

# How fast do amphibians disperse? Introductions, distribution and dispersal of the common frog (*Rana temporaria*) and the common toad (*Bufo bufo*) on a coastal island in Central Norway

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The common frog (*Rana temporaria*) and the common toad (*Bufo bufo*) were introduced successfully to the coastal island of Frøya in Central Norway several times during 1960–2012. There is still a very high degree of conformity between sites where they were introduced and the present distribution of the two species. However, in western Frøya, a release of frogs about 1996 was followed by a quick expansion of their distribution area; in 2012 and 2013, breeding was registered close to 7 km westwards and eastwards, respectively, i.e. a population dispersal speed of approximately 0.4 km/yr. On eastern Frøya and some small islands in the archipelago, area expansions at another four frog localities have been prevented by ecological barriers like unfavourable limnetic or terrestrial habitats or salty water. Two local common toad populations on eastern Frøya do not show any expansion either. However, an apparently isolated record of the species on western Frøya in 2011 can possibly be explained by the expansion westwards of a population in northern central Frøya, where toads were introduced around 1995. This stretch is about 9.9 km, i.e. an average population dispersal speed of 0.6 km/yr.

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## INTRODUCTION

The known distributions of the common frog (*Rana temporaria* Linnaeus, 1758) and the common toad (*Bufo bufo* (Linnaeus, 1758)) in Norway have been mapped by Dolmen (2008) and Artsdatabanken (2015a, b). The common frog is distributed practically all over the country, while the common toad is mostly confined to the lowlands north to Dønna in the county of Nordland. However, in coastal areas, the toad is much more common than the frog. In fact, if it had not been for anthropogenic introductions, the common frog may have been

a very rare species on, for instance, Norwegian coastal islands (Nilssen et al. 1994). In accordance with this, the large islands of Hitra and Frøya, right outside the mouth of Trondheimsfjord in Central Norway, have had no known frog populations (Dolmen 2008), while the common toad is very abundant on Hitra (Salvidio et al. 1993).

During late April 2000, zoologists from the NTNU University Museum visited Frøya and the Frøøyane archipelago on the coast of Sør-Trøndelag (Grendstad et al. 2000). On the western part of Frøya, D. Dolmen unexpectedly found common

frog spawn in a small pond at Singstad, midway between Daløya and Kverva. This was the first known record of frogs on Frøya.

The pond at Singstad (UTM: 32V MR 726624) is situated only 10 m from the road (county road 410) and is barely 900 m<sup>2</sup> large, partly drained and quite shallow, and for the most part overgrown by sedges *Carex* spp., yellow iris *Iris pseudacorus*, lesser duckweed *Lemna minor* etc., and partly filled in with boulders. The pH of the water on 27 April 2000 was measured at 6.8, conductivity at 290 µS/cm and water colour at 110 mg Pt/L.

A total of 71 egg clusters were recorded in the pond, all of them confined to the very shallow northern part. People in the house nearby, having lived there for 20 years, told us that frogs had been unknown on Frøya until 1998, when they started to appear in increasing numbers around the houses at Singstad. An obvious first hypothesis was that people had introduced frogs to Frøya quite recently and probably released them in the pond at Singstad or its close vicinity.

We now wanted to investigate this further by looking for possible proof of an anthropogenic introduction of the common frog. Furthermore, considering a related topic, invasive species, an additional interesting question was: How quickly does the species disperse and expand its distribution in this coastal lowland, where competitors are virtually lacking and there are no, or only very few, experienced predators? Moreover, in the course of our investigations, it also turned out that there could have been more than one introduction of frogs to Frøya. In addition, there could also be a connection between the few occurrences of the common toad we came across on the island and the prior release of toads there.

Some preliminary data on the distribution of the common frog on the western part of Frøya were published by Seland (2014), and that article includes a more detailed description and a photograph of the Singstad pond.

## MATERIAL AND METHODS

We considered requests for information and interviews as ways of solving the apparently mysterious occurrence of frogs, and also toads, on Frøya, and extensive fieldwork to trace possible expansions of their distribution areas.

D. Dolmen had already in 2000 contacted the local newspaper, Hitra–Frøya, which then published an article on 26 September 2000 about the record of frogs on Frøya (Støen 2000). The article included a request that anyone who had observed frogs on the island should ring Dolmen at the NTNU University Museum.

