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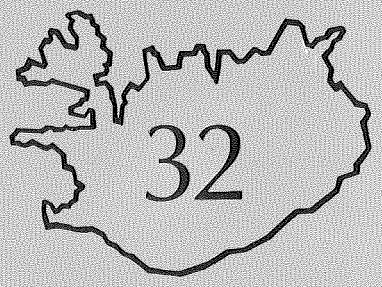

Tick-borne viruses in Icelandic seabird colonies

Stephen R. Moss
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Abstract. Nine virus isolations were made from 16 pools of *Ixodes uriae* ticks collected during three summers from seabird colonies around the coasts of Iceland. The viruses were isolated from four of nine different collection sites. Five viruses were isolated from ticks collected at Elliðaey in Breiðafjörður, West Iceland, two from Grímsey, off North Iceland, and one each from Flathólmi and Þormóðseyjarklettur, both in Breiðafjörður. Complement fixation, immunofluorescent antibody and neutralization tests showed that the viruses belonged to three different serogroups: three were orbiviruses of the Kemerovo serogroup, two were nairoviruses of the Hughes serogroup and four were uukuviruses of the Uukuniemi serogroup. A short discussion is given of the transportation of viruses between seabird colonies in Iceland and other parts of the world.

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INTRODUCTION

Ixodes (*Ceratixodes*) *uriae* White, 1852 (= *Ixodes putus* Pickard-Cambridge, 1878), a species of hard or ixodid tick, is a common ectoparasite of seabirds. It has a remarkable bipolar distribution, and is circumpolar in its northern and southern distributions (Clifford 1979). Zumpt (1952) suggested that this bipolar distribution may have resulted from ticks being transported by seabirds between the two regions. Although *I. uriae* feeds on almost any available seabird hosts, in the northern hemisphere the preferred hosts appears to be auks, particularly the Common Guillemot *Uria aalge*, and in the southern hemisphere, penguins (Murray & Vestjens 1967, Karpovich 1970, Eveleigh & Threlfall 1974, 1975, Kelly 1982, Mehl & Traavik 1983). In Iceland, *I. uriae* is most commonly associated with Puffins *Fratercula arctica* (Hantzsch 1905, Sæmundsson 1936, Timmermann 1949, Lindroth *et al.* 1973, Æ.P., pers. obs.), see Fig. 1. Other recorded hosts include gulls, petrels, cormorants and shearwaters (Neumann 1901, Nuttall *et al.* 1911, Cooley & Kohls 1945, Bequaert 1946, Gregson 1956, Anastos 1957, Arthur 1963, 1965, Murray & Vestjens 1967, Wilson 1970). *Ixodes uriae* will also feed on mammals, including humans (Nuttall *et al.* 1911, Mehl & Traavik 1983, Æ.P. and P.A.N., personal experience).

At least 53 viruses have been isolated from *I.*

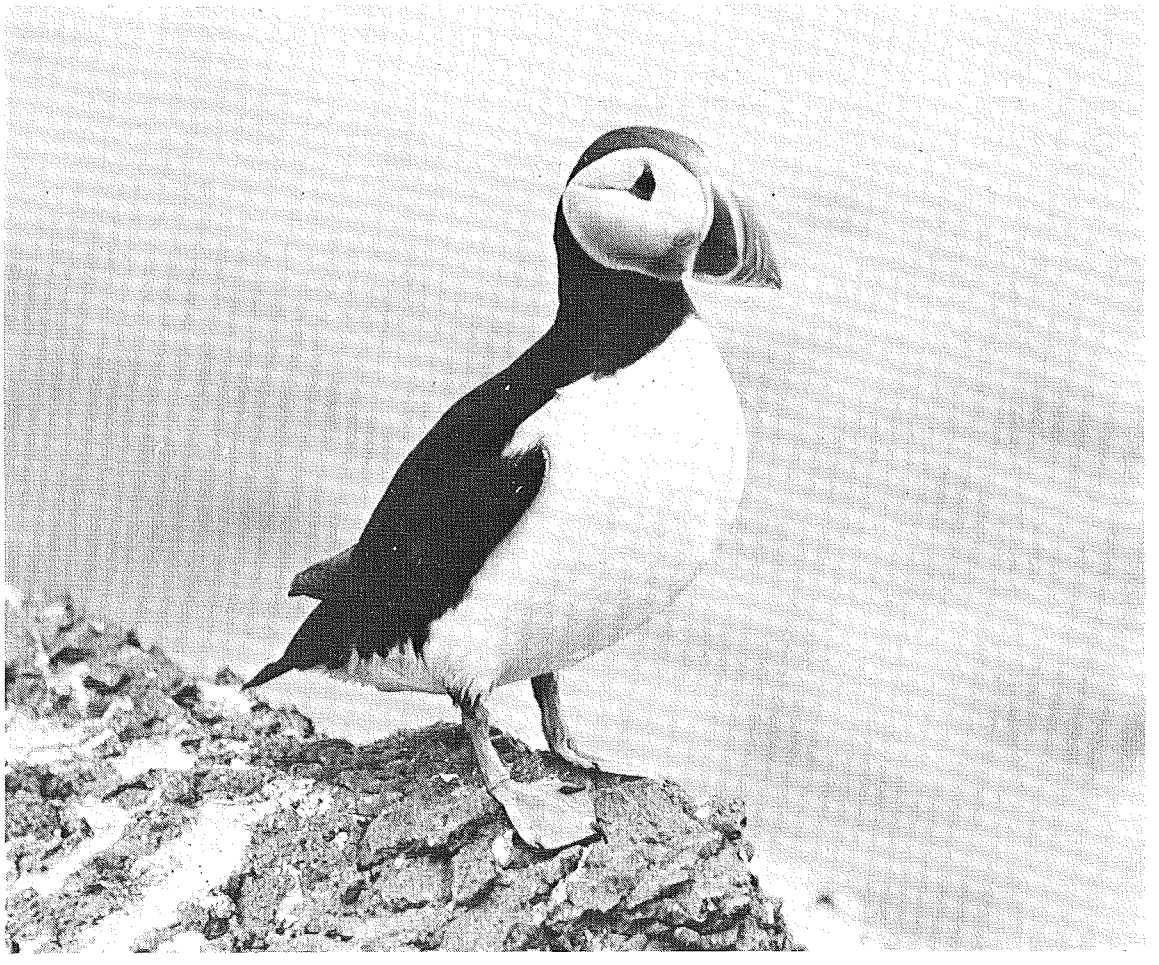

Fig. 1. Puffins are the most important hosts for *Ixodes uriae* in Iceland. Photo: Björn Björnsson.

uriae. They include members of the Kemerovo serogroup (Reoviridae: *Orbivirus*), group B serogroup (Flaviviridae: *Flavivirus*), Sakhalin serogroup (Bunyaviridae: *Nairovirus*), Uukuniemi serogroup (Bunyaviridae: *Uukuvirus*), and Runde virus a possible member of the family Coronaviridae (reviewed by Clifford 1979 and Nuttall 1984) and Hughes serogroup (Bunyaviridae: *Nairovirus*) (Nuttall *et al.* 1986). All of these viruses are considered to be arboviruses (=**ar**thropod-**bo**rne viruses). They are thought to replicate in the arthropod vector (i.e. *I. uriae*) and be transmitted to the vertebrate host (i.e. seabird) when the ticks feed on susceptible hosts. The virus then replicates in the seabird producing viraemia (=virus in the blood), infecting more ticks when these feed on the viraemic seabird. Evidence that viruses, isolated from *I. uriae*, infect seabirds has been gained from the isolation of tick-borne viruses from the blood and other tissues of seabirds (Main *et al.* 1976a, Nuttall *et al.* 1981, Eley & Nuttall 1984) and by the detection of neutralizing antibodies, to the viruses, in the sera of seabirds (Main *et al.* 1976a, b, Doherty *et al.* 1975, Yunker 1975, Nuttall *et al.* 1984a, St. George *et al.* 1977). Direct evidence that viruses isolated from *I. uriae* are indeed arboviruses (by demonstrating virus replication in, and transmission by the ticks) has not been obtained.

