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Circulation of influenza viruses and paramyxoviruses in waterfowl originating from two different areas of North America

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Migratory waterfowl and shore birds harbour a wide range of influenza viruses, some of which have been implicated in influenza outbreaks in mammals and domestic birds. In the present study, a comparison was made of two marshalling areas for different migratory flyways of waterfowl in North America over a 6-8-year period. Virtually all known influenza subtypes were isolated and the predominant subtype changed from year to year. A marked difference between the two locations was that the predominant subtypes circulating were never the same, even though in both areas, most virus isolations were made from the same duck species (mallard duck). Isolations of paramyxovirus were characterized mainly as avian PMV-1.

Viruses isolated from ducks included those antigenically related to viruses causing disease in birds and mammals, although the viruses did not necessarily appear in ducks immediately before they appeared in other species. For example, H5N2 isolates antigenically related to the virus causing severe disease outbreaks in chickens in the USA in 1983, were detected in ducks from both areas at different times (1976, 1980 and 1982). These studies indicate that ducks in different areas represent a continual source of orthomyxoviruses and paramyxoviruses of potential disease significance to other species.

During the past few years, severe disease outbreaks associated with avian influenza viruses have occurred in both birds and mammals, e.g., seals in the USA in 1979-80 (*1*) and in 1982-83 (Hinshaw et al., unpublished data); pigs in Europe in 1981-82 (*2*); turkeys in the USA (*3, 4*); and more recently, chickens in Pennsylvania, USA (Bean et al., unpublished data). Although the source of these viruses has never been fully elucidated, it is possible that waterfowl and shore birds are involved. Over the past 8 years, longitudinal studies have been done to determine the incidence and number of different subtypes of influenza viruses present in wild ducks that originate in Alberta, Canada. Earlier reports on this study (*3*) indicated that many influenza haemagglutinin and neuraminidase subtypes could be isolated from ducks in Alberta and that the predominant subtype changed from year to year. Comparative studies have never been done to determine if the influenza viruses prevalent in ducks on one migratory flyway were also prevalent in ducks on other flyways and whether there is any correlation between disease outbreaks and the prevalence of viruses in the wild duck species.

In the present study, influenza A strains and paramyxovirus strains circulating in feral ducks from two regions of Alberta from 1976 to 1983 were examined and compared with viruses isolated from ducks in New York, USA, from 1978 to 1983. Ducks from these regions of Alberta migrate primarily along the Pacific, Central and Mississippi flyways, whereas ducks from New York migrate along the Atlantic flyway. Comparisons were made between viruses from feral ducks and viruses causing disease outbreaks in other animal species along the migratory flyways.

This study demonstrates that: (*a*) many different ortho- and paramyxoviruses circulate in ducks from both Alberta and New York; (*b*) the antigenic subtypes and frequency of strains are different in ducks from different flyways and change from year to year; (*c*) changes in the predominant strains infecting

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ducks takes place rapidly; and (*d*) H5N2 viruses, antigenically similar to a virulent chicken virus, circulated in feral ducks in 1976, 1980 and 1982.

MATERIALS AND METHODS

Collection of samples

Waterfowl and shore birds were trapped in the month of August at the end of the breeding season on several lakes near Vermilion, Alberta, Canada, from 1976 to 1978; on lakes near Grande Prairie, Alberta, Canada, from 1979 to 1983 (some 480 km NW of Vermilion); at Howland Island, Cayuga County, New York, USA, from 1978 to 1982; and at Three Rivers Wildlife Management Area, Onondaga County, New York, in 1983 (16 km NE of Howland Island). Waterfowl trapped in Alberta during August were mainly mallard ducks and pintail ducks assembling to begin migration south. Mallard ducks from the Grande Prairie region used the Pacific flyway, whereas those from Vermilion mainly used the Central and Mississippi flyways. Pintail ducks from both regions of Alberta migrated along the Pacific flyway. Birds trapped in New York were congregating to begin migration south along the Atlantic flyway. Birds were classified as juveniles (birds born within the year) or adults (sexually mature birds in the second calendar year of life or later).