After we started our investigations (in 2010), a second article was published in Hitra–Frøya (6 May 2011) with new information and appeals for information (Brendboe 2011). Letters were also sent to schools and preschools. An extensive round of interviews started in January 2013, mostly

by telephone. These interviews, however, revealed that people very probably easily confused frogs and toads, and that claimed observations of frogs in reality had been toads. This problem could sometimes only be solved by fieldwork.

In spring 2010 (27 April), we revisited the place at Singstad where D. Dolmen had first seen the frog spawn, and from there we started to investigate ponds and lakes in the district. New investigations were made later in 2010 (total no. of man-days: 5), 2011 (6) and 2012 (14) by J. Seland and in 2013 (20) by D. Dolmen and J. Seland, and others, while in 2014 (5) and 2015 (7) they were made by J. Seland.

The aim was to visit at least a few potential egg-laying localities within each 1x1 km UTM square on western Frøya, but other parts of Frøya were also covered. In the period 2010–2015, about 580 ponds and lakes were checked for amphibians.

Data were collected on occurrences, number of egg clutches, tadpoles and metamorphosed frogs and toads. Any amphibians caught were immediately released at the place of capture. In spring (April and early May), we especially looked for egg clutches and egg strings in ponds and along sheltered bays of larger water bodies, i.e. biotopes where our experience shows that frogs and toads lay their eggs. Later in summer, tadpoles were sought visually or by netting in the same biotopes.

When we measured the dispersal distance of the frogs or the frog population on the map, we usually measured this in a straight line, i.e. the real distance covered by the frogs is probably much underestimated. The calculated speed of dispersal is also a minimum value, since we do not know which year the frogs came to the locality, only that they were present in the year of investigation.

## Study area

Frøya is one of three large coastal islands belonging to an archipelago situated just west of the entrance to Trondheimsfjord in Central Norway. Its main area is about 150 km<sup>2</sup> (240 km<sup>2</sup> when a number of smaller islands are included). The human population is about 4 600, mostly concentrated in the southeastern part of the main island. Frøya is relatively flat and has large areas of bare rock, mainly gneiss and granite; the eastern part is more elevated and hilly, and the highest point is 76 m a.s.l. Most of the island lies below the marine limit (40 m a.s.l.), and in the lowest parts the soil has a large proportion of shell sand. The vegetation is mostly heath with heather *Calluna vulgaris*, mosses *Racomitrium* spp., lichens *Cladonia* spp. etc., but some leaside slopes and crevices may have juniper *Juniperus communis* shrubs or deciduous trees. A few small areas have been planted with conifers *Pinus montana* and *Picea sitchensis* (see Seland 2014). The climate is oceanic and the average annual temperature is 6–8 °C (Moen 1999). The density of potential frog-spawning places is high; the number of ponds and small lakes over most of Frøya varies from about 10–15 per km<sup>2</sup> and upwards, according to the Series M711 topographical maps (1:50 000).

