canada. Committee on the Status of Endangered Wildlife in Canada. 48 pp.

3. Additional copies of this report may be obtained at nominal cost from Canadian Nature Federation, 453 Sussex Drive, Ottawa, Ontario, K1N 6Z4.

DEFINITIONS

SPECIES: "Species" means any species, subspecies, or geographically separate population.

VULNERABLE SPECIES: Any indigenous species of fauna or flora that is particularly at risk because of low or declining numbers, occurrence at the fringe of its range or in restricted areas, or for some other reason, but is not a threatened species.

THREATENED SPECIES: Any indigenous species of fauna or flora that is likely to become endangered in Canada if the factors affecting its vulnerability do not become reversed.

ENDANGERED SPECIES: Any indigenous species of fauna or flora that is threatened with imminent extinction or extirpation throughout all or a significant portion of its Canadian range.

EXTIRPATED SPECIES: Any indigenous species of fauna or flora no longer known to exist in the wild in Canada but occurring elsewhere.

EXTINCT SPECIES: Any species of fauna or flora formerly indigenous to Canada but no longer known to exist anywhere.

STATUS REPORT ON THE PASSENGER PIGEON *ECTOPISTES MIGRATORIOUS* IN CANADA

BY

DAVID A. KIRK

'Here in the fall, large flocks of pigeons fly,So num'rous, that they darken the sky.'[1]

'The Passenger Pigeon needs no protection. Wonderfully prolific, having the vast forests of the north as its breeding grounds, travelling hundreds of miles in search of food, it is here today, and else-where tommorow, and no ordinary destruction can lessen them or be missed from the myriads that are yearly produced'[2].

[1] A poem by Thomas Makin (1729) cited in Schorger 1955

[2] By a committee reporting on a game bill to the State Legislature of Ohio in 1857 (cited in Schorger 1955).

Contents

Executive Summary

Description. The Passenger Pigeon *Ectopistes migratorius* was a large, arboreal pigeon (average length in males was 41 cm, in females 35 cm). It resembled a Mourning Dove *Zenaida macroura* but was half as big again as this species. The head of the male was slaty blue, being more pale on the chin and throat. The hindneck had an area of metallic iridescence. The upper back was slate-grey with greyish or olive brown tinges (and metallic iridescence), the lower back and rump were greyish-blue, grading to brownish-grey on the upper tail coverts. The wing coverts were brownish grey with irregular black markings. Primaries were grey-brown, with whitish edgings (except the tenth), and rufous towards the inner edge. Except for the two central tail feathers, which were dark grey, the remaining rectrices were white. The upper breast was cinnamon or russet, to vinous and eventually white on the vent and under tail coverts. The bill was black, legs and feet red and the iris was scarlet; the orbital ring was flesh or purple-coloured. Females were similar but smaller with duller plumage.

Distribution. The Passenger Pigeon was endemic to North America. It was previously found throughout the eastern deciduous forests of Canada and the United States within the range of three preferred mast-producing tree species; American beech *Fagus grandifolia*, oak *Quercus* spp. and American Chestnut *Castanea dendata*. In Canada, highest numbers bred in southern Manitoba, southern Ontario, Nova Scotia and south-western Quebec. In the United States, Passenger Pigeons bred in the north-eastern Atlantic coast states (New York, Maine, New Hampshire, Vermont) and northern Lake states (Minnesota, Michigan and Wisconsin). They also bred in Georgia, Kansas, Mississippi, Montana, New Jersey, North and South Carolina (possible), North and South Dakota, Oklahoma, Tennessee (possible), Virginia (possible) and West Virginia.

Protection. Laws enforced to protect the declining Passenger Pigeon in the 1880s were either too late

or not enforced and so did not halt the demise of the species.

Population size and trends. A population size of 3-5 billion birds was estimated at the time of the arrival of the European settlers. One Passenger Pigeon flock was estimated at over 3.7 billion birds. By the late 18th century the numbers of pigeons appearing in the spring had declined, although population fluctuations were normal because of the unpredictability of its mast food supply. Numbers declined in Quebec by the 19th century, and in Ontario, large flocks were seen only every 4-5 years by the mid 1800s. The last nesting in Ontario was in 1898. After 1878, the Passenger Pigeon population was too small to support pigeon netters. Declines were probably caused by forest fragmentation and a reduction in the average age of the deciduous forests following cutting. Fragmentation may have caused pigeon populations to become scattered and socially disfunctional.