MATERIALS AND METHODS

Collection of ticks

Ixodes uriae were collected during three summers (1981, 1982, 1983). Table 1 lists the collection sites and dates, the host species from which the ticks were collected or else where they were found, and the numbers of ticks in each tick pool. All ticks examined for viruses were adult females.

Descriptions of seabird colonies

Ixodes uriae were collected from nine seabird colonies around the coasts of Iceland. The geographical location of these is shown in Fig. 2, and a brief description of each site is given below. The information on seabird numbers is either unpublished and collected by Æ.P. or Trausti Tryggvason on expeditions to these colonies, or published in Garðarsson (1979), Einarsson (1979), and Petersen (1979, 1981). These population estimates have all been collected within the last 10 years. If estimates have been published, these are used and of these the most recent one.

Grímsey, off N.-Iceland (Fig. 3): Well-known in the literature as a seabird station (e.g. Hantzsch 1904, Foster *et al.* 1951). This island is approx. 5.3 km^2 in area. It slopes gently from max. 105 m high cliffs on the east side towards 10–20 m high cliffs on the west side. The numbers of breeding seabird pairs run into hundreds of thousands. The steep eastfacing cliffs are packed with breeding Fulmars *Fulmarus glacialis*, Kittiwakes *Rissa tridactyla*, Common Guillemots, Brünnich's Guillemots *Uria lomvia*, Puffins, and Razorbills *Alca torda*. A few Great Black-backed Gulls *Larus marinus* nest on the island, and inland Arctic Terns *Sterna paradisaea* abound, with Black-headed Gulls *Larus ridibundus* occurring in much fewer numbers. Puffins, from which the ticks were collected, nest in three main habitats: (a) in cracks on the cliff face, (b) on grassy slopes below cliffs, on the cliff or at the cliff edges, and (c) in boulder scree. One of two of our tick pools was collected in the soil around Puffin nesting burrows at the edge of a cliff (at Básavík) whereas the other was found on our clothes and could have come from anywhere on the island.

Efri-Langey, Breiðafjörður: A long, narrow island, grassy on top, with ca. 15 m high cliffs on its north side, under which is a boulder scree; slopes towards the south where there are sandy and gravelly beaches intermittent with rocky outcrops. Size ca. 0.25 km^2. Principal seabird species: A large colony of Puffins, a few hundred pairs of Eiders *Somateria mollissima*, several hundred pairs of Fulmars, ca. 25 pairs of Shags *Phalacrocorax aristotelis*, and approximately 100 pairs of Black Guillemots *Cepphus grylle*. Puffins nest in two different habitats: (a) the boulder scree and (b) grassy periphery of the island.

Sýrey, Breiðafjörður: A low island (max. 10 m), largely covered with Lymegrass *Leymus arenarius*, with sandy and gravelly beaches and stony outcrops. Size ca. 0.05 km^2. The Puffin outnumber other seabird species by far numbering thousands of pairs. There are many hundreds to a few thousand pairs of Arctic Terns, 7–12 pairs of Black Guillemots, less than 100 pairs of

Table 1. Tick collections and virus isolations from Icelandic seabird colonies.

Collection sites		Date	Tick		Virus	
Site name	Co-ordinates		Source[1]	Pool[2]	Serogroup[3]	Isolate
Grímsey, off N.-Iceland	66°33'N 18°00'W	17.7.81 25.7.81	CL	5	–	None
Grímsey, off N.-Iceland	66°33'N 18°00'W	11.7.82	P	8	KEM HUG	GRIMS82-1a GRIMS82-1b
Efri-Langey, Breiðafjörður	65°24'N 22°57'W	24.7.83	P	1	–	None
Sýrey, Breiðafjörður	65°23'N 22°56'W	18.7.83	BG	1	–	None
Hrólfsklettur, Breiðafjörður	65°23'N 22°54'W	11.7.81	CO	5d	–	None
Hrólfsklettur, Breiðafjörður	65°23'N 22°54'W	21.7.83	F	2	–	None
Klofningur, Breiðafjörður	65°22'N 22°57'W	18.7.83	F	5	–	None
Flathólmi, Breiðafjörður	65°22'N 22°54'W	20.7.83	P	2e	UUK	FLAT-1
Elliðaey, Breiðafjörður	65°08'N 22°49'W	20.7.81 23.7.81	P	6 6 4e 1e 5e	UUK UUK KEM HUG UUK –	ELL-1 ELL-2 ELL-3a ELL-3b ELL-4 None
Þormóðseyjarklettur, Breiðafjörður	65°04'N 22°56'W	13.6.82	CO	6	KEM	THOR-1
Elliðaey, Vestmannaeyjar	63°28'N 22°10'W	1.8.82	P	10 3e	– –	None None

[1] CL= on researcher's clothes; P= from Puffin; BG= from Black Guillemot; CO= free in colony; F= from Fulmar.
[2] Number of ticks in tick pool; all were female *Ixodes uriae*; d= dead; e= engorged.
[3] Kem= Kemerovo; HUG= Hughes; UUK= Uukuniemi.

Black-headed Gulls, and a few hundred pairs of Eider Ducks.

Hrólfsklettur, Breiðafjörður: A small, knolly islet, grassy on top, and bordered with low cliffs (max. 10 m). Size ca. 0.02 km^2. Main seabird species nesting: Kittiwake, ca. 190 pairs, Puffin a few hundred pairs, Shag 44 pairs, Black Guillemot 4–6 pairs, and Fulmar 4 pairs.

Klofningur, Breiðafjörður: This island is elongated with low cliffs on its north side (10 m), and grass on the highest points becoming rocky as it slopes towards the south. The islet is