The birds sampled included the following species: western grebe (*Aechmophorus occidentalis*); horned grebe (*Podiceps auritus*); Canada goose (*Branta canadensis*); mallard (*Anas platyrhynchos*); American black duck (*Anas rubripes*); pintail (*Anas acuta*); gadwall (*Anas strepera*); American wigeon (*Anas americana*); northern shoveler (*Anas clypeata*); blue-winged teal (*Anas discors*); green-winged teal (*Anas crecca*); wood duck (*Aix sponsa*); redhead (*Aythya americana*); canvasback (*Aythya valisineria*); lesser scaup (*Aythya affinis*); bufflehead (*Bucephala albeola*); ruddy duck (*Oxyura jamaicensis*); moorhen (*Gallinula chloropus*); American coot (*Fulica americana*); greater yellowlegs (*Tringa melanoleuca*); lesser yellowlegs (*Tringa flavipes*); long-billed dowitcher (*Limnodromus scolopaceus*); and sandpiper (*Calidris* spp.) The procedures for virus isolation have been described previously (*5*).

Viruses

Viruses used in antigenic comparisons are shown in Table 5. Viruses were grown in the allantoic cavity of 11-day-old embryonated chickens' eggs.

Serological tests and virus identification

Haemagglutination inhibition (HI) tests were performed in microtitration plates using sera treated with receptor-destroying enzyme (RDE) (*6*). The neuraminidase inhibition (NI) tests have already been fully described (*7*). All haemagglutinating agents were identified in HI and NI tests with specific antisera to the isolated surface antigens of reference influenza viruses (*5*). Antisera to selected avian isolates were prepared in chickens according to standard procedures (*5*).

RESULTS

Influenza virus isolation

During the period from 1976 to 1983, 2422 influenza A viruses were isolated from 9195 birds in Alberta. The frequency of virus isolation was much higher in juvenile birds (mean, 30%) than in older birds (mean, 11%) and varied from year to year, the highest frequency (61%) occurring in 1978 (Table 1). In New York, from 1978 to 1983, 166 influenza A viruses were isolated from 1560 birds; the number of birds sampled and the overall rates of virus isolation (12% in juveniles, 4% in adults) were lower than in Alberta. All virus isolations in both regions were from apparently healthy birds.

In Alberta, birds trapped were mainly mallard ducks and pintail ducks, whereas in New York, wood ducks were the predominant species (46%). Relatively few mallard ducks (19%) and pintail ducks (0.5%) were trapped in New York. The proportion of virus isolations was highest in mallard ducks and pintail ducks in Alberta (31% and 29%, respectively) and highest in mallard ducks in New York (39%), whereas virus isolations were seldom made in wood ducks (8%). No influenza viruses were isolated from 277 Canada geese sampled.

Paramyxovirus isolation

During the study period, 237 paramyxoviruses were isolated from waterfowl in Alberta and 88 paramyxoviruses were isolated in New York (mean isolation rates, 3.5% and 6.3%, respectively). Antigenic characterization on 316 of these isolates (232 from Alberta, 84 from New York) (Table 2) showed that they were mainly avian paramyxovirus-1 (Alberta, 224 isolations; New York, 70 isolations).

Antigenic characterization of influenza viruses

Alberta. Throughout the study, 44 different antigenic combinations of influenza virus were isolated (Table 3). These combinations involved 12 different haemagglutination subtypes and 9 different neuraminidase subtypes. Thus, of the 13 haemag-

Table 1. Isolation of influenza viruses from juvenile and adult waterfowl in Alberta and New York

Year of study	Alberta						New York					
	No. of birds sampled		No. of virus isolates		Isolation rate (%)		No. of birds sampled		No. of virus isolates		Isolation rate (%)	
	J[a]	A[a]	J	A	J	A	J	A	J	A	J	A
1976[b]	473	463	85	20	18	4						
1977[b]	973	1 073	190	116	19	11						
1978	1 098	747	666	203	61	27	260	89	27	3	10	3
1979	1 041	253	480	50	46	20	253	106	18	3	7	3
1980	684	53	148	8	22	15	242	94	0	0	0	0
1981	611	145	93	9	15	6	211	28	13	1	7	4
1982	468	344	167	41	36	12	180	20	63	5	34	25
1983	634	135	133	13	21	10	69	8	30	3	43	38
Total	5 982	3 213	1 962	460	30	11	1 215	345	151	15	12	4

[a] J = juvenile, A = adult.
[b] No samples from New York in 1976 and 1977.