Habitat. Passenger Pigeons were found in the eastern deciduous and Columbia forest zone, which is the distribution center for the main mast-bearing trees, beech, oak, chestnut and chickory, on which Passenger Pigeons relied for food.

General Biology. Passenger Pigeons bred in dense colonies beginning in early April, following their return migration from wintering areas, until late June. They arrived early on the breeding grounds, before snow melt to ensure access to mast from the previous autumn, buried under the snow. Nesting colonies were sometimes huge (one covered 2,202 km^2). The nest was a loose structure built of twigs, and situated on tree branches. A single egg was laid, although hunters sometimes reported two eggs being found. Laying dates were highly synchronous within colonies. Although previously thought to be single brooded, Passenger Pigeons may have bred several times in one season, in different places. The breeding cycle was about 30 days. Passenger Pigeons were nomadic and irruptive, and movement from their wintering grounds in the southern states to the northern deciduous forests was a key factor in their ability to track mast food resources. They migrated on a broad front,

enabling them to search huge areas for food. Flock-foraging (possibly involving information transfer at roosts, as well as local enhancement - the mechanism by which other birds are attracted to aggregations of individuals) was essential for the pigeons to locate food. Their peak numbers coincided with large mast crops that were produced every 2-5 years. During the breeding season, the chief food of the Passenger Pigeon was mast, while in the summer they switched to fruit.

Limiting factors. Mast production, acting in a density-dependent manner was a principal factor limiting the size of the Passenger Pigeon population. Passenger Pigeons had a very restricted diet. Clearance of forests by European settlers altered the pattern of mast production and reduced the amount of mast available.

Special significance of the species. Extinction of the Passenger Pigeon serves as a warning of how habitat alteration on a regional or continental scale can jeopardize even a species with extremely large populations.

Conclusions. The Passenger Pigeon became extinct in 1914, when the last individual died in captivity in Cincinnati Zoo.

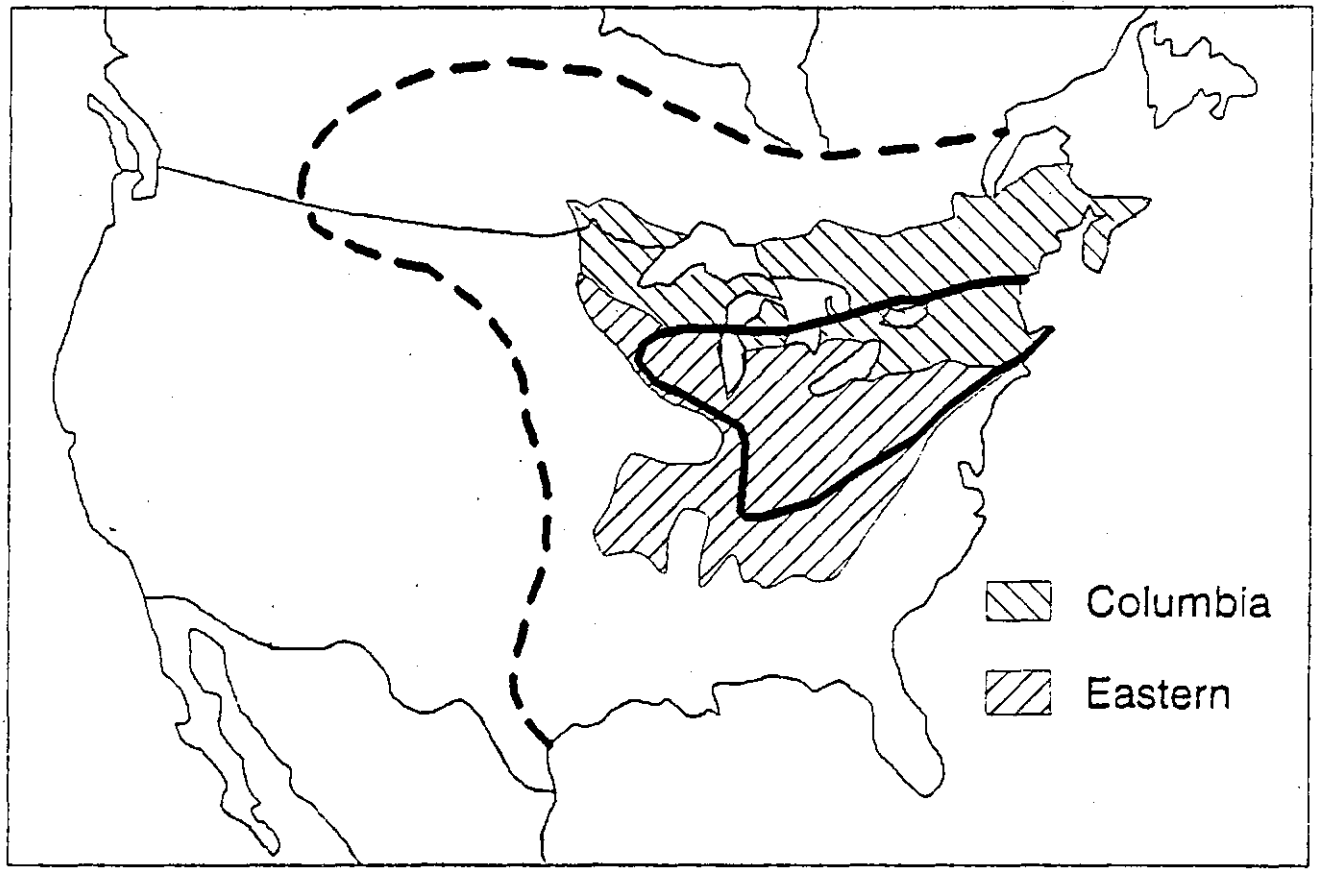
A. Abstract.