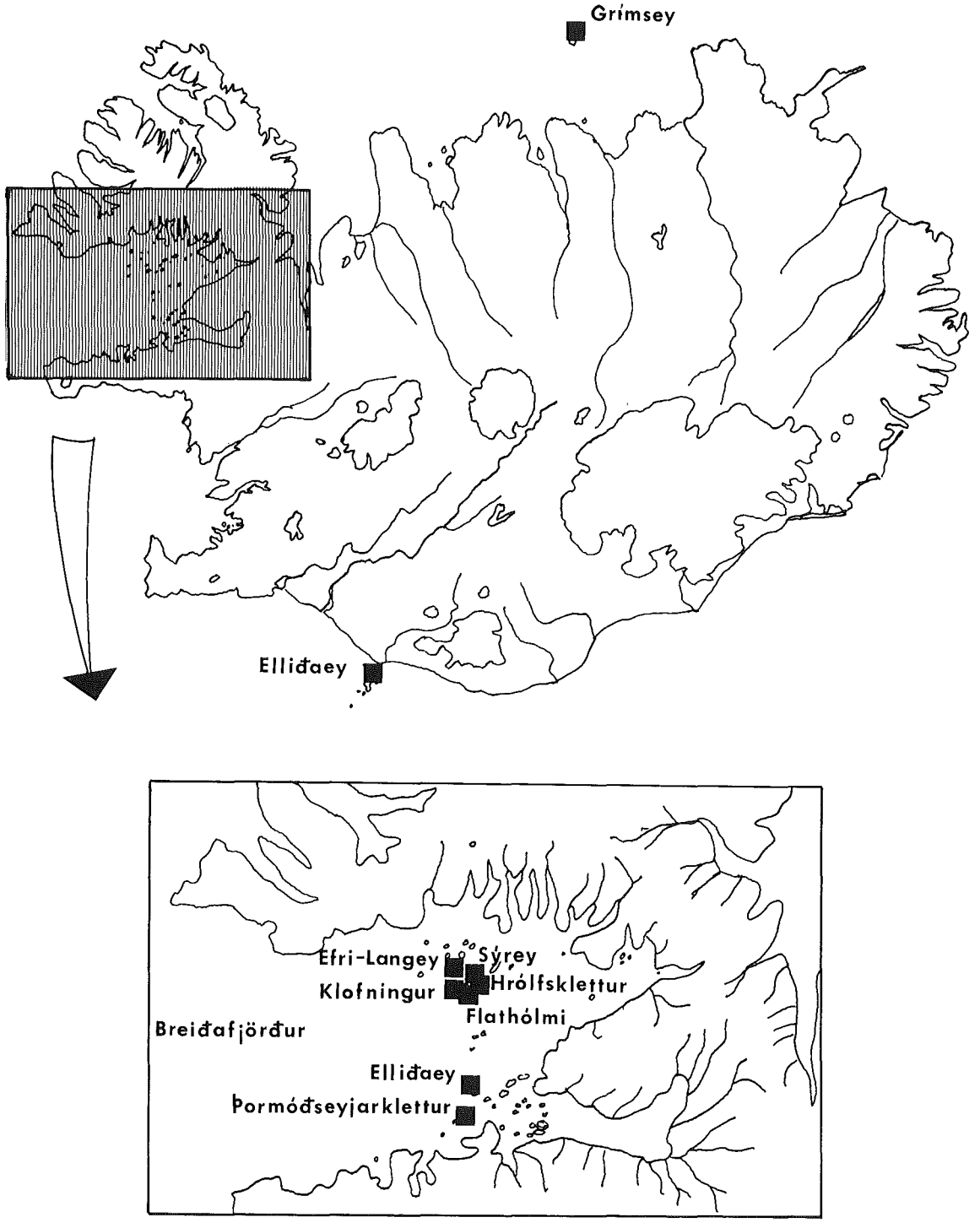

Fig. 2. The geographical location of seabird colonies around the coasts of Iceland, at which ticks were collected.

Fig. 3. From Grímsey, off North Iceland. July 13, 1982. Photo: Ævar Petersen.

intersected by crevices. Size ca. 0.04 km^2. Main seabird species nesting: Kittiwake ca. 760 pairs, Shag 510 pairs, Puffin a few hundred pairs, Eider pairs in low tens, Fulmar ca. 20 pairs, Black Guillemot 9 pairs, Arctic Tern a few pairs, and Lesser Black-backed Gull *Larus fuscus* 1–2 pairs.

Flathólmi, Breiðafjörður (Fig. 4): Low and grassy, with gravelly and stony beaches, except for a headland on its southeast side. Size ca. 0.04 km^2. Puffins outnumber all other seabirds, numbering thousands of pairs and possibly in the low ten thousands; Eider just under 100 pairs, Black Guillemot 9–10 pairs, and Arctic Tern hundreds of pairs.

Elliðaey, Breiðafjörður: A semi-circular island, bordered with cliffs (up to 41 m) on its west, north and east sides, grassy on top; used to be inhabited. Size ca. 0.3 km^2. Principal seabird species: Kittiwake thousands of pairs, Puffins thousands, Eider a small colony, Shag 5 pairs, Fulmar a few dozen pairs, Black Guillemot many dozen pairs to low hundreds, Arctic Tern a few pairs, and Great Black-backed Gull a few pairs.

Pormóðseyjarklettur, Breiðafjörður: A small knolly island with high, dense vegetation, low cliffs (11 m), and with sandy and stony beaches. At low tide an unvegetated skerry can be reached from the main island. Size ca. 0.06 km^2. Puffin is the most common seabird species, thousands of pairs, with Cormorant *Phalacrocorax carbo* 85 pairs, Fulmar ca. 50 pairs, Black Guillemot ca. 10 pairs, Eider 5–7 pairs, Shag ca. 12 pairs, Arctic Tern 1–2 pairs, and Great Black-backed Gull ca. 10 pairs.

Elliðaey, Vestmannaeyjar: Much larger than the Breiðafjörður islands, ca. 0.6 km^2. The Vestmannaeyjar islands are well-known as a seabird breeding station (Annandale 1904, Petersen 1982). High cliffs (up to 145 m) border the island's periphery, but on top the island is grassy with a rolling landscape. Alcids predominate: Puffins in tens of thousands, Razorbill common, Common Guillemot very common, Brünnich's Guillemot a few pairs, Black

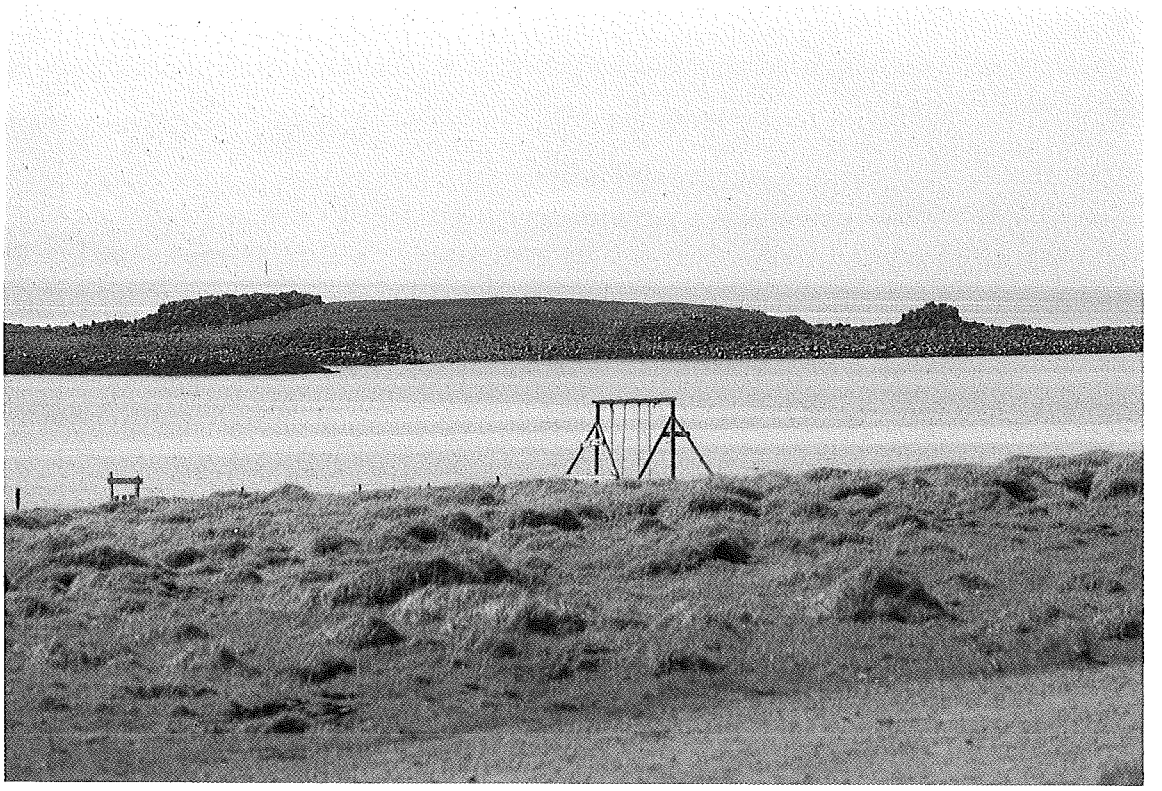

Fig. 4. A view to the islet of Flathólmi off Flatey Island in Breiðafjörður, West Iceland. June 1982. Photo: Ævar Petersen.

