

## Host Specificity and Pathogenicity of Pox Viruses from Wild Birds

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# Host Specificity and Pathogenicity of Pox Viruses from Wild Birds

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## Abstract

An attempt was made to differentiate avian pox viruses by means of transmission experiments and cross-immunity tests, and to compare the results with those of other workers. It is concluded that a further clarification of the differences in susceptibility of bird hosts and in virulence of virus strains can only be achieved when the immune status of the experimental birds can be determined by reliable tests.

## Introduction

As early as 1873, when Bollinger<sup>1</sup> described the pathology of fowl pox, he mentioned the susceptibility of pheasants to the causative virus. Although wild birds were considered to be possible sources of fowl pox, research at the time was usually limited to domestic fowl, pigeons and canaries. In general, studies of avian pox viruses have not included interspecies transmission experiments and cross-immunity tests with strains isolated from different host species. However, Eberbeck et al.<sup>15</sup> found a fowl pox strain that was "bipathogenic", producing less marked lesions in pigeons than in chickens. These authors concluded that there are pox strains which are specifically pathogenic for either the chicken or the pigeon, and that there are also strains which are pathogenic in a varying degree to both species of birds. A strain of canary pox, studied by Reis et al.,<sup>16</sup> was "tripathogenic", infecting chickens, pigeons and passerine birds. Irons,<sup>10</sup> who made a comparative study of the behaviour of nine strains of avian pox virus, over a period of 4 years and involving more than 1400 animals, came to the conclusion that he could not distinguish different immunological strains of avian pox virus. The purpose of the present study was to attempt further to differentiate avian pox viruses by means of transmission experiments and cross-immunity tests.

## Materials and Methods

The viruses studied included avian pox viruses purchased from the American Type Culture Collection (fowl pox strains F228 and F229 and canary pox strain C3) and pox viruses isolated from pox infections in wild and domestic birds.

All strains were maintained by serial passage on the chorioallantoic membranes (CAM) of 9 to 14 day embryonated chicken eggs, except the strains from the following wild birds: Yellow-shafted Flicker (*Colaptes auratus*), Slate-colored Junco (*Junco hyemalis*) and American Robin (*Turdus migratorius*), from which I was unable to propagate the viruses on the CAM, and thus only lesion material from the host species was used as inocula. All wild bird strains were from birds trapped in Canada or Panama, which bore tumorous lesions suggestive of avian pox infection.

Skin biopsies were preserved by freezing, then ground to make 10% suspensions in sterile buffered saline, pH 7.5, containing 750 units of penicillin, 750 mg of streptomycin and 750 mg of neomycin per ml. The suspensions were centrifuged at 1500 rpm for 20 minutes and the supernatant fluids were used as inocula. The route of inoculation and the species used are listed in Table I.

Cross immunity tests were made by exposing a bird to a pox virus isolated from a different species, then re-exposing it to a pox virus isolated from a member of its own species.

Common and scientific names of wild birds used in this study follow Peterson<sup>38</sup> and Meyer de Schauensee.<sup>39</sup>

## Results

### TRANSMISSION EXPERIMENTS WITH WILD BIRD POX STRAINS

#### *Flicker Pox Virus:*

Two Yellow-shafted Flickers were infected with a pox virus obtained from cases of natural infection in Flickers. One was exposed by cage contact through pecking, the other by intradermal inoculation of Flicker pox lesion material. A third Flicker was resistant to all routes of exposure. Attempts to infect 15 species of wild birds other than the Flicker, three species of domestic birds and three species of mammals with the Flicker virus were unsuccessful.<sup>25</sup>

#### *Creeper Pox Virus:*

Attempts to transmit the virus isolated from the Brown Creeper (*Certhia familiaris*) to chickens were unsuccessful.<sup>28</sup>

#### *Thrush Pox Virus:*

The viruses isolated from the Swainson's Thrush (*Hylocichla ustulata*), the Gray-cheeked Thrush (*Hylocichla minima*) and the Wood Thrush (*Hylocichla ustulata*) were each injected into chickens. Primary lesions were observed only in chickens which had been inoculated with CAM-passaged virus. No attempts were made to infect wild birds because they were not available at the time.