glutinin subtypes known to exist in different animal species, 12 were detected in wild ducks. All of the 9 known neuraminidase subtypes were detected in ducks. The frequency of isolation of each influenza virus strain varied from year to year. Only 2 antigenic combinations (H3N8 and H4N6) were isolated every year, whereas 19 combinations (H1N2, H1N5, H1N6, H1N8, H2N9, H3N3, H3N4, H4N3, H4N4, H6N9, H7N2, H7N5, H7N8, H10N3, H11N1, H11N3, H11N4, H11N8, H12N1) were isolated in only one year. Isolations of H5N2 strains in mallard ducks were made in 1976 and 1980. The predominant subtype for 5 of the 8 years was H3N8, and in the remaining 3 years it was H6N2, H6N5 or H6N6 (Fig. 1). In 1978 and 1982, the predominant subtypes circulating were completely different from those circulating previously. In 1978, H6N2 virus accounted for 60% of all virus isolations, yet this strain was not isolated in the previous 2 years and accounted for only 9% of isolations in the following year. In 1982, H6N6 virus accounted for 75% of all isolations, although this strain had been isolated only twice before in 1979, and it was not detected in 1983. In all years except 1979 and 1983, one strain clearly

Table 2. Paramyxoviruses isolated from waterfowl in Alberta and New York

Location	Year of isolation							
	1976	1977	1978	1979	1980	1981	1982	1983
Alberta	1 PMV1 1 PMV6	43 PMV1 2 PMV2 1 PMV6	37 PMV1 2 PMV6	10 PMV1	49 PMV1	36 PMV1	12 PMV1 1 PMV4 1 PMV6	36 PMV1 4 PMV4 1 PMV6
Total	2	46	39	10	49	36	14	41
New York	No samples	No samples	18 PMV1 1 PMV4 4 PMV6	19 PMV1 1PMV2 2 PMV4 2 PMV6	19 PMV1 1 PMV4 1 PMV6	8 PMV1 2 PMV4 3 Unchar[a]	4 PMV1 1 Unchar[a]	2 PMV1
Total	–	–	23	24	21	13	5	2

[a] Uncharacterized.

Table 3. Antigenic classification of influenza A viruses isolated from feral ducks in Alberta from 1976 to 1983

Antigenic subtype	No. of influenza viruses isolated in:							
	1976	1977	1978	1979	1980	1981	1982	1983
H1N1	14	33	5	4	6	9		5
H1N2				2				
H1N5						1		
H1N6		1						
H1N8		1						
H2N3		1	1	2	8			
H2N9		1						
H3N1	1					1		25
H3N2	2		7	8	5	3		
H3N3			1					
H3N4				1				
H3N5				3				1
H3N6	7	21	5	8	10	1		15
H3N8	54	135	162	126	112	50	6	40
H3N9		1						3
H4N1	3	2						5
H4N2			8	37	1			
H4N3		1						
H4N4								1
H4N6	16	90	122	51	7	16	28	31
H4N8	1	5	22				1	3
H5N2	3				1			
H6N1				1		1	4	
H6N2			523	47		9	2	
H6N4				8			1	
H6N5			1	152		1		
H6N6				2			165	
H6N8			5	67		6		
H6N9				4				
H7N2				1				
H7N3	3	6	1	1		1		
H7N5		1						
H7N8				1				
H8N4		1	1	1	2		1	
H9N1			1					7
H10N3			1					
H10N7		1	2			2		
H11N1								1
H11N3								1
H11N4					1			
H11N8								1
H11N9		4		3	3			5
H12N1								2
H12N5	1	1				1		3
Total	105	306	869	530	156	102	208	149

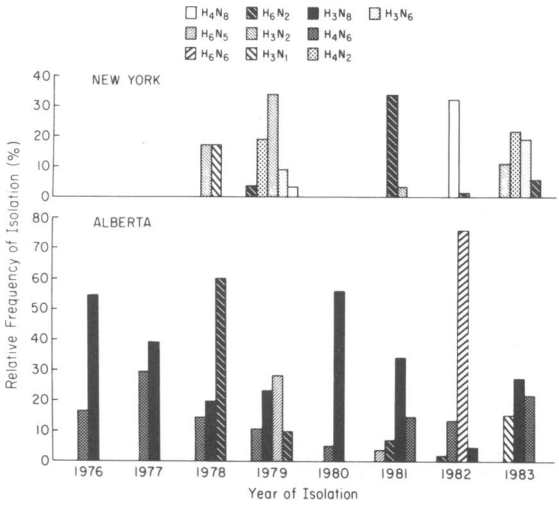

Fig. 1. The predominant influenza A subtypes isolated in feral ducks from New York and Alberta, 1976–1983.

predominated, but in 1979 there were twice the usual number of strains isolated, with two of them (H3N8 and H6N5) accounting for most isolations, and in 1983 both H3N8 and H4N6 strains were predominant.