Guillemot rare. In addition Leach's Petrel *Oceanodroma leucorhoa* low thousands of pairs, Storm Petrel *Hydrobates pelagicus* many hundreds or low thousands of pairs, Manx Shearwater *Puffinus puffinus* thousands of pairs, Fulmar thousands of pairs, and Herring Gull *Larus argentatus* a few pairs.

Virus isolation procedures

Viruses were pooled according to site and then homogenized in phosphate buffered saline containing 1% bovine plasma albumin, 200 units/ml penicillin, 20 mcg/ml streptomycin, 200 mcg/ml kanamycin and 5 mcg/ml fungizone (PBSA). Clarified suspensions were inoculated intracerebrally (i.c.) into 1 to 2 day-old Swiss-bred mice (Pathology Oxford strain), and into chick embryo fibroblast (CEF), baby hamster kidney (BHK), and *Xenopus laevis* cell lines. Primary CEF cultures were prepared from 10 day-old fertile hens' eggs. All cell lines except *Xenopus* were grown in Eagle's minimum essential medium supplemented with 10% heat-inactivated foetal calf serum (FCS), at 37°C. *Xenopus* cell cultures were grown in Leibovitz's medium supplemented with 10% FCS and 10% tryptose phosphate broth, at 28°C. When inoculated mice showed clinical signs of infection they were killed, and the brains were removed and homogenized to form a 20% suspension in PBSA. Mouse brain was then diluted 1/2 an 1/10 and passaged in mice and in cell cultures. Inoculated cell cultures were examined for development of a cytopathic effect and then frozen and thawed and the clarified supernatant titrated. Titrations were carried out in either Vero or *Xenopus* cells cultures in Linbro plates (Flow Laboratories) with Leibovitz's medium supplemented with 3% FCS and 0.75% (w/v) carboxymethylcellulose (BDH). Vero cells were not used for virus isolation as they had been found previously to be less sensitive that BHK cells for plaque titration.

Characterisation of viruses

Infected cell cultures were examined for the presence of viruses by electron microscopy. Pelleted cells were fixed for 1 hour at 4°C in 2% glutaraldehyde followed by 1% osmic acid for 1½ hours at 4°C; 0.2 M phosphate buffer pH 7.2 was used as a dilutant for the fixatives and for intermediate washes. Fixed cells were dehydrated in a graded ethanol series followed by acetone, and embedded in Epikote. Sections were cut on a Reichert Ultracut microtome, collected on grids, and stained with 2% (w/v) uranyl acetate and lead citrate. Stained sections were examined with a JEOL 100S electron microscope at 100 kv.

The viruses isolated were characterised serologically by complement fixation (CFT), immunofluorescent antibody (IFAT) and neutralization tests (NT).

Complement fixation tests were carried out using antigens prepared from suckling mouse brain by sucrose acetone extraction (Clarke & Casals 1958). Immune ascitic fluids were prepared as described by Shope & Sather (1979) using Landshultz's strain of Ehrlich's ascites cells. Clo Mor ScotAr 7 (Sakhalin serogroup) and Cape Wrath (Kemerovo serogroup) immune ascitic fluids (AF) were kindly supplied by Dr. A.J. Main (Yale Arbovirus Research Unit). Polyvalent Kemerovo group AF, raised against Kemerovo, Chenuda, Mono Lake, Wad Medani, Tribec and Huacho viruses, was obtained from the US National Institute of Allergy and Infectious Diseases. Ascitic fluid to FT363 (Kemerovo serogroup) and St. Abb's Head virus M349 (Uukuniemi serogroup) were prepared from viruses isolated from ticks collected at St. Abb's Head, Scotland (Nuttall *et al.* 1981). GS80-3 (Hughes serogroup) and GS80-11 (Uukuniemi serogroup) ascitic fluids were prepared from viruses isolated from ticks collected on Gt. Saltee Island, Eire (Nuttall *et al.* 1984a). Titres were expressed as the 50 per cent end-point using two units of antigen (calculated from the homologous reaction).

Immunofluorescent antibody tests were carried out using the indirect technique with fluorecein-conjugated swine anti-mouse globulin, and infected *Xenopus* cell cultures. Neutralization tests were performed using the plaque reduction technique in Linbro plates (Madrid & Porterfield 1969). Equal volumes of virus and two-fold dilutions of head-inactivated ascitic fluid were allowed to react together overnight at 4°C and then titrated.

RESULTS

The basic results, viruses isolated and serogroups, together with the names of isolates, are given in Table 1.

Virus isolation

Three isolations were made by inoculation into mouse brain (one from ticks collected at Þormóðseyjarklettur, THOR-1, and two from Grímsey, GRIMS82-1a and GRIMS82-1b), and six isolations were from inoculated cell cultures (Flathólmi, FLAT-1, and Elliðaey, ELL-1, -2, -3a, -3b, and -4), see Table 2.

Four of 7 mice developed clinical signs 8–9 days after inoculation with tick pool THOR-1; on passage in mice the incubation period was reduced to 5–6 days. When the pool of ticks from Grímsey were inoculated into mice, 3 of a litter of 9 mice showed clinical signs 12–13 days later, the incubation period being reduced to 3–4 days on passage. Infected mouse brain extracts were inoculated into BHK and CEF cell cultures. THOR-1 infected mouse brain produced a cytopathic effect in both cell lines; virus harvested from infected BHK cell cultures had a titre of 5.8 Log_{10} pfu/ml in Vero cell cultures but did not produce plaques in *Xenopus* cell cultures. Mouse brain inoculated with the Grímsey tick pool produced a cytopathic effect in BHK cells, 7–8 days post-infection, but not in CEF cultures; virus from BHK cells had a titre of 5.3 Log_{10} pfu/ml in Vero cell cultures and 6.0 Log_{10} pfu/ml in *Xenopus* cell cultures.

Three tick pools (Elliðaey, ELL-3 and ELL-4, and Flathólmi, FLAT-1) produced clinical signs of infection when inoculated into mice but had little or no effect on passage. Tick pools ELL-1 and ELL-2 did not show evidence of infection in mice.

Five viruses (ELL-1, ELL-3a, ELL-3b and ELL-4, and FLAT-1) were isolated by inoculation of tick pools into CEF cultures. ELL-1 produced a cytopathic effect 3 days after infection and had a titre of 5.0 Log_{10} pfu/ml in *Xenopus* cells but did not produce plaques in Vero cell cultures; ELL-3 (a mixture of ELL-3a

Table 2. Virus isolations from tick pools.