#### *Junco Pox Virus:*

Five chickens, three pigeons and ten Slate-colored Juncos exposed to the Junco virus from lesion biopsies showed no sign of infection after several months of observation. Other wild birds exposed by cage contact without infection were two European Sparrows (*Passer domesticus*), three Red-winged Blackbirds (*Agelaius phoeniceus*), one Brown-headed Cowbird (*Molothrus ater*), three Starlings (*Sturnus vulgaris*) and one American Robin.

#### *Field Sparrow Pox Virus:*

The exposure of 31 chickens, three pigeons, three Red-winged Blackbirds, two Savannah Sparrows (*Passerculus sandwichensis*) and one Indigo Bunting (*Passerina cyanea*) to the Field Sparrow (*Spizella pusilla*) strain did not result in clinical disease, but it was possible to infect one group of chickens, which had primary lesions 10 days post-exposure.

#### *Song Sparrow Pox Virus:*

Three pigeons, 35 chickens, three Song Sparrows (*Melospiza melodia*), one Connecticut Warbler (*Oporornis agilis*), and four Red-winged Blackbirds were exposed to the Song Sparrow strain. Attempted transmission was successful only to Red-winged Blackbirds. The first case developed a pinhead-sized lesion on the tarsus of the right leg and a similar lesion at the angle of the mouth 36 days after exposure. The virus was re-isolated in chicken embryos inoculated with a suspension of lesion tissues. In two other Red-winged Blackbirds exposed, pox lesions developed 25 and 32 days later, respectively.

TABLE 1. *Transmission Experiments with Avian Pox Viruses*

SUBGROUP	STRAIN	ROUTE	SPECIES INOCULATED	RESULT*
Fowl pox	Game Cock	i.m.**	chicken	+
		s.c.	turkey	+
		i.d.	pigeon	—
			wild birds	—
			mice	—
			rabbits	—
	F 228	i.d.	chicken	+
		i.m.	pigeon	—
		s.c.	duck	+
			geese	+
			wild birds	—
	F 229	i.d., s.c.	chicken	+
		i.mu.	pigeon	—
			wild birds	—
Pigeon pox	Oshawa	i.d.	chicken	—
		s.c.	pigeon	+
		i.mu.	wild birds	—
Canary pox	C 3	i.d.	chicken	—
		s.c.	pigeon	—
		i.mu.	wild birds	—
	C 4494	i.d.	chicken	—
		s.c.	pigeon	—
		i.mu.	wild birds	+
Creepers pox	Breakwater	i.d., s.c.	chicken	—
Junco pox	Museum	i.d.	chicken	—
		i.mu.	pigeon	—
			wild birds	—
	Breakwater	i.d.	chicken	—
		s.c.	pigeon	—
		i.mu.	wild birds	—
Flicker pox	Toronto	i.d.	chicken	—
		s.c.	turkey	—
		i.mu.	pigeon	—
		i.mu.	flicker	+
			wild birds	—
			mice, hamsters, rabbits	—
Song Sparrow pox	Dundas	i.d.	chicken	—
		s.c.	pigeon	—
		i.mu.	Song Sparrow	—
			wild birds	+
Field Sparrow pox	Lighthouse	i.d.	chicken	+
		s.c.	pigeon	—
		i.mu.	field sparrow	—
			wild birds	—
Robin pox	Guelph	i.d.	chicken	—
		i.mu.	robin	—
Gray-cheeked Thrush	Panama	i.d.	chicken	+
Swainson's Thrush pox	Panama	i.d.	chicken	+
Wood Thrush pox	Panama	i.d.	chicken	+

\* = Plus signs denote development of lesions; minus signs, no reaction

\*\* i.m. = intramuscular; s.c. = subcutaneous; i.d. = intradermal; i.mu. = intramucosal

*Song Sparrow Pox from First Passage in the Red-winged Blackbird:*

Five apparently healthy Red-winged Blackbirds were exposed to the Song Sparrow strain which had been re-isolated from lesion tissues of a Red-winged Blackbird infected with Song Sparrow pox. No lesions developed.