In 1979, there was a clear distinction between the strains isolated during the first 12 days of sampling and those isolated later (Fig. 2). This comparison was done with isolates from 2 lakes where similar numbers of ducks (mainly juvenile mallard and pintail) were sampled each day. Before 16 August, 54% of all virus strains were H3N8 and only 11% were of the H6 subtype; after 16 August, 91% of all virus strains isolated were H6 subtype with the H6N5 strain predominating. In addition, before 16 August only 17% of virus isolations were made in adult ducks, whereas later the number of virus isolations in adult ducks increased to 37%. This was more than twice the normal isolation frequency for adult ducks in this area (Table 1). These changes took place within the space of 5 days.

New York. Ducks from this area excreted influenza viruses with 23 different antigenic combinations (Table 4), which included 8 different haemagglutinin subtypes and 7 different neuraminidase subtypes. Two of the strains (H1N3, H2N2) isolated in New York were not isolated in ducks from Alberta. The frequency of isolation of different strains varied each year; the most frequently isolated strains were H4N8, H4N2, H6N2 and H3N2. In 1980, there were no influenza virus isolations and only 2 paramyxovirus isolations, even though 336 waterfowl were examined. One isolation of H5N2 virus was made in a mallard duck in 1982. The predominant subtypes appearing each year in New York ducks were different from those appearing in ducks from Alberta (Fig. 1). Even in 1978 and 1982, when the majority of ducks from Alberta were shedding H6N2 and H6N6 viruses, respectively, these viruses were not isolated in New York. The only strain that was isolated to any significant extent in both duck populations was H6N2 but there was a 3-year interval between the times of predominance in each duck population.

Antigenic comparison between H5 viruses from different avian species

Isolations of H5N2 viruses were made from ducks trapped in Alberta in 1976 and 1980, and New York in 1982. These viruses were compared antigenically with an H5N2 virus recently isolated from sick chickens in Pennsylvania in 1983 (A/chick/Pa/6/83). Results of HI tests (Table 5) showed that the isolates from feral ducks and the isolate from a domestic chicken were all closely related serologically.

DISCUSSION

This comparison of viruses circulating in feral ducks in marshalling areas for the Pacific, Central,

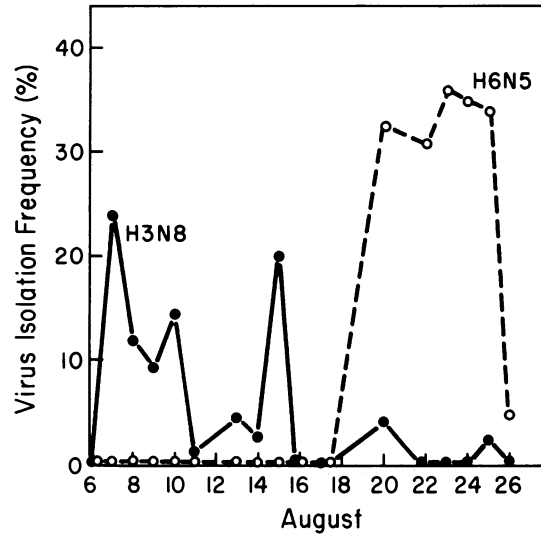

Fig. 2. Isolation of influenza A virus from feral ducks on 2 lakes in Alberta during August 1979. The frequency of virus isolation of the predominant subtypes, H3N8 (•——•) and H6N5 (○——○), are illustrated for each day of sampling.