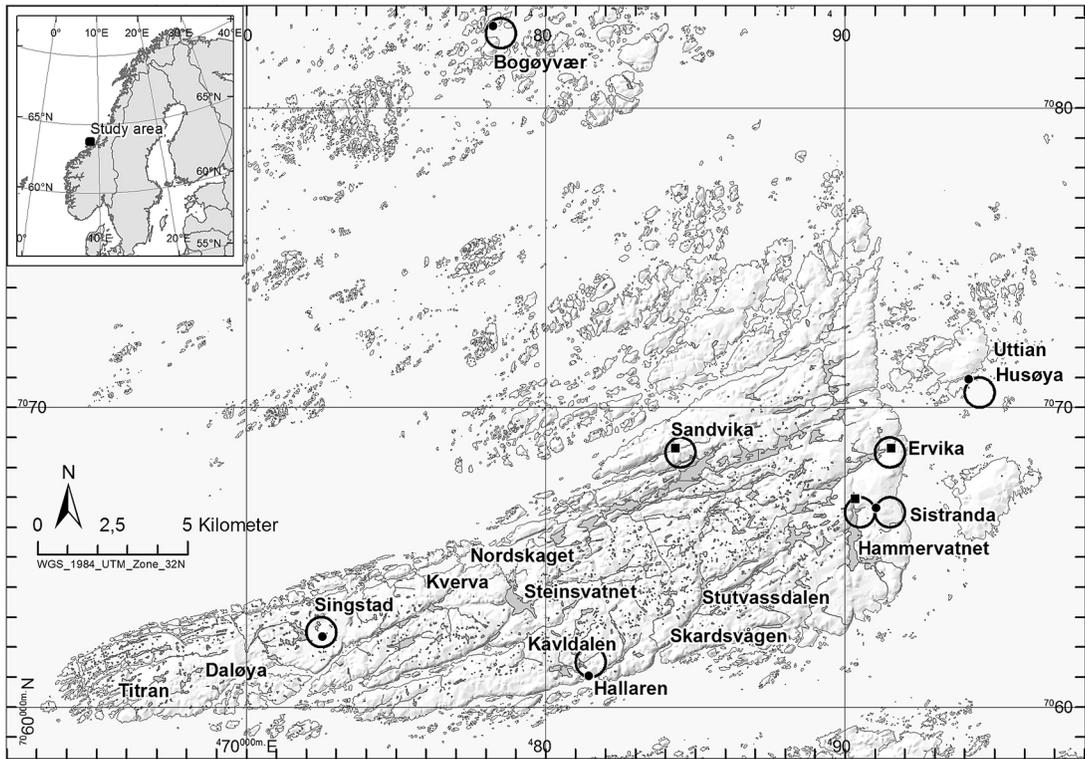


Figure 1. The island of Frøya and its archipelago. Large circles show 1x1 km UTM squares (WGS84) where amphibians have been introduced. Small dots show more precisely the known introductions of the common frog (*Rana temporaria*), and small squares the known introductions of the common toad (*Bufo bufo*).

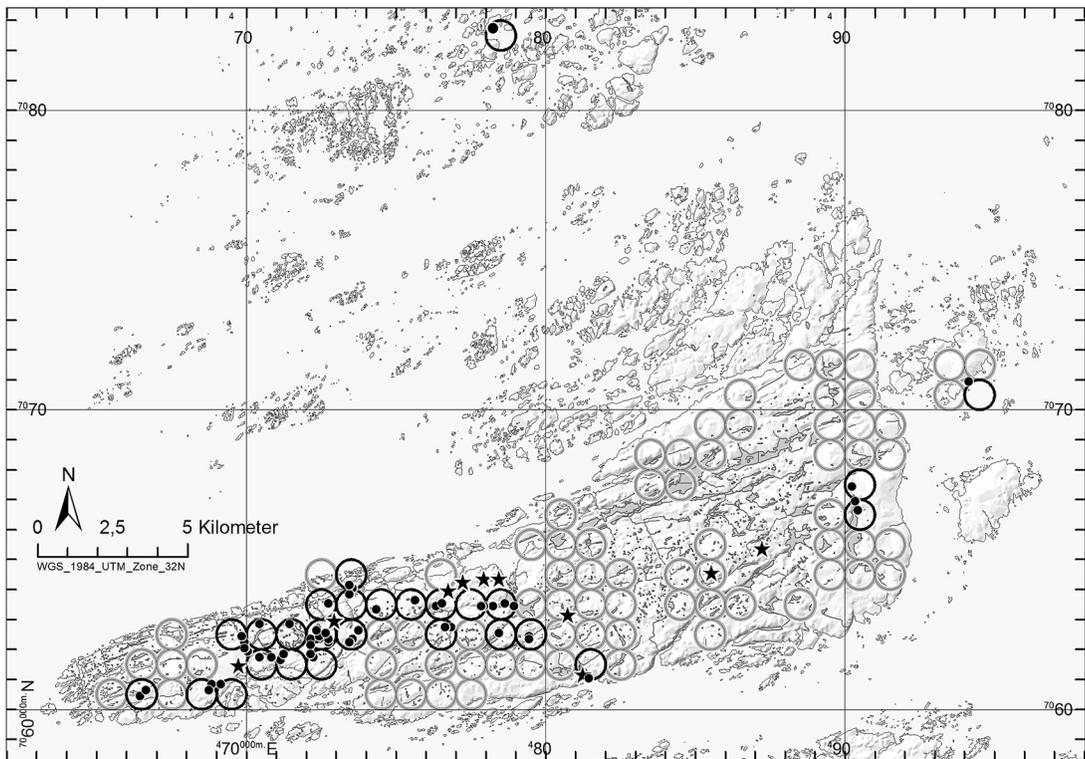


Figure 2. The known distribution of the common frog (*Rana temporaria*) on Frøya. Large grey circles show 1x1 km UTM squares where investigations have taken place and black circles where common frogs were also found (with the addition of Bogøyvær). Small dots show the frog breeding localities more precisely, while small stars denote terrestrial individuals outside the main distribution area.