*Robin Pox Virus:*

Three chickens and two American Robins were exposed without result to the Robin pox strain. This strain was not successfully propagated on the CAM.

## TRANSMISSION EXPERIMENTS WITH DOMESTIC BIRD POX STRAINS

*Fowl Pox Virus:*

Several different fowl pox strains (F228, F229, Game Cock) were inoculated into the following wild and domestic birds and mammals: 24 chickens, 24 turkeys, 12 pigeons, six ducks, six geese, 12 Ring-billed Gulls (*Larus delawarensis*), 11 Red-winged Blackbirds, one European Sparrow, two Evening Grosbeaks (*Hesperiphona vespertina*), two Catbirds (*Dumetella carolinensis*), two Baltimore Orioles (*Icterus galbula*), one Starling, one Indigo Bunting, one American Goldfinch (*Spinus tristis*), two White-throated Sparrows (*Zonotrichia albicollis*), one Brown-headed Cowbird, three Song Sparrows, five American Robins, one Brown Thrasher (*Toxostoma rufum*), two Eastern Kingbirds (*Tyrannus tyrannus*), one Common Grackle (*Quiscalus versicolor*), six rabbits and two white mice.

In chickens and turkeys infection became generalized and after five weeks all lesions had disappeared and the birds appeared healthy. Mortality occurred only in birds in which lesions completely covered the eyes or obstructed the mouth and nasal cavities.

The pigeons and all wild birds and mammals showed no evidence of clinical disease during an observation period of five to eight weeks.

In all experimentally infected domestic ducks and geese, spherical elevated lesions, which grossly resembled vesicles appeared between the 4th and 8th days post-exposure. They were seen mainly on the plantar side of the webs in both web compartments but also occurred on the dorsal side and on the digits. Approximately at the same time, a non-purulent conjunctivitis occurred in all birds. The foot lesions persisted four to six weeks. During the progress of the disease, the general health of the birds seemed not affected, though the disease was readily transmitted from infected to healthy birds by cage contact.<sup>20</sup>

*Pigeon Pox Virus:*

Birds exposed to the pigeon strain were 17 chickens, 12 pigeons, three Slate-colored Juncos, two Red-winged Blackbirds, one White-throated Sparrow, one Fox Sparrow (*Passerella iliaca*), two Brown-headed Cowbirds, two Yellow-bellied Sapsuckers (*Sphyrapicus varius*), one Field Sparrow and one Song Sparrow. All chickens were refractory. In juvenile and adult pigeons, primary lesions developed around the eyes and beak and on the feet. However, 5-day-old pigeons developed very severe primary and secondary lesions which persisted for more than 10 weeks. The wild birds showed no evidence of infection during a 3-month observation period.

*Canary Pox Virus:*

The two canary strains (C3 and C4494) were inoculated into 22 chickens, 13 pigeons, seven Red-winged Blackbirds, six Slate-colored Juncos, one Yellow-shafted Flicker, one Brown-headed Cowbird, one European Sparrow, six Tree Sparrows (*Spizella arborea*), two White-throated Sparrows, three Song Sparrows, two Catbirds, one Starling and one Budgerigar (*Melopsittacus undulatus*). No evidence of pox infection was found during the four weeks observation period after exposure in chickens, pigeons and most of the wild birds.