Isolate	Virus Serogroup	Locality	Method of isolation[1] Mice	CEF	BHK	*Xenopus*
ELL-1	UUK	Elliðaey, Breiðafjörður	−2	+	ND	ND
ELL-2	UUK	Elliðaey, Breiðafjörður	−	−	−	+
ELL-3a &	KEM	Elliðaey,	(+)	+	ND	ND
ELL-3b	HUG	Breiðafjörður	(+)	+	ND	ND
ELL-4	UUK	Elliðaey, Breiðafjörður	(+)	+	ND	ND
GRIMS-1a &	KEM	Grímsey	+	−	ND	−
GRIMS-1b	HUG		+	−	ND	−
THOR-1	KEM	Þormóðseyjarklettur	+	−	−	ND
FLAT-1	UUK	Flathólmi	(+)	+	−	ND

[1] Tick pool inoculated into either mice, or chick embryo fibroplast (CEF), baby hamster kidney (BHK), or *Xenopus leavis* cell lines; −= virus not isolated, += virus isolated, ND= not done, (+)= virus lost on passage.

and ELL-3b) did not produce a cytopathic effect but had a titre of 4.3 Log_{10} pfu/ml in Vero and 5.0 Log_{10} pfu/ml in *Xenopus* cell cultures; ELL-4 produced a slight cytopathic effect with a titre of 2.0 Log_{10} pfu/ml in *Xenopus* cells and no plaques in Vero cells. FLAT-1 produced a cytopathic effect 4 days after inoculation of CEF but did not effect BHK cells; virus harvested from infected CEF cell cultures had a titre of 5.0 Log_{10} pfu/ml in *Xenopus* cells but did not produce plaques in Vero cell cultures. ELL-2 tick pools did not produce a cytopathic effect when inoculated into CEF, BHK, Vero or *Xenopus* cell cultures, and virus was not detected by titration in either Vero or *Xenopus* cells. However, when inoculated *Xenopus* cell cultures were passaged in *Xenopus* cells, 5.1 Log_{10} pfu/ml was produced although a cytopathic effect was not observed; plaques were produced in *Xenopus* but not in Vero cell cultures.

Electron microscopy

Cultures of CEF infected with ELL-1 or ELL-4 isolates contained bunyavirus-like particles. The particles were spherical, approximately 90 nm in diameter, and comprised an electron dense area surrounded by a closely adherent membrane. Intracellular particles were localized within smooth membrane-bound vesicles; occasionally particles were observed budding into the vesicles (Fig. 5). Some particles, both intracellular and extracellular, appeared to have a fringe of surface projections (Fig. 6).

Similar bunyavirus-like particles were observed in CEF cultures infected with the ELL-3 isolate and BHK cell cultures infected with the Grímsey isolate. However, they appeared to be more variable in size and had a less pronounced fringed appearance (Fig. 7).

In addition to the bunyavirus-like particles, BHK cell cultures infected with the Grímsey isolate also contained orbivirus-like particles. Similar virus particles were observed in Vero cell cultures infected with the THOR-1 isolate. The virus particles had an electron dense core surrounded by an electron dense shell (Fig. 8). They were associated with tubules, fibrils and electron dense granular areas of viral matrix

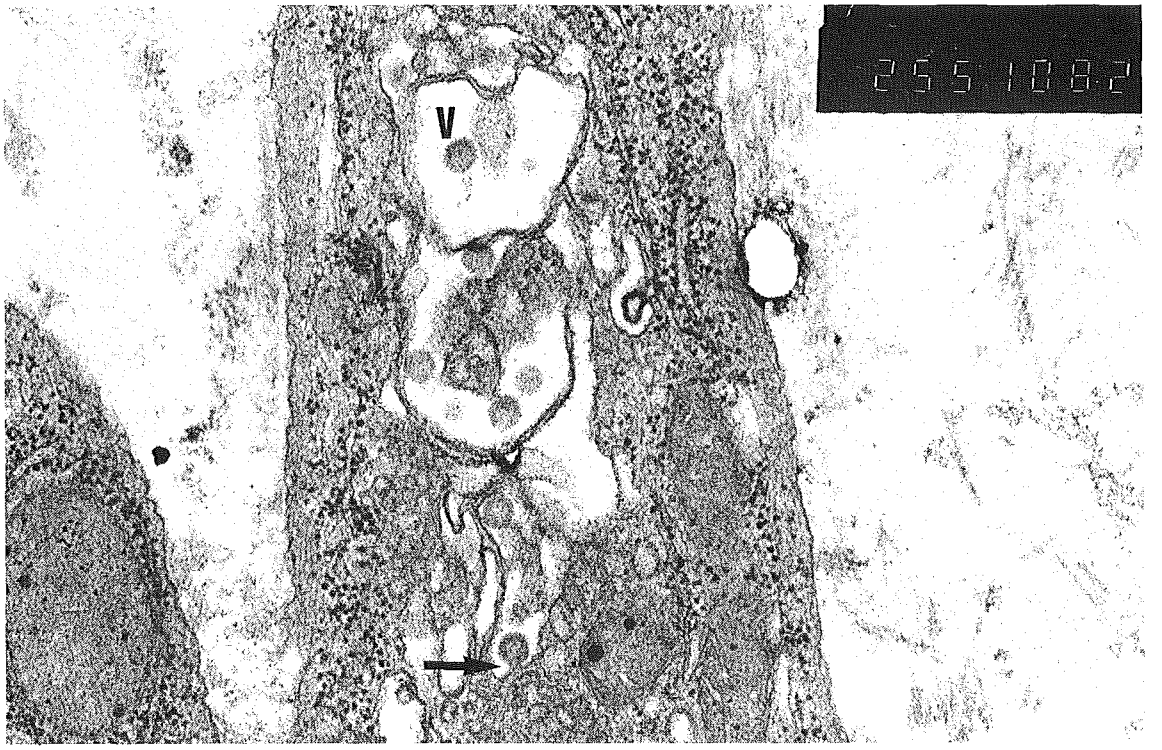

Fig. 5. Chick embryo fibroblast culture infected with ELL-1 virus. Intracellular virions (V) budding (arrow) into intracytoplasmic vesicles.

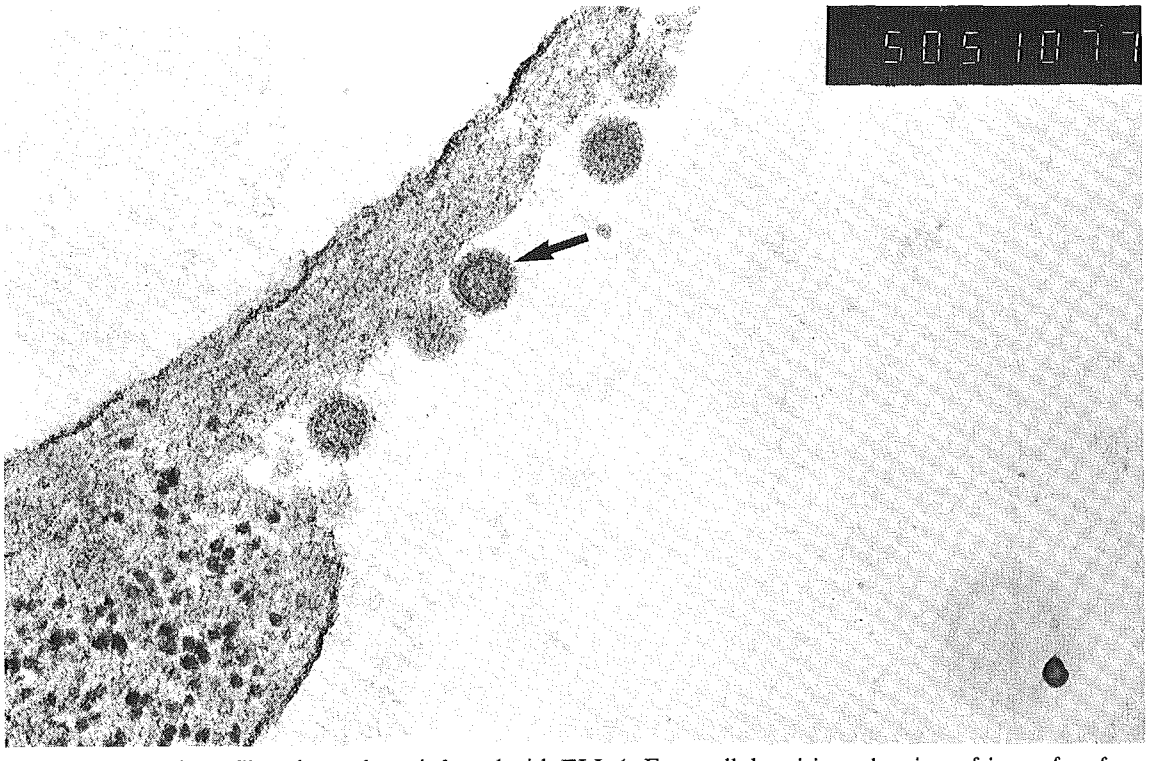

Fig. 6. Chick embryo fibroplast culture infected with ELL-1. Extracellular virions showing a fringe of surface projections (arrow).