The Passenger Pigeon *Ectopistes migratorius*, a nomadic specialist species, endemic to the deciduous forests of eastern Canada and the United States, became extinct in 1914, when the last known individual, 'Martha', died in Cincinnati Zoo. Incredibly, its status changed from being probably the most abundant bird in the world, to becoming extinct in only 300 years. Whilst it was previously thought that human predation and disturbance were alone responsible for its extinction, it is now believed that forest fragmentation and habitat loss caused by humans was probably the primary underlying factor, combined with lack of social facilitation (in finding sporadic food resources and in nesting colonies) at small population sizes. The Passenger Pigeon specialized in exploiting sporadic mast crops of nut-bearing trees and had an extremely large home range. It relied solely on social facilitation to locate sporadic food sources. It was the sheer size of their flocks that led to reports that they darkened the skies with their numbers. Once populations were reduced to low levels, the birds simply could not locate irregular mast crops, which occur synchronously over a large region, even though apparently suitable nesting and foraging habitat was still available. Forest fragmentation probably resulted in separation of the Passenger Pigeon population into subpopulations which subsequently became subject to random demographic and environmental events. Human persecution certainly exacerbated these primary causes of extinction. Development of the eastern railroad network allowed most nesting colonies of Passenger Pigeons to be within easy access of a market and telegraph communication enhanced information transfer about nesting colony locations.

B. Distribution

Previously found throughout the eastern deciduous forests of Canada and the United States (Fig. 1), the Passenger Pigeon was most abundant within the range of three tree species groups, American

Figure 1 Distribution of the Passenger Pigeon showing total range (dotted line) and main breeding area (solid line) (Columbia forest and Eastern Deciduous Forest zones; Schorger 1955)



beech *Fagus grandifolia*, oak *Quercus* spp., and American chestnut *Castanea dendata*, the nuts of which were their preferred food. Its restricted distribution was somewhat surprising, given the abundance of mast-bearing trees in western North America (Mershon 1907, Schorger 1955).

1. In Canada.

Although there are records of Passenger Pigeons from British Columbia and Alberta, it is unlikely that the species bred in these provinces (see Schorger 1955). Small numbers bred in central-eastern Saskatchewan (Drummond in Greenway 1967, Houston 1972), but it was in southern Manitoba (Portage La Prairie), southern Ontario, Nova Scotia and south-western Quebec that the species reached its highest abundance in Canada. Passenger Pigeons bred in huge numbers in southern Ontario. They also nested in western Ontario to northern Lake of the Woods and north to Moose Factory (Godfrey 1986). Other breeding records from the Boreal forest region were presumably of birds ranging further afield to locate breeding sites (e.g., Smoky Falls on the Mattagami River in northern Ontario, Canyon to Alter Falls, Abitibi River, Cochrane; Mitchell 1935). However, the pre-requisite for large sources of mast for nesting (Schorger 1955, 125) casts some doubt as to whether these northerly breeders were successful in rearing offspring, given that in the Canadian boreal forest zone, beech, oak and chestnut are essentially absent. For example, Kalm (1911) stated that Passenger Pigeons were not found more than 20 miles (c. 32 km) north of Quebec city because of the lack of mast-bearing trees. It was only in poor mast years that Passenger Pigeons dispersed to the northern Great Lake States and Canada to feed on alternative foods (see Behaviour/Adaptability) (Blockstein and Tordoff 1985).