Two of the Tree Sparrows exposed to canary pox strain C4494 developed lesions around the eyelids and in the mouth and diphtheritic patches were seen also covering the pharynx, and the upper part of the trachea. Both eyes were closed by the severity of the lesions and the birds died eight and ten days post-exposure, respectively. Inclusion bodies were found in histological sections of eye lesions but not elsewhere. The European Sparrow developed similar eye and foot lesions and died six days post exposure. Pox inclusions were demonstrated in sections of the lesions.

### Immunity Reactions

*Pigeons* exposed to avian pox strains from pigeons, chickens, canaries, the Song Sparrow and Field Sparrow were infected only with the pigeon pox strain. Subsequent exposure of these pigeons with pigeon pox virus revealed partial immunity in pigeons previously infected with the pigeon strain but no immunity in the birds which had been exposed to the other strains (Table 2).

TABLE 2. *Cross-Immunity Reactions to Avian Pox Viruses*

BIRDS	FIRST EXPOSURE—RESULT		SECOND EXPOSURE—RESULT	
Pigeons	Pigeon pox	+	Pigeon pox	—/+*
	Fowl pox F228	—	"	+
	Fowl pox F229	—	"	+
	Fowl pox Game C	—	"	+
	Canary pox C3	—	"	+
	Canary pox C4494	—	"	+
	Song Sparrow pox	—	"	+
	Field Sparrow pox	—	"	+
	Junco pox	—	"	+
	Flicker pox	—	"	+
Chickens	Pigeon pox	—	Fowl pox	+
	Fowl pox F228	+	"	—
	Fowl pox F229	+	"	—
	Fowl pox Game C	+	"	—
	Canary pox C3	—	"	+
	Canary pox C4494	—	"	+
	Song Sparrow pox	—	"	+
	Field Sparrow pox	—/+*	"	±
	Brown Creeper pox	—	"	+
	Flicker pox	—	"	+
	Junco pox	—	"	+
	Robin pox	—	"	+
	Graycheeked Thr.	+	"	+
	Swainson's Thr.	+	"	+
	Wood Thrush pox	+	"	+
Turkeys	Fowl pox Game C	+	Fowl pox	—
	Flicker pox	—	"	+
Flickers	Flicker pox	+	Flicker pox	±
	Flicker pox	+	Pigeon pox	—

\* —/+ = variable results or partial susceptibility (see text)

*Chickens* were inoculated with strains from the pigeon, chicken, canary, Song Sparrow, Field Sparrow, Brown Creeper, Flicker, Junco, Robin, Gray-cheeked Thrush, Swainson's Thrush and Wood Thrush. Immunity was observed only in chickens which had previously been exposed to a fowl pox virus and were challenged with a heterologous strain of fowl pox and in one group of chickens infected with the Field Sparrow strain and challenged with fowl pox. All other strains did not protect chickens against infection with fowl pox virus, even when, as with the Thrush viruses, primary lesions had developed.<sup>27</sup>

*Turkeys* were exposed only to fowl pox and Flicker pox strains. Homologous immunity developed with the fowl pox strain but the Flicker strain did not protect turkeys against re-infection with a fowl pox virus.

*Flickers* were the only wild bird species in which immunity trials were carried out. Two infected birds were challenged with the Flicker strain two months after the first lesions had disappeared. One Flicker had developed immunity, the other Flicker developed small transient lesions at the site of inoculation.<sup>25</sup>

### Discussion

Inter-species transmission experiments with avian pox viruses have been made by others<sup>19</sup> but the numbers of wild birds used were limited. The susceptibility of wild and domestic birds to different avian pox strains varied greatly from species to species.

#### HOST SPECIFICITY OF AVIAN POX STRAINS

##### *Chickens:*

All attempts in the present study to infect chickens of different age groups with a strain highly virulent for pigeons were unsuccessful. Irons,<sup>10</sup> however, was able to induce mild disease in chickens with a pigeon pox virus.

Exposure of chickens to both canary pox strains did not produce clinical disease, though the viruses were readily maintained on the CAM of the embryonated chicken egg.