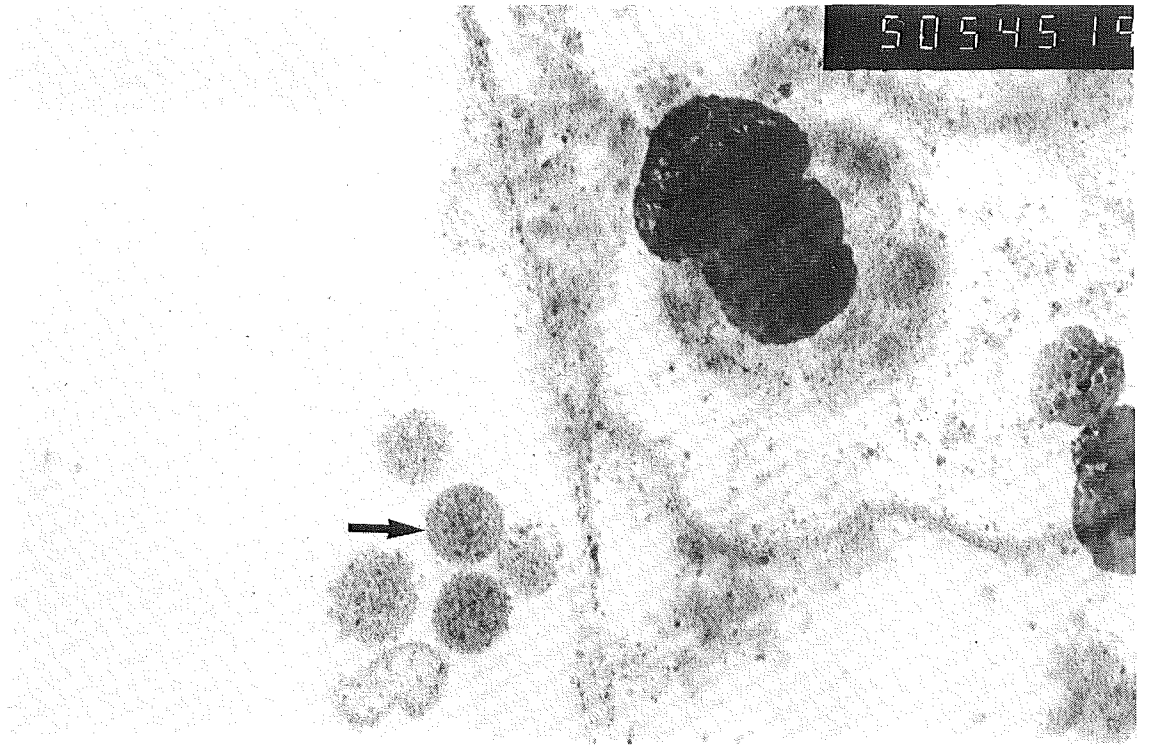

Fig. 7. BHK cells infected with Grímsey virus. Extracellular virions showing a closely adherent membrane (arrow) surrounding an electron dense area.

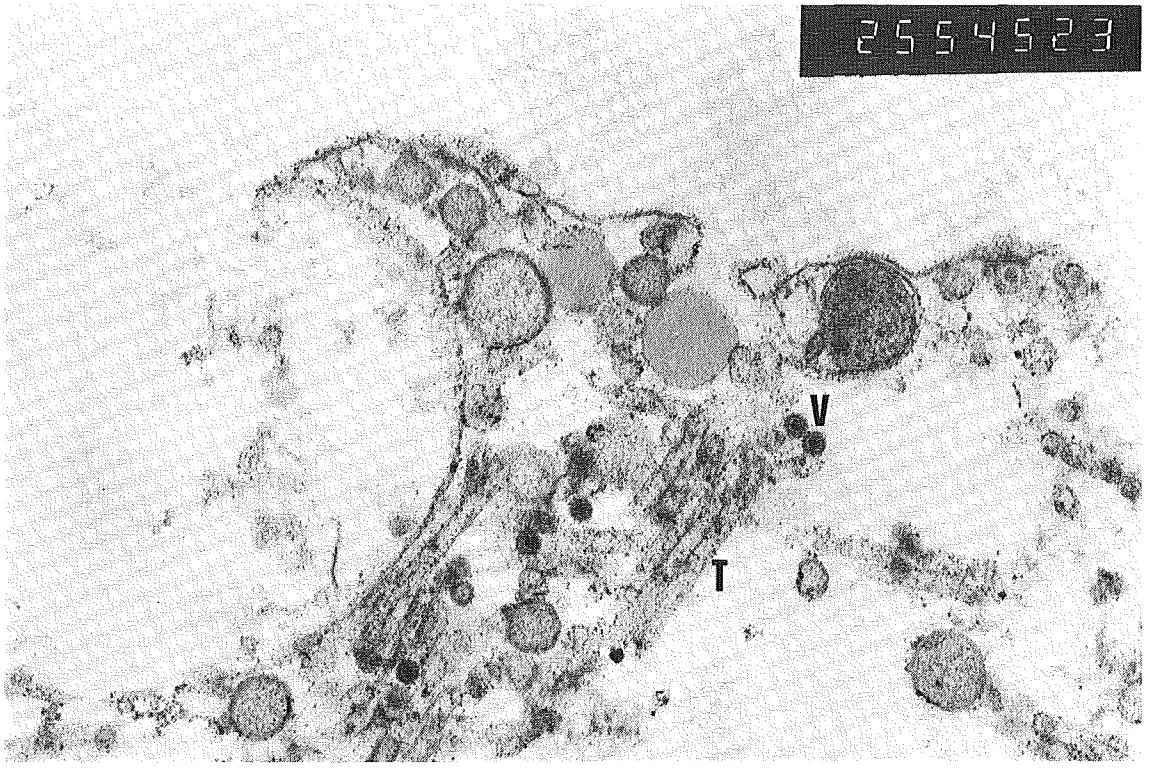

Fig. 8. BHK cells infected with Grímsey virus. Intracellular virions (V) associated with tubules (T).

similar to the structures in cell cultures infected with viruses of the Kemerovo serogroup (Nuttall *et al.* 1982).

Serological tests

Three different virus serogroups, Kemerovo, Hughes and Uukuniemi, were distinguished by complement fixation and immunofluorescent antibody tests.