Table 4. Antigenic classification of influenza A viruses isolated from ducks in New York from 1978 to 1983

Antigenic subtype	No. of influenza viruses isolated in:					
	1978	1979	1980	1981	1982	1983
H1N2					6	
H1N3					1	
H1N5	1					
H1N8					8	
H2N2	1					
H2N3	1					
H3N1	9					
H3N2	9	9		1		4
H3N3					1	
H3N6		2				6
H3N8	2	1			1	4
H3N9	1					
H4N1	1					
H4N2		4		1	2	7
H4N3					17	
H4N6	1	3				4
H4N8		1			23	
H5N2					1	
H6N1	2					
H6N2		1		10	1	2
H6N6				2		
H11N9	2				1	
H12N5						1
Uncharacterized					6	5
Total	30	21	0	14	68	33

Mississippi and Atlantic flyways over a 6–8-year period, has shown that both influenza A viruses and paramyxoviruses are widely distributed. All 9 influenza neuraminidase subtypes and all, except H13, of the haemagglutinin subtypes were detected in the virus isolates. However, there is evidence that ducks may not be natural hosts for viruses of the H13 subtype, since this subtype has only been detected in gulls (*8*, *9*). The predominant strains circulating in ducks from Alberta and in those from New York were never the same and were rarely the same in consecutive years. For example, in 1982 when 75% of all influenza virus isolations in Alberta were of the H6N6 virus, this strain was not isolated in ducks from New York. The differences between strains circulating in Alberta and New York may be due to the limited mixing of ducks from different flyways (*10*) and the high frequency of virus isolations in juvenile birds that had not left the hatching areas.

In 1979 there was an example in Alberta of the rapid emergence of a new dominant H6 subtype (H6N5) strain), which replaced existing subtypes within the space of 5 days. This rapid mid-season change in dominant subtypes has not previously been documented. The emergence of a dominant strain may involve various mechanisms, but would depend on the availability of a large number of susceptible ducks. In addition to infections of juvenile ducks, the H6N5 virus infected an unusually high proportion of adult ducks, possibly as a result of the H6 haemagglutinin being an antigenic variant of previously circulating H6 haemagglutinins (data not provided) and the N5 neuraminidase being rarely isolated in the previous year.

Owing to the enormous numbers of strains circulating in ducks and the long distances travelled by the ducks during migration, there has been speculation about the importance of duck viruses in relation to influenza outbreaks in other animal species. In the present study, viruses antigenically related to H1N1 viruses of pigs (*5*, *12*); H7N2, H6N8, H6N2 and H4N8 viruses of turkeys (*3*, *12*); and H3N8 viruses of horses (*13*) have been isolated in feral ducks. Although viruses antigenically similar to all antigenic combinations that infected man in the past (H1N1, H2N2 and H3N2) have been isolated in these studies, there were 9 HA subtypes and 7 NA subtypes in the duck population that man has not yet experienced. This represents a large gene pool of potential disease significance for man.

Influenza viruses of avian origin have been implicated in outbreaks of disease in mammals such as seals in New England, USA (*1*; Hinshaw et al.,

Table 5. Haemagglutination-inhibition reactions of H5 influenza viruses from ducks and chickens

Antigen	HI titres[a] with chicken antisera to:	
	Dk/Alb/57/76	Ck/Pa/6/83
Dk/Alb/7/76 (H5N2)	160	160
Dk/Alb/57/76 (H5N2)	160	320
Dk/Alb/11/76 (H5N2)	160	80
Dk/Alb/645/80 (H5N2)	160	80
Dk/NY/189/82 (H5N2)	160	160
Ck/Pa/6/83 (H5N2)	80	320

[a] HI titre is the reciprocal of the highest dilution of antisera inhibiting 4 haemagglutinating doses of virus.

unpublished data) and pigs in Europe (*2*, *14*). There is also good evidence for involvement of duck influenza viruses in outbreaks of disease in domestic birds, especially turkeys (*4*, *15*). Influenza viruses of the H5 subtype have periodically caused severe outbreaks in different avian species such as terns (H5N2 virus) (*15*); chickens (H5N1 virus); and turkeys (H5N9 virus) (*16*). Recently, a highly pathogenic H5N2 virus appeared in domestic chickens, turkeys and game birds in Pennsylvania, USA, and resulted in destruction of over 12 million birds from November 1983 through May 1984. We have demonstrated that the chicken H5N2 virus was antigenically related to viruses circulating in wild ducks from 1976 to 1982 and further studies have shown that the chicken and duck H5N2 viruses were genetically related (Bean et al., unpublished data). However, duck H5N2 viruses are avirulent for chickens (Wood, unpublished data) and the chicken H5N2 virus does not replicate in the intestinal tract of ducks (Webster and Kawaoka, unpublished data). Thus, it is unlikely that the pathogenic chicken virus originated directly from ducks, but may have emerged from an avirulent duck virus by selective adaptation in chickens.