**Table 1.** Reported releases (R), and observations (O) of the common frog *Rana temporaria*. Locality numbers refer to our field protocol. Distances and years are calculated for the most important stretches. Coordinates with only 2x2 digits may not be fully correct, and the record may belong to a neighbouring square. DD = Dag Dolmen, JS = Jan Seland, ET = Eva Tilsteth, JT = Jan Trøan.

Loc. no.	Release/observ.	Loc. name/ area	UTM 32V MR		Number, life stage	Donor place	Year	Released by/ observed by	Information by	Distance (km) from release loc.	No. of years	No. of km/yr
			east	north								
1	R	Anne-Britt-tjørna, Singstad	7266	6242	ca. 30 tadpoles	Buenget, Trondheim	ca. 1996	boys from Trondheim	Anon. 2000	0	0	
1	O	Anne-Britt-tjørna, Singstad			71 clutches		2000	DD				
1	O	crossroad at Lunheim/Sørgård	729	629	1 terr. frog or toad		around 1996?	Harald Johansen	Harald Johansen 2015	0.5		
1	O	Daløya	69	61	3 terr. ads		2000	Bjørng Stoen's son	Bjørng Stoen/ Hitra-Froya 26.09.2000	3.2	4	0.8
1	O	pond at Kverva kinderg., Nordskag	779	643	2 ads (photo)		2009	Nordskag Kindergarden	Hitra-Froya 08.09.2009, Siv Tove Skarshaug 2013	5.7	13	0.4
1	O	Nordskag, W of	77	64	frog (photo)		?		Eskil Sandvik? 2012	5.9		
1	O	Vassbukta, Kverva	767	639	frog(s)		2010	?	Ola Vie 2013	4.3	14	0.3
1	O	Nordskag/ Kverva	77	64	frog or toad		?	a contractor	Roger Lyngvær 2013	5.9		
1	O	Anne-Britt-tjørna, Singstad			≥ 93 clutches		2010	DD, JS				
1	O				12 clutches		2011	JS				
1	O				21 clutches		2013	JS				
1	O				ca. 15 clutches		2014	JS				
1	O				ca. 14 clutches		2015	JS				
2	O	marsh at farm W of Singstad	727	622	3 clutches		2010	DD, JS				
3	O	large, rectangular pond, Singstad	727	623	remains		2010	DD, JS				
4	O	bog puddle, Singstad	724	623	7-8 clutches		2010	DD, JS				
5	O	peat pit, Singstad	723	623	25 clutches		2010	DD, JS				
6	O	Kystadvatnet, SE narrow bay	721	623	ca. 25 clutches		2010	DD, JS				
7	O	lakelet SW of loc. 6	721	621	ca. 120 clutches		2010	DD, JS				
8	O	pond NW of Singstad	724	624	10-20 clutches		2010	DD, JS				
9	O	lakelet NW of Singstad	723	626	17 clutches		2010	DD, JS				
10	O	pond N of Singstad	726	625	4 clutches		2010	DD, JS				
13	O	cattlepond SW of Nordhaug	727	635	34 clutches		2010	DD, JS				
14	O	lakelet N of road, Malmmyran	743	633	41 clutches		2010	DD, JS				
15	O	ponds S of road, Flatmyran	756	636	1 clutch		2010	DD, JS		3.3 km	14	0.2

Table 1. Continued.

Loc. no.	Release/observ.	Loc. name/ area	UTM 32V MR east north	Number, life stage	Donor place	Year	Released by/ observed by	Information by	Distance (km) from release loc.	No. of years	No. of km/yr
15	0			4 clutches		2012	JS				
15	0			12 clutches		2014	JS				
15	0			57 clutches		2015	JS				
20	0	middle lakelet SW of Nordvågen, Kvisten	734 641	1 clutch		2010	JS				
21	0	eastern three-lakelets, Kvisten	735 640	1 gelatinous mass		2010	JS				
22	0	pond W of Veisan, Kvisten	734 638	1 clutch		2010	JS				
26	0	pond at crossroad Lunheim/Sørgard	729 629	2 dead frogs		2010	JS				
28	0	ponds at Halthøia SW	735 623	5 clutches		2010	JS				
29	0	ponds at Halthøia NW	737 626	26 clutches		2010	JS				
31	0	ponds NE of Setra	734 622	3 clutches		2010	JS				
32