2. United States.

Passenger Pigeons previously bred in Georgia, Kansas, Mississippi, Montana, New Jersey, North and South Carolina (not definite), North Dakota, Oklahoma, South Dakota, Tennessee (not definite),

Virginia (not definite) and West Virginia (Schorger 1955). They also bred in the north-eastern States bordering the Atlantic coast (i.e. New York, Maine, New Hampshire, Vermont) as well as the northern Lake States of Minnesota, Michigan and Wisconsin (see Greenway 1967).

Passenger Pigeons wintered in the southeastern United States.

C. Protection

First discovered by Cartier in 1534 on Prince Edward Island, by the 1880s the Passenger Pigeon population had declined drastically, hence laws were passed in a number of states to limit human persecution (Halliday 1980). Unfortunately, these were not enforced (Brewster 1889, Schorger 1955) and so had little effect in protecting the species. Revoil (1859) predicted the extinction of the Passenger Pigeon. Prohibiting live pigeons being used in shooting galleries in New York came too late in 1907; no further sightings of Passenger Pigeons in the wild were made after this date.

D. Population size and trends

It was extremely difficult to estimate accurately the total size of the Passenger Pigeon population. However, there are several estimates of the size of flocks and nestings; in about 1810, Wilson (1832) estimated a flock of Passenger Pigeons at 2,230,272,000 birds, the first and one of the largest flocks ever recorded. Schorger (1955), using details provided by Major King, at Fort Mississisaugua, Ontario, calculated a flock of over 3.7 billion birds. Dionne (1906) described a flock near Henderson, near the Ohio border, which he estimated at 1,115,156,000. The largest known nesting was in Wisconsin in 1871 and was composed of an incredible 135 million birds (Schorger 1937). Schorger (1955; 204) further guessed a total population between three and five billion Passenger Pigeons when the first European settlers arrived in North America. Thus, Schorger (1955)

speculated, based on figures given by Wing (1941) and Peterson (1941) that the Passenger Pigeon comprised 25-40% of the entire bird population in North America.

By the late 18th century, the numbers of pigeons appearing in the spring had declined, although this did not necessarily indicate a decline in the total population; fluctuations were a normal event because of the periodicity of mast production. However, by the 19th century, numbers had declined in Quebec (Lambert 1814). Dionne (1906) recorded that 20 years prior to the time of writing 'Les oiseaux de la province de Quebec' the last specimens known to him were killed in a forest near Charlesbourg. However, large numbers were still found in many parishes on the south side of the St. Lawrence river, as well as Trois-Pistoles, St. Paschal, St-Phillipe de Néri, Mont-Carmel and St-Nicholas (Dionne 1906). In Ontario, large flocks were only seen every 4-5 years by the mid 1800s (Small 1867); their last nesting in the Province was in 1898 in Frontenac Co. (20 birds) and the last sighting of a wild bird in Simcoe Co in 1902 (Mitchell 1935). The last year in which the Passenger Pigeon population was large enough to support professional pigeon netters was in 1878 (Mershon 1907: p. 118). Schorger (1955) recorded the decline in the Passenger Pigeon population as being 'precipitous' between 1871 and 1880.

Many explanations have been advanced for the extinction of the Passenger Pigeon and these are not mutually exclusive. Those listed by Bucher (1992) include the following (presented in order of increasing likeliness): 1) inbreeding, 2) climatic changes or disasters, 3) diseases and parasites, 4) competition, 5) persecution by humans and 6) habitat alteration.

1) since inbreeding depression affects small isolated populations it is unlikely that it could account for the decline of the Passenger Pigeon (Bucher 1992).

2) No evidence exists for climatic changes concomittant with the period of decline and extinction of Passenger Pigeons (Bucher 1992). Spring snow storms may have caused local mortality

in nesting colonies (Schorger 1955) but not on a scale sufficient to affect the entire population.

3) Whilst Passenger Pigeons were likely candidates for transmitting disease and parasites it is unlikely that these played a role in the species' extinction for three reasons. Extinction from disease would likely occur at a much faster rate than the actual decline observed from 1830-1900. Also, it is difficult to see how a disease could be effective during years when there were few pigeons, owing to lack of mast. Lastly, no other pigeons have shown large scale population decreases attributable to disease or parasitic infection.