The high incidence of infection of ducks in Alberta (up to 61%) and New York (up to 43%) was probably due to large numbers of susceptible juvenile birds in these areas at the end of the breeding season. When ducks have begun migration and are examined later in the year, the isolation rates are much lower, e.g., 1.5% in Arkansas from November 1974 to January 1975 (*18*) and 3% in Delaware and Maryland in November 1973 (*19*), presumably because of developing immunity and dispersal of duck populations so that they are below the critical levels necessary to maintain infections.

Paramyxovirus isolations in feral ducks were mainly of PMV-1, although PMV-2, PMV-4 and PMV-6 were also isolated. The importance of these viruses circulating in ducks is difficult to assess, although their existence has been known for a number of years (*18*, *19*). All the virus isolations in the present study were from apparently healthy ducks, but antigenically related viruses have caused considerable mortality in domestic turkeys and chickens, psittacines, and other exotic birds (PMV-1 and PMV-2) (*20*).

These studies have established that feral ducks are very effective hosts for a large number of different influenza A viruses and paramyxoviruses. Several factors may contribute to this, including annual infection of susceptible juvenile birds; ease of transmission by the faecal/oral route (*21*); genetic reassortment during mixed infection of duck intestine (*11*); lack of disease symptoms shown by ducks; and effective transport to different locations during migration. This diversity of influenza genes circulating in the duck population may be important as a recurring source of viruses for other animal species, especially domestic birds.

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RÉSUMÉ

CIRCULATION DES VIRUS GRIPPAUX ET DES PARA-MYXOVIRUS CHEZ LE GIBIER D'EAU PROVENANT DE DEUX RÉGIONS DIFFÉRENTES D'AMÉRIQUE DU NORD

Le gibier d'eau migrateur héberge toute une gamme de virus grippaux, dont certains ont été à l'origine de poussées de grippe chez les mammifères et les oiseaux domestiques. La présente étude s'attache à la comparaison qui a été faite sur une durée de 6 à 8 ans entre deux zones de rassemblement (l'Alberta, au Canada, et l'État de New York, aux Etats-Unis d'Amérique), au départ des différentes routes de migration du gibier d'eau en Amérique du Nord. La fréquence d'isolement du virus grippal a varié selon les années et les endroits (de 0% à 61%), mais elle était plus élevée chez les juvéniles que chez les adultes. La fréquence d'isolement des para-myxovirus a été bien plus faible (de 0,2% à 7%).

Tous les sous-types grippaux définis à partir de l'hémagglutinine, sauf l'H13, ainsi que tous les sous-types connus définis à partir de la neuraminidase ont été isolés. Chaque année, un ou deux sous-types grippaux dominent en général, mais ils changent d'une année à l'autre. Un exemple de ce remplacement rapide d'un sous-type dominant par un autre a été observé chez les canards de l'Alberta en 1979, où des changements se sont produits à la mi-saison en l'espace de 5 jours. Les isolements effectués en Alberta et dans l'Etat de New York diffèrent systématiquement par la nature du sous-type circulant dominant, alors pourtant que, dans les deux régions, la plupart de ces isolements sont effectués à partir de la même espèce de canard (canard col-vert). Par exemple, en Alberta, le virus H3N8 a dominé pendant 5 des 8 années étudiées, tandis que cette souche n'était que rarement isolée dans l'Etat de New York. De plus, en 1982, 75% des isolements des virus grippaux étaient des H6N6 en Alberta, alors que cette souche n'a pas été isolée chez les canards de l'Etat de New York. Ces poussées localisées reflètent probablement la fréquence élevée des isolements effectués chez des juvéniles n'ayant pas encore quitté la zone d'éclosion.

Parmi les virus isolés des canards, il y en avait qui étaient apparentés du point de vue antigénique aux virus pathogènes pour les oiseaux et les mammifères; pourtant, leur apparition chez les canards n'a pas toujours immédiatement précédé leur manifestation chez les autres espèces. Par exemple, le sous-type H5N2, qui a une parenté antigénique avec le virus responsable de graves épizooties chez les poulets aux Etats-Unis en 1983, a été isolé chez les canards des deux régions à différentes époques (1976, 1980 et 1982). Bien que les virus des sous-types H5 aient causé de graves flambées épizootiques chez diverses expèces d'oiseaux comme la sterne, le poulet et le dindon, même le virus hautement pathogène A/chick/Pa/83 (H5N2) n'est pas virulent pour le canard. On peut donc penser que les canards peuvent héberger un virus virulent pour d'autres espèces aviaires sans présenter aucun symptôme de maladie. Dans ces conditions, les canards de différentes régions constituent une source permanente d'orthomyxovirus et de paramyxovirus éventuellement pathogènes pour d'autre espèces animales.