Varying results have been obtained by other workers. Burnet<sup>6</sup> and Lahaye<sup>29</sup> were not able to infect chickens with canary pox; however, Kikuth et al<sup>22</sup> infected chickens with the first strain of canary pox isolated, and similar results were obtained by Jactot et al.<sup>20</sup> A "tripathogenic" canary pox strain infectious for chickens was described by Reis et al,<sup>10</sup> but these authors also described two other strains from canaries which were not pathogenic for the chicken. Durant et al<sup>14</sup> were able to transmit a canary pox virus to young chickens but they failed to infect 6- to 8-month-old chickens.

I was able to infect chickens with the pox strains of three Thrush species, but only with CAM propagated material, not by direct exposure to lesion biopsy material. Only minimal primary lesions developed at the inoculation sites. This is similar to the observations of Goodpasture et al,<sup>15</sup> who studied a Junco pox strain (see below).

Several attempts were made to infect chickens with the Field Sparrow strain. The first results were negative, however, with material of higher subsequent passages on the CAM, it was possible to produce primary lesions in chickens. All other wild bird pox strains used in this study were not pathogenic for chickens, even when repeated exposures were made and virus was available in abundance.

Similar apparently inconsistent results in the susceptibility of chickens to wild bird pox strains have been observed by others also. Strains from gallinaceous wild birds have been generally transmitted to chickens without difficulty: Pheasant (*Phasianus colchicus*);<sup>10</sup> Sooty Grouse (*Dendragapus fuliginosus*);<sup>11</sup> Blue Grouse (*Dendragapus obscurus*);<sup>9</sup> Sage Grouse (*Centrocercus urophasianus*); Ruffed Grouse

(*Bonasa umbellus*), and Prairie Chicken (*Tympanuchus cupido*).<sup>12</sup> However, Findlay<sup>10</sup> was unable to infect chickens with a pox strain from the European Partridge (*Perdix perdix*).

Fewer attempts were made to infect chickens with pox strains from passerine birds. A pox strain from a sparrow was not virulent for chickens.<sup>20</sup> Worth<sup>45</sup> was able to infect chickens with a Junco strain. However, in experiments by Goodpasture et al.,<sup>18</sup> transmission failed with lesion material from a Junco and was only successful with CAM material. It was possible to infect chickens with a strain from the Jackdaw (*Corvus monedula*)<sup>21</sup> and with a sparrow pox strain<sup>35</sup> but not with a strain from a Cowbird<sup>31</sup> and a strain from Starlings.<sup>43</sup>

#### Pigeons:

All attempts in this study to infect pigeons with strains from wild and domestic birds, other than pigeons, failed. This shows the strict host specificity and monopathogenicity of this pigeon pox strain. However, I did not attempt to infect other wild species of the family Columbidae, which are known to be susceptible to avian pox viruses.<sup>3, 28, 31, 32</sup>

The infection of pigeons with fowl pox viruses seems to be more easily achieved than the reciprocal.<sup>15</sup> However, one strain of fowl pox was transmissible with gradually increasing virulence to pigeons, but two other strains failed to infect.<sup>19</sup> Tietz,<sup>42</sup> also failed to infect pigeons with a fowl pox virus.

"Tripathogenic" strains of canary pox were transmitted to pigeons by Reis et al.<sup>40</sup> and by Jactot et al.,<sup>20</sup> but the latter failed to infect pigeons with another canary strain, as did Kikuth et al.<sup>22</sup> and Durant et al.<sup>14</sup>