4) A fourth hypothesis rests on the dubious assumption that prehistoric populations of Passenger Pigeons were very low due to competition for food with humans, and that this competitive system collapsed with the arrival of Europeans (Neumann 1985). Also, early settlers killed many of the mast-consuming species that competed with Passenger Pigeons for food, thus enabling the latter species to dramatically increase. It is virtually impossible for the native population in eastern North America either to have been large enough or to have sufficient mobility to have competed with Passenger Pigeons for mast and thereby kept the population in check. However, the lack of archaelogical remains of Passenger Pigeon bones, as well as the conspicuous absence of mention of the species in many early accounts (Neuman 1985) is more difficult to explain, although it may have been due to decreased periodicity of heavy mast years resulting in low pigeon populations. It could also have been due to extremely low human population levels which decreased the chances of seeing the highly mobile pigeon flocks that ranged throughout eastern North America. Competition from hogs and other domestic animals has also been suggested as a cause of the decline of the Passenger Pigeon (see Smith in Schorger 1955).

5) Schorger (1955) maintained that direct human persecution was alone responsible for the decline and subsequent extinction. Halliday (1980) postulated that social facilitation in their huge

nesting colonies was essential for effective breeding in Passenger Pigeons and that it was the reduction in colony size caused by humans that resulted in their decline. Blockstein and Torduff (1985) believed that the advent of the railroad effectively opened up all parts of the species' range to easy market access and the telegraph enhanced communication about nesting colonies among the 1000 or so professional pigeoners. They attribute the Passenger Pigeon's extinction, not to direct hunting of flocking adults, but to the disruption of breeding activities at colonies through destroying trees and nests for their eggs and nestlings.

Pigeon hunters concentrated their efforts at the large colonies, so it is unlikely that this alone was responsible for the species' extinction (Bucher 1992). Also, if food supply was the ultimate factor determining the Passenger Pigeon population, as postulated by some authors (e.g. Bucher 1992) this would suggest that human predation was not the cause of extinction. Moreover, other populations of Columbidae can support heavy human predation pressure (up to 10% of the entire population for the Eared Dove; Bucher 1982, 1989 and Woodpigeon control campaigns; Murton and Westwood 1977) with little sign of declines.

6) As far back as 1907, Audubon (in Mershon 1907) suggested that direct human exploitation alone could not fully explain the precipitous decline in such an abundant species, but rather forest loss was the principal factor involved. Likewise, Dionne (1906) suggested that both human persecution and removal of the forests where they roosted caused their gradual decline. Forest cover in North America is thought to have declined by 30-40% since since the arrival of Columbus (Terborgh 1980) due to clearance for agriculture and settlement. It is notable that the beech and maple *Acer* spp. forests, largely restricted to the low hills and valleys, were extensively cleared by 1880 to provide rich agricultural land for early European settlers (Forbush 1929, Irland 1982). Oak, hickory and chestnut were most abundant at higher elevations and were cut intensively for firewood. The

clearance of forests by Europeans reached a peak in 1880 and this coincided almost exactly with the sudden increased rate of decline in the Passenger Pigeon population (Schorger 1955: p 207, Irland 1982).

Removal of forest cover by European settlers also reduced the average age of forests to fewer than 40 years (when mast is first produced by beech; Kricher and Morrison 1988) and resulted in domination by younger brushy growth where pigeons found it hard to forage (Bucher 1992).

Passenger Pigeons needed vast forested areas so that their sporadic and periodic food source could be located (Bucher 1992). They also probably required large forested areas for breeding (Bucher 1992). Once nesting or roosting colonies were separated in increasingly smaller woodlots, the population could have become disfunctional because of lack of social facilitation.

A further related factor not hitherto considered is that predation on Passenger Pigeon nests would be increased in these small fragments (see Wilcove 1985, Yahner and Scott 1988; see Bohning-Gaese 1993), particularly as Passenger Pigeon nests were open, flimsy structures (Schorger 1955).

E. Habitat

Previously found in southern Canada and the United States, the Passenger Pigeon was endemic to the Eastern Deciduous and Columbia forest zone. This region is the distribution centre (Braun 1950) for the main nut-bearing tree species, beech, oak, chestnut and hickory, on which Passenger Pigeons relied for food (Kalm 1911, Cotton and Knappen 1939, Schorger 1955, Bucher 1992) from September to May.