REFERENCES

1. WEBSTER, R. G. ET AL. Characterization of an influenza A virus from seals. *Virology*, **113**: 712-724 (1981).
2. SCHOLTISSEK, C. ET AL. Genetic relatedness of hemagglutinins of the H1 subtype of influenza A viruses isolated from swine and birds. *Virology*, **129**: 521-523 (1983).
3. HINSHAW, V. S. ET AL. The perpetuation of orthomyxoviruses and paramyxoviruses in Canadian waterfowl. *Canadian journal of microbiology*, **26**: 622-629 (1980).
4. HALVORSON, D. ET AL. Epizootiology of avian influenza—simultaneous monitoring of sentinel ducks and turkeys in Minnesota. *Avian diseases*, **27**: 77-85 (1983).
5. HINSHAW, V. S. ET AL. Novel influenza A viruses isolated from Canadian feral ducks, including strains antigenically related to swine influenza (HswlN1) viruses. *Journal of general virology*, **41**: 115-127 (1978).
6. PALMER, D. F. ET AL. *Advanced laboratory techniques for influenza diagnosis*. United States Department of Health, Education and Welfare, 1975 (Immunology Series No. 6).
7. AYMARD-HENRY, M. ET AL. Influenza neuraminidase and neuraminidase-inhibition test procedures. *Bulletin of the World Health Organization*, **48**: 199-202 (1973).
8. HINSHAW, V. S. ET AL. Antigenic and genetic characterization of a novel hemagglutination subtype of influenza A viruses from gulls. *Journal of virology*, **42**: 865-872 (1982).
9. BEAN, W. J. Correlation of influenza A virus nucleoprotein genes with host species. *Virology*, **133**: 438-442 (1984).
10. ANDERSON, D. R. & HENNY, C. J. *Population ecology of the mallard. 1. A review of previous studies and the distribution and migration from breeding areas*. United States Department of the Interior. Fish and Wildlife Service. Bureau of Sport Fisheries and Wildlife, 1972 (Resource Publication 105).
11. HINSHAW, V. S. ET AL. The ecology of influenza viruses in ducks and analysis of influenza viruses with monoclonal antibodies. *Comparative immunology, microbiology and infectious diseases*, **3**: 155-164 (1980).
12. EASTERDAY, B. C. Animal influenza. In: Kilbourne, E.D., ed. *The influenza viruses and influenza*. New York, Academic Press, 1975, pp. 462-463.
13. WADDELL, G. H. ET AL. A new influenza virus associated with equine respiratory disease. *Journal of the American Veterinary Medical Association*, **143**: 587 (1963).
14. OTTIS, K. & BACHMANN, P. A. Occurrence of HswlN1 subtype influenza A viruses in wild ducks in Europe. *Archives of virology*, **63**: 185-190 (1980).
15. HINSHAW, V. S. & WEBSTER, R. G. The natural history of influenza A viruses. In: Beare, A. S., ed. *Basic and applied influenza research*. Boca Raton, Florida, CRC Press, 1982, pp. 79-104.
16. BECKER, W. B. The isolation and classification of tern virus: influenza virus A/tern/South Africa/1961. *Journal of hygiene*, **64**: 309-320 (1966).

17. LANG, G. ET AL. A new influenza A virus infection in turkeys. II. A highly pathogenic variant, A/turkey/Ontario/7732/66. *Canadian veterinary journal*, **9**: 151-160 (1968).
18. WEBSTER. R. G. ET AL. Ortho- and paramyxoviruses from migrating feral ducks. Characterization of a new group of viruses. *Journal of general virology*, **32**: 217-225 (1976).
19. ROSENBERGER, J. K. ET AL. Isolation of Newcastle disease and type A influenza viruses from migratory waterfowl in the Atlantic flyway. *Avian diseases*, **18**: 610-613 (1974).
20. ALEXANDER, D. J. Avian paramyxoviruses. *Veterinary bulletin*, **50**: 737-752 (1980).
21. WEBSTER, R. G. ET AL. Intestinal influenza: replication and characterization of influenza viruses in ducks. *Virology*, **84**: 268-278 (1978).