Varying results were obtained also in infecting pigeons with wild bird pox strains. A strain from a Bull Finch (*Pyrrhula vulgaris*) was successfully transmitted to two pigeons.<sup>8</sup> A strain from an outbreak of pox in pheasants was transmitted to pigeons by Dobson.<sup>10</sup> "Sparrow" pox was not virulent to pigeons<sup>20</sup> but transmission of other wild bird pox strains to pigeons was achieved with material from the Jackdaw,<sup>21</sup> "wild sparrows"<sup>35</sup> and the Junco.<sup>45</sup> In the latter case only pigeon squabs were susceptible. It is interesting to note that the only reported attempt to transmit a pox virus from Mourning Doves (*Zenaidura macroura*) to pigeons, i.e. in the same family Columbidae, was unsuccessful.<sup>32</sup>

#### Canary:

Canaries have been rarely used in cross-species transmission experiments. Unsuccessful attempts were made by Tietz<sup>42</sup> to transmit pigeon pox and fowl pox viruses to canaries, but Burnet<sup>6</sup> found that canaries exposed to fowl pox virus died after six to eight days with typical lesions, whereas two other fowl pox strains and one pigeon pox strain failed to induce specific lesions. Transmission was achieved with strains from a Pine Siskin (*Spinus pinus*),<sup>2</sup> a "sparrow",<sup>20</sup> and "wild sparrow".<sup>35</sup> All other reported attempts to transmit pox viruses from wild birds to canaries have been unsuccessful.

#### Ducks and Geese:

In this study, it was possible to infect both ducklings and goslings with a fowl pox virus, to re-isolate the virus on the CAM and to infect chickens with lesion tissues from the ducks and geese.<sup>20</sup>

Doyle et al.,<sup>12</sup> Findley<sup>10</sup> and Tietz<sup>42</sup> were unable to infect ducks with fowl pox virus. Negative results were obtained also by Irons,<sup>19</sup> who inoculated young ducks repeatedly with strains of fowl pox and pigeon pox. Other attempted transmission of canary pox to ducks<sup>10</sup> and of pigeon pox to geese and ducks<sup>42</sup> failed also. As reports in recent literature indicate,<sup>11</sup> avian pox seems unlikely to be observed under natural conditions in domestic waterfowl.



*Wild Birds:*

A wide variety of wild birds was found in nature to be hosts of avian pox virus.<sup>21,27</sup> Wild birds, however, are difficult to maintain in numbers in captivity for experimental purposes, not only because of their feeding habits but also because of objections from naturalists organizations. This has hindered research, especially inter-species transmission experiments.

In the present study it was possible to infect Tree Sparrows and one European Sparrow with a canary pox strain but 28 other wild birds of nine different species were not susceptible.

All attempts in this study to infect wild birds with a pigeon pox strain failed, but blind passages of virus material in wild birds has not been attempted.

It was impossible to infect a number of wild birds with three different fowl pox virus strains.

A Flicker pox virus strain was transmitted from Flicker to Flicker. However, 78 other wild birds of 15 different species were not susceptible to this strain. It was even impossible to infect related species of the same family, *Picidae*, such as the Downy Woodpecker (*Dendrocopus pubescens*), and the Yellow-bellied Sapsucker.<sup>25</sup>

The only positive result in cross-species transmission of wild bird pox strains was the successful transmission of a Song Sparrow strain to Red-winged Blackbirds, but it was not possible to infect Song Sparrows and other wild birds with the same strain.

## IMMUNITY STUDIES

In the present study, experimental infection of chickens with three different fowl pox strains resulted in complete immunity in cross-infection trials; also, turkeys infected with a fowl pox strain were protected against subsequent infection with another fowl pox strain. Chickens infected with strains of three Thrushes, however, were not immune against reinfection with a fowl pox strain; chickens were protected against a fowl pox strain when first infected with a Field Sparrow strain.

It was found in precipitation tests that chickens were very poor pox virus antibody producers,<sup>11</sup> but Goodpasture<sup>17</sup> in his review of fowl pox states that "recovery from attacks is associated with immunity", though he also agrees that immunity in some cases is not of long duration and that partial immunity may be observed, depending on the fowl pox strain used in the experiment. Andrewes<sup>1</sup> states that "immunity in chickens is not as permanent as could be desired".