F. General Biology

1) Reproductive

Passenger Pigeons returned from their wintering areas in the southern United States in March, prior to snow melt. They bred in dense colonies between early April and late June, peaking in mid-April and mid-May, at sites in forests where there was an abundance of mast (Schorger 1936, Roney [in Mershon 1907], Audubon [in Mershon 1907]). No evolutionary advantages accrued to their being philopatric (i.e. returning to their natal site) because of the unpredictability and sporadic nature of their food supply. Bucher (1992) suggested that by arriving in the spring in northern areas where deep snow persisted until April, Passenger Pigeons were ensured access to mast from the previous autumn that was buried under the snow. Snow cover prevented numerous other predators of mast from exploiting the food resource. This would account for the seemingly inexplicable fact that the species did not breed south of Kentucky despite the abundance of mast-bearing species in that region (see Bucher 1992).

The 'nestings' varied greatly in size; in Ontario, colonies were reported to extend over an area of 350 km^2 (Mitchell 1935). The most accurately recorded colony in 1871 in Wisconsin was also the largest, covering an area of 2,202 km^2 (850 square miles; Schorger 1937). Nests were apparently loose structures of twigs on tree branches that were vulnerable to wind-blow (Schorger 1955, Greenway 1967). Usually a single egg was laid, although hunters reported that occasionally two were found (Craig 1911, Whitman in Greenway 1967). Laying dates were highly synchronous within colonies (Blockstein and Tordoff 1985) and this may have been an important adaptation for successful reproduction. Although many pigeon species can rear several broods during a breeding season, through their adaptation of producing crop-milk, Schorger (1955) previously believed that the Passenger Pigeon had only one brood each year. However, Bucher (1992) suggested that some

Passenger Pigeons may have bred several times during the season, in different places, following the pattern in other itinerant breeders such as the Red-billed Quelea *Quelea quelea* (Ward 1971) and probably Eared Doves (Bucher 1992). The breeding cycle of Passenger Pigeons occupied about 30 days (the 13 days incubation was the shortest incubation period for any Columbid; Schorger 1955) which meant that one breeding season was sufficiently long for two broods, taking into account dispersal time to a new second nest site (Bucher 1992). According to some sources, three or four broods were possible in high mast years (Wilson in Mershon 1907, Dickinson in Schorger 1955) and this was much more likely (Halliday 1978) considering the extremely high population level of the species.

2) Movement

The Passenger Pigeon was a nomadic, irruptive species (Bucher 1992). The movement of Passenger Pigeons between their wintering grounds in the southern United States and the northern deciduous forests was a key factor in their ability to track mast food resources. Their migration was on a broad front (Bucher 1992), so that they covered huge areas in their search for mast. In this respect the Passenger Pigeon resembled the Eared Dove of north-eastern Brazil and central Argentina (Bucher 1982). Large mast crops in the eastern forest are produced every 2-5 years and several tree species bearing mast do so synchronously over very large regions (Smith and Scarlett 1987). Beech mast is produced every two years but very heavy crops are irregular in occurrence (Schorger 1936). Thus, in even years when beech mast was available in large quantities in Michigan and Pennsylvannia, Passenger Pigeons moved to this state, while in odd years acorns were abundant in Wisconsin and Minnesota and pigeons moved there (Schorger 1955).

Because the crops of Passenger Pigeons killed in the New York area were still full of rice ,

and that this food source was available only in Georgia or North or South Carolina, Audubon (in Dionne 1906) believed that within six hours they could fly 300-400 miles (483-644 km). Thus he proposed that they must fly at a speed of one mile (1.609 km) per minute. This is based on the assumption that Passenger Pigeons had rapid digestion and that all food is digested within 12 hours.

3) Behaviour/Adaptability

Three of the most striking adaptations of the Passenger Pigeon were first, its ability to detect food in open-fronted flocks over a huge area, second the use of birds feeding on the ground as cues for good feeding areas, and third, possible information transfer at roosts about the location of food sources (Bucher 1992). Flock-foraging was essential for this species and it is likely that subordinates were most successful in large groups, as shown for Woodpigeons *Columba palumbus* (Murton and Westwood 1977). Evidence also suggests that individuals that had knowledge of mast food sources in the previous autumn could return to them in the following spring and lead unsuccessful birds to the food (e.g. a case documented by Schorger 1955 in Wisconsin in 1881, also in Kalm 1911). Unlike other pigeons, feeding Passenger Pigeons had a special call to attract other flocks to the ground, and this may have evolved in response to the need for communication in dense deciduous forest (Schorger 1955).