Isolates ELL-3a and GRIMS82-1a contained viruses that reacted in complement fixation tests with each other and with ascitic fluid to the Kemerovo serogroup, and to Cape Wrath and FT363 viruses, members of the Great Island subgroup of the Kemerovo serogroup (Table 3). The antigen ELL-3a was produced from mouse brain inoculated with virus harvested from infected CEF cultures; antigen GRIMS82-1a was produced from the second mouse brain passage of the virus following isolation in mice. Antigen ELL-3b, produced from mouse brain inoculated with *Xenopus*-grown virus, reacted in CFT only with Great Saltee (GS80-3) virus, a member of the Hughes serogroup. None of the isolates reacted with Clo Mor virus, a member of the Sakhalin serogroup.

Since attempts to produce antigens to the other isolates were unsuccessful, the remaining isolates (except THOR-1) were characterised by immunofluorescence using infected *Xenopus* cell cultures (Table 4). Immunofluorescent antibody tests showed that ELL-1,2,4 and FLAT-1 were of the Uukuniemi serogroup: they all produced positive results with St. Abb's Head and GS80-11 viruses, both members of this group. These tests also confirmed that ELL-3b was a member of the Hughes serogroup, together with GRIMS82-1b, since both cross-reacted with GS80-3 virus. In addition, members of the Hughes serogroup (ELL-3b, GRIMS82-1b and GS80-3) cross-reacted in IFAT with Clo Mor virus, a member of the Sakhalin serogroup.

Neutralization tests confirmed the presence of three serogroups (Table 5). The THOR-1 isolate was identified as a member of the Kemerovo serogroup, reacting with ascitic fluids to ELL-3a and GRIMS82-1a isolates, and FT363 virus. Ascitic fluid raised against THOR-1 did not contain neutralizing activity. The ELL-3a and GRIMS82-1a isolates showed only one way cross-neutralization (ascitic fluid to ELL-3a neutralized both isolates whereas ascitic fluid to GRIMS82-1a did not neutralize the ELL-3a isolate), and only GRIMS82-1a reacted with FT363 ascitic fluid. These three isolates, containing viruses of the Kemerovo serogroup, did not react with any of the other isolates.

Of the four isolates (ELL-1, ELL-2, ELL-4, and FLAT-1) containing viruses of the Uuku-

Table 3. Results of complement fixation tests.

Ascitic fluid	Antigen[1]			
	ELL-3a	ELL-3b	G82-1a	Clo Mor
ELL-3a	32/8	<8/8	256/16	<8/16
ELL-3b	<8/8	64/8	<8/16	<8/16
GRIMS82-1a	16/8	<8/8	64/16	<8/16
GS80-3[2]	<8/8	16/8	<8/16	<8/16
Clo Mor[3]	<8/8	<8/8	<8/8	128/16
CAPE WRATH[4]	16/8	<8/8	32/16	ND
FT363[4]	64/8	<8/8	128/16	ND
ST. ABBS[5]	<8/8	<8/8	<8/16	ND
KEM[4]	8/8	<8/8	8/8	ND

[1] Reciprocal of ascitic fluid titre/ antigen titre; ND= not done.
[2] Hughes serogroup.
[3] Sakhalin serogroup.
[4] Kemerovo serogroup.
[5] Uukuniemi serogroup.

Table 4. Results of immunofluorescent antibody tests.

Virus	Ascitic Fluid				
	ELL-3b	St. Abbs	GS80-11	GS80-3	Clo Mor
ELL-1	–	+	+	–	–
ELL-2	–	+	+	–	–
ELL-3b	+	–	–	+	+
ELL-4	–	+	+	–	–
GRIMS82-1b	+	–	–	+	+
FLAT-1	–	+	+	–	–
St. ABBS	–	+	+	–	+
GS80-11	–	+	+	+	–
GS80-3	+	–	–	+	–
Clo Mor	+	–	–	+	+

niemi serogroup, two (ELL-1 and ELL-2) reacted in neutralization tests with ascitic fluid to St. Abb's Head virus, a member of this serogroup. Attempts to raise ascitic fluid to the Icelandic Uukuniemi-group isolates were unsuccessful.

Isolates ELL-3b and GRIMS82-1b were both neutralized by ascitic fluid to GS80-3 virus, a member of the Hughes serogroup. Ascitic fluid raised against ELL-3b did not neutralise isolate GRIMS82-1b. Attempts to raise ascitic fluid to GRIMS82-1b were unsuccessful.

DISCUSSION

Nine virus isolations were isolated from *I. uriae* collected from four seabird colonies in Iceland (Table 1). They belonged to three different serogroups: three were members of the Kemerovo serogroup (ELL-3a, GRIMS82-1a, and THOR-1), two Hughes (ELL-3b and GRIMS82-1b) and four Uukuniemi (ELL-1, ELL-2, ELL-4, and FLAT-1). The presence of these viruses in *I. uriae* ticks infesting seabirds constitutes a similar situation to that found in other seabird colonies in the northern and southern hemispheres (Yunker 1975, Clifford 1979, L'vov *et al.* 1979, Nuttall 1984, Nuttall *et al.* 1986). Often, as in the case of Elliðaey in Breiðafjörður, and Grímsey, more than one type of virus circulates in a colony (Nuttall 1984).

All the ticks screened for viruses were female *I. uriae*. They were collected on a casual basis during ringing expeditions. Most of them were removed from seabirds which would account for the lack of male ticks in the collections since male *I. uriae* do not take a blood meal and are seldom found on the host (Nuttall *et al.* 1911). The absence of nymphs from the samples is unusual, but may just indicate that they were overlooked on the birds which were not thoroughly examined and ticks only collected incidentally. Isolates ELL-1, ELL-2, GRIMS82-1a and -1b and THOR-1 were from unfed females. Presumably, the infections had been present or acquired at the nymphal stage and survived trans-stadially. In contrast, ELL-3a and -3b, ELL-4 and FLAT-1 were from engorged females; viruses may have been present in the blood meal rather than in the tick *per se*.

ELL-3a, ELL-3b and GRIMS82-1a were characterised using CFT; antigens to the other six viruses could not be produced from suckling mouse brain (Table 3). The THOR-1 isolate was neutralized by ascitic fluids to ELL-3a and GRIMS82-1a and was therefore placed in the Kemerovo serogroup. Differences in neutralization titres between ELL-3a, GRIMS82-1a and THOR-1, and FT363 (a member of the Kemerovo serogroup from a seabird colony in Scotland) indicate that the isolates from Iceland were antigenically distinct from each other and therefore represent different serotypes.

Isolates ELL-1, 2, 4, FLAT-1 and GRIMS82-1b were characterized using the immunofluorescent antibody test (Table 4). ELL-1, 2, 4 and FLAT-1 showed positive fluorescence with ascitic fluids to St. Abb's Head and GS80-11 viruses, members of the Uukuniemi serogroup. Neutralization tests confirmed these results

Table 5. Results of neutralization tests.