Partial immunity in pigeons infected and re-exposed with a highly virulent monopathogenic pigeon pox strain was seen in this study. Some of the pigeons developed localized primary lesions when re-challenged three months after previous lesions had disappeared.

Burnet<sup>7</sup> found strong immunity in pigeons but of short duration. In some cases reinfection was possible after two months, but other pigeons were still immune after four to five months. He relates partial immunity to varying severity of infection and states that "in a mild disease reinfection occurs also with mild lesions". Loewenthal also found partial immunity in pigeons.<sup>26</sup>

In the present experiments, cross-immunity trials were made only with one strain of wild bird pox virus, the Flicker strain. These experiments were limited by the number of birds available. Partial immunity was observed in the Flickers.

Cross-species immunity studies on avian pox viruses carried out in the past are summarized in Table 3.

As evidenced by partial immunity in Flickers and by no immunity in Chipping Sparrows (*Spizella passerina*) and Field Sparrows,<sup>27</sup> recovered wild birds can sometimes be reinfected with avian pox viruses. It is thus ensured that the disease will be maintained for long periods in wild bird populations.

The varying susceptibility of birds, whether domestic or wild, to avian pox virus strains may be explained by adaptation to a specific host and differences in virulence of the strain.

Until it is feasible to rear experimental wild birds in captivity under specific-pathogen-free conditions, there will be no further clarification of the differences in susceptibility of wild bird hosts, since the immune status and prior infection of trapped wild birds is unknown.

A promising step in this direction has been made recently by Williamson et al.,<sup>43</sup> who were able to propagate the pox virus strain from the Starling on the CAM of Starling eggs, with production of typical intracytoplasmic inclusion bodies. They also used embryonic birds for inoculation with the virus.

Since birds appear to be poor antibody producers against pox viruses, one cannot rely on presently available serologic tests to determine their immune status.

TABLE 3. *Results of Comparative Immunity Studies on Avian Pox Viruses*

PRIMARY HOST	EXPERIMENTAL HOST	CHALLENGE VIRUS	RESULT	REFERENCE
Blue Grouse	Chicken	Fowl pox	immune	9
Canary	Chicken	Fowl pox	susceptible	14
	Turkey	Fowl pox	susceptible	
	Quail	Fowl pox	susceptible	
	Chicken	Fowl-Pigeon pox	immune	40
	Pigeon	Fowl-Pigeon pox	immune	
	"passerines"	Fowl-Pigeon pox	immune	
	Pigeon	Pigeon Pox	susceptible	15
Chipping Sparrow	Chipping Sparrow	Chipping Sparrow	susceptible	37
Field Sparrow	Field Sparrow	Field Sparrow Pox	susceptible	37
Fowl	Chicken	Fowl Pox	immune	45
	Chicken	Junco Pox	susceptible	
	Chicken	Sage Grouse Pox	immune	13
	Chicken	Ruffed Grouse Pox	immune	13
	Chicken	Canary Pox	immune	40
	Pigeon	Canary Pox	immune	
	"passerines"	Canary Pox	immune	
	Chicken	Junco Pox	immune	18
Junco	Chicken	Junco Pox	immune	45
	Chicken	Fowl Pox	susceptible	18
Pigeon	Chicken	Canary Pox	immune	40
	Pigeon	Canary Pox	immune	
	"passerines"	Canary Pox	immune	
	Pigeon	Pigeon Pox	immune	5, 29, 30
	Pigeon	Pigeon Pox	susceptible	30
	Pheasant	Pheasant Pox	susceptible	10
	Pheasant	Pheasant Pox	immune	10
	Mourning Dove	Mourning Dove	immune	29
Ruffed Grouse	Chicken	Fowl Pox	immune	13
Sage Grouse	Chicken	Fowl Pox	immune	9
Sooty Grouse	Chicken	Fowl Pox	immune	41

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