Pigeons can produce crop-milk for their young which makes them independent of animal food (Bucher 1992). Thus, a further adaptation was that Passenger Pigeons could possibly shift their breeding season or have an extended breeding season, as in other pigeons (e.g., Murton and Westwood 1977), depending on the availability of mast crops.

Although Schorger (1955) records that Passenger Pigeons had a varied diet, their chief food for most of the year was beech mast, acorns and chestnuts. Food preferences of Passenger Pigeons

were based on observations of birds disgorging crop contents when a preferred food was available. In the summer months, Passenger Pigeons fed on fruit. Seeds, insects and worms were also taken (Schorger 1955).

G. Limiting factors

Mast production, acting in a density-dependent manner, was the principal, but not only, factor limiting the size of the Passenger Pigeon population, as in both Eared Doves in South America (Bucher 1989) and Woodpigeons *Columba palumbus* in Britain (Murton and Westwood 1977). The erratic nature of this mast production, although synchronous on a regional scale, meant that Passenger Pigeons had to cover a massive area encompassing the whole eastern deciduous forest both on their migration routes, and on nomadic movements. Unlike its extant ecological congener, the Band-tailed Pigeon *Columba fasciata*, the Passenger Pigeon relied mainly on mast. Other species that rely on mast do so predominantly in winter, or they have a wider diet and can thus switch to alternative food if mast crops fail. However, as humans cleared the eastern deciduous forests for agriculture, altering the spatial pattern of mast production, it probably became increasingly difficult for pigeons to find food.

H Special significance of the species

Extinction of the Passenger Pigeon serves as a particularly poignant warning as to how habitat alteration on a regional or continental scale can jeapordize even a species with extremely large populations. Extant dove species which had previously large populations and are now threatened by habitat loss include the Eastern White-winged Dove *Zenaida asiatica asiatica* (Purdy and Tomlinson 1991). Also, nomadic, itinerant species, like the Passenger Pigeon, that depend on a single food resource may be especially vulnerable to extinction (see Terborgh and Winter 1980; e.g., Red

Crossbill *Loxia curvirostra*; Benkman 1993).

I. Evaluation and Proposed Status

The Passenger Pigeon was extirpated from Manitoba and from Ontario in 1902; in Quebec the last certain sighting was made in 1902. It became extinct in 1914 when the last individual died in captivity.

J. References

Benkman, C.W. 1993. Logging, conifers, and the conservation of crossbills. Conservation Biol. 7:473-479.

Blockstein, D.E. and Tordoff, H.B. 1985. A contemporary look at the extinction of the Passenger Pigeon. Am. Birds 39:845-852.

Bohning-Gaese, K., Taper, M.L. and Brown, J.H. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biol. 7:76-86.

Braun, E.L. 1950. Deciduous forests of Eastern North America. Klakiston, Philadelphia.

Brewster, W. 1889. The present status of the wild pigeon (*Ectopistes migratorius*) as a bird of the United States, with some notes on its habits. Auk 6:285-291.

Bucher, E.H. 1982. Colonial breeding of the Eared Dove (*Zenaida auriculata*) in north-eastern Brazil. Biotropica 14:255-261.

Bucher, E.H. 1989. The influence of changes in regional land-use patterns on *Zenaida* dove populations. Pp. 291-303 *in* Granivorous birds in the agricultural landscape. (J. Pinowsky and J.D. Summers-Smith, eds.). Polish Academy of Sciences, Warsaw.

Bucher, E.H. 1992. The causes of extinction of the Passenger Pigeon. Pp. 1-36. *in* Current

Ornithology, Volume 9. (D.M. Power, ed.). Plenum Press, New York.

Cotton, C. and Knappen, P. 1939. Food of some uncommon North American birds. Auk 56:138-169.

Craig, W. 1911. The expression of emotions in the pigeons. III: The Passenger Pigeon *Ectopistes migratorius* Linn.). Auk 28:408-427.

Dionne, C.-E. 1906. *Ectopistes migratorius*, (Linn.) Pp. 182-187 *in* Les oiseaux de la province de Quebec. Dussault and Proulx, Québec.

Forbush, E.H. 1929. The birds of Massachusetts and other New England States. Part 2: Land birds from bob-whites to grackles. Massachusetts Department of Agriculture, Boston.

Godfrey, W.E. 1986. The birds of Canada. Revised edition, National Museum of Canada, Ottawa.

Greenway, J.C. Jr. 1967. Extinct and vanishing birds of the world. Dover Publ., New York.