Virus isolate	Ascitic fluid[1]					
	ELL-3a	ELL-3b	GRIMS82-1a	GS80-3	ST. ABBS	FT363
ELL-1	<16	<16	ND	<16	>32<64	ND
ELL-2	<16	<16	ND	<16	>32<64	ND
ELL-3a	64	<16	<16	ND	ND	<16
ELL-3b	<16	64	ND	>32<64	<16	ND
ELL-4	<16	<16	ND	<16	<16	ND
GRIMS82-1a	64	<16	512	ND	ND	32
GRIMS82-1b	<16	<16	<16	>32<64	<16	ND
FLAT-1	<16	<16	ND	<16	<16	ND
THOR-1	32	<16	128	ND	ND	64

[1] Reciprocal of neutralization titre of immune ascitic fluid; ND= not done.

with ELL-1 and ELL-2, both being neutralized by ascitic fluids to St. Abb's Head and GS80-11 viruses, however, no evidence of neutralization was observed with ELL-4 and FLAT-1 against any of the ascitic fluids used. This suggests that ELL-4 and FLAT-1 represented serotypes that were distinct, antigenically, from the other two isolates (ELL-1 and ELL-2) belonging to the Uukuniemi serogroup. GRIMS82-1b showed positive fluorescence with ascitic fluid to ELL-3b and Great Saltee (GS80-3), members of the Hughes serogroup. GRIMS82-1b was also neutralized by Great Saltee ascitic fluid, but not by ascitic fluid to ELL-3b, indicating that the two Icelandic members of the Hughes serogroup, ELL-3b and GRIMS82-1b, were different serotypes. The Hughes group viruses cross-reacted in immunofluorescent antibody tests with Clo Mor virus, a Sakhalin group virus, however, no evidence of positive reactions were observed in CFT or NT. The Hughes and Sakhalin serogroups belong to the genus *Nairovirus* of the family, Bunyaviridae (Casals & Tignor 1980). Cross-reactions between these two serogroups in IFAT, but not in CFT and NT, indicate that antigenically they are distantly related.

The viruses were isolated by inoculation of tick pool extracts into mice and into cell cultures (Table 2). Isolates of the Uukuniemi serogroup (ELL-1, ELL-2, ELL-4, and FLAT-1) were either non-pathogenic or of low pathogenicity for mice; all the isolates from tick pools were made in cell culture. In contrast, the Þormóðseyjarklettur (Kemerovo serogroup) and the two Grímsey isolates (Kemerovo and Hughes serogroups) were isolated in mice but not in cell culture. The remaining isolates ELL-3a and ELL-3b had low pathogenicity for mice and were isolated in cell culture. The reasons for these differences in the method by which the isolates were achieved are unknown. They suggest that different serotypes or strains may vary in pathogenicity, rather than differences being a characteristic of the serogroup. Previous experience had shown that members of the Uukuniemi serogroup varied in their pathogenicity for mice, whereas members of the Hughes serogroup were generally non-pathogenic (Nuttall *et al.* 1984b, 1986). All the Kemerovo group isolates produced plaques in Vero cell cultures but not in *Xenopus* cells whereas the Uukuniemi and Hughes group isolates produced plaques in *Xenopus*, but not in Vero cell cultures. This phenomenon has been reported previously (Nuttall *et al.* 1981) and was used as a means of separating the mixed isolates (ELL-3a, and -3b; GRIMS82-1a and -1b).

The relationship of viruses in Icelandic seabird colonies to those found in other parts of the world has yet to be determined. The nearest colonies to Iceland, from which virus-infected *I. uriae* have been recorded, are in the Faeroes (Main 1978, Jacobs *et al.* 1986) and, a little further afield, in Scotland (Main *et al.* 1976a, Moss & Nuttall 1985, Nuttall *et al.* 1981, 1982), Norway (Saikku *et al.* 1980), and Newfoundland, Canada (Main *et al.* 1973). The isolation of closely related viruses, from ticks collected in seabird colonies of different geographical loca-

tions, suggests that viruses are transported from one colony to another (Nuttall 1984, Moss & Nuttall 1985), rather than they have evolved in isolation.

Viruses could be transported by viraemic seabirds, or by virus-infected ticks carried by seabirds. Viraemia has been detected in seabirds naturally infected with viruses transmitted by *I. uriae* (Main *et al.* 1976b, Nuttall *et al.* 1981, Eley & Nuttall 1984), and viruses have been isolated from ticks found on seabirds away from their breeding sites (Converse *et al.* 1976, Moss & Nuttall 1985). *Ixodes uriae*, like most other ixodid ticks, takes several days to complete engorgement before it drops off its host (Murray & Vestjens 1967, Eveleigh & Threlfall 1974): the duration of feeding may allow sufficient time for transportation of infected ticks to a new geographical site. Factors affecting successful virus transportation by seabirds *per se* include the duration of viraemia, and the effect of virus infection on the health and behaviour of seabirds. Hoogstraal & Feare (1984) suggested that illness, resulting from virus infections, may alter the behaviour of seabirds and cause them to visit sites where normally they would not be found.

The extent of virus transportation, both in distance and frequency, is undetermined. Seabirds are known to travel great distances and Icelandic seabirds are no exception (Tuck 1971, Petersen 1982). The greatest movement of seabirds, in terms of both numbers of birds and distance, occurs during the off-season although visits to colonies are less frequent at that time of year than during the breeding season. However, during the off-season, *I. uriae* is mostly inactive, overwintering in cracks in the rock face and under stones of seabird breeding sites. Therefore, transportation of viruses is more likely during the breeding season, mediated by viraemic or tick-infested birds that either visit different seabird colonies temporarily (the so-called prospectors) or settle down at a site other than their natal colony.

The relative importance of different seabird species, with regard to the transportation of viruses, depends on the abundance of a particular species (Evans 1984) and the degree of tick infestation of that species (Flint & Kostyrko 1967, Karpovich 1970, Eveleigh & Threlfall 1975). In addition, characteristics of the life history of a species, such as fidelity to natal colony and degree of colony exchange (Lack 1968, Nelson 1980), will have important bearings on their role as virus vectors. Generally, seabirds breed in the same colony during successive years, once they have become mature and commenced breeding (Nelson 1980). Some species, such as cormorants, terns, and gulls change breeding colony more readily than others (Karpovich & Pilipas 1972, Nelson 1980). There is considerable evidence that young, immature birds show less site-fidelity than the adult breeders (Monaghan & Coulson 1977, Brooke 1978, Nelson 1980), and that in their immature years they also visit other colonies during the breeding season (Scott 1970, Petersen 1976, Fowler & Swinfen 1984, Harris 1984). Although a number (perhaps the majority) of the immatures will eventually return and breed at their natal colony, many nest in new sites (Karpovich & Pilipas 1972, Harris 1984). Thus virus transportation is more likely to be mediated by immature rather than adult breeding birds. Failed breeders and adult non-breeders may also be important in this respect. However, it is important to note that seabird species probably differ considerably in importance as potential vectors, owing to differences in their life histories and numbers.

Despite the similarity of viruses at geographically distant sites, many viruses from different colonies, and even within colonies, are antigenically distinct. It seems probable that viruses circulating in a seabird colony evolve in isolation, and that the exchange of viruses between colonies is a relatively rare event (Doherty *et al.* 1975, Main 1978).

The majority of viruses isolated from ticks inhabiting seabird colonies (all the virus types from Iceland, described in this paper), carry their genetic information in the form of segmented genomes. Evolution of segmented-genome virues can occur by genome reassortment or recombination (Ramig 1985). When two such viruses that are closely related, co-infect a cell, they produce progeny reassortant viruses containing genetic information derived from both parental viruses. Reassortment has been demonstrated between Broadhaven and Wexford, two serotypes of the Kemorovo serogroup (Moss *et al.* in prep.). Both viruses were isolated from *Ixodes uriae* collected from seabird colonies: Broadhaven virus at St. Abb's Head, Scotland, and Wexford virus from Gt.

Saltee Island, Eire (Nuttall *et al.* 1981, 1984a). Reassortment of viruses associated with seabirds compounds the problem of virus identification. Current studies are aimed at determining whether viruses from Icelandic seabird colonies can reassort with similar viruses from Newfoundland and the U.K. Such detailed studies may help elucidate the origins of these viruses, and thus provide information on the interactions of seabirds from different parts of the world.

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