Halliday, T.R. 1978. Vanishing birds. Sidgewick and Jackson, London.

Halliday, T.R. 1980. The extinction of the Passenger Pigeon *Ectopistes migratorius* and its relevance to contemporary conservation. Biol. Conserv. 17:157-162.

Houston, C.S. 1972. The Passenger Pigeon in Saskatchewan. Blue Jay 30 (2): 77-83.

Irland, L.C. 1982. Wildlands and woodlots, the story of New England's forests. University Press of New England, Hanover, New Hampshire.

Kalm, P. 1911. A description of the wild pigeons which visit the southern English colonies in North America, during certain years, in incredible multitudes. Auk 28:53-66.

Kricher, J.C. and Morrison, G. 1988. A field guide to eastern forests in North America. Houghton Mifflin Company, Boston.

Lambert, J. 1814. Travels through Canada, and the United States of North America, in the years 1806, 1807 and 1808. Second edition, London, I, 78.

Mershon, W.B. 1907. The Passenger Pigeon. The Outing Publishing Company, New York.

Mitchell, M.H. 1935. The Passenger Pigeon in Ontario. Toronto.

Murton, R.K. and Westwood, N.J. 1977. Avian breeding cycles. Clarendon Press, Oxford.

Neumann, T.W. 1985. Human-wildlife competition and the Passenger Pigeon: Population growth from system destabilization. Human Ecology 13:389-410.

Peterson, R.T. 1941. How many birds are there? Audubon Mag. XLIII: 182.

Purdy, P.C. and Tomlinson, R.E. 1991. The Eastern White-winged Dove: factors influencing use and continuity of the resource. Pp. 255-265 *in* Neotropical wildlife use and conservation. (J.G. Robinson and K.H. Redford, eds.). The Univ. of Chicago Press, Chicago.

Revoil, B.-H. 1859. Chasse dans l'Amerique du Nord. P. 132. English translation from 1869 ed. in Wild Life Bull. No. 8, Penn. Alpine Club (Altoona, Penn.).

Schorger, A.W. 1936. The great Wisconsin nesting of 1871. Proc. Linnean Soc. 48:1-26.

Schorger, A.W. 1937. The great Passenger Pigeon nesting of 1871. Proc. Linnean Soc. of N.Y. 48:1-26.

Schorger, A.W. 1955. The Passenger Pigeon: Its natural history and extinction. University of Oklahoma Press, Norman.

Small, H.B. 1867. A Canadian handbook and tourist's guide. Montreal 1867.

Smith, K.G. and Scarlett, T. 1987. Mast production and winter populations of Red-headed Woodpeckers and Blue Jays. J. Wildl. Manage. 5:459-467.

Terborgh, J. 1980. The conservation status of neotropical migrants: Present and future. Pp. 21-30. *in* Migrant birds in the neotropics: Ecology, behavior, distribution and conservation. Smithsonian Instit. Press, Washington D.C.

Terborgh, J. and Winter, B. 1980. Some causes of extinction. Pp. 119-134 *in* Conservation Biology: An evolutionary perspective. (M.E. Soule and B.A. Wilcox, eds.). Sinauer Associates,

Sunderland, Mass.

Ward, P. 1971. The migration patterns of *Quelea quelea* in Africa. Ibis 113:275-297.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Wilcove, D.S., McLellan, C.H. and Dobson, A.P. 1986. Habitat fragmentation in the temperate zone. Pp. 273-256. *in* Conservation biology. The Science of scarcity and diversity. (M.E. Soule, ed.). Sinauer associates, Sunderland, Mass.

Wilson, A. 1832. American Ornithology Vol. 5, Philadelphia, PA.

Wing, L. 1941. Wildlife populations. Mimeographed Washington State Wildlife Management Notes (State College Wash.), III (Dec. 28, 1941): 1.

Yahner, R.H. and Scott, D.P. 1988. Effects of forest fragmentation on depredation of artificial nests. J. Wildlife Manage. 52:158-161.

K. Acknowledgements

I would like to thank the Canadian Wildlife Federation for funding and C. Hyslop for the opportunity to prepare this report. The Canadian Wildlife Service, Ontario Region and CWS headquarters, Hull provided administrative support. I am grateful to C. Hyslop and R.D. James who improved earlier drafts by their comments. M. Huot provided a useful reprint from 'Les oiseaux de la province de Quebec'. Staff at the Environment Canada Library, Place Vincent de Massey, Hull, helped with literature searches, photcopying and inter-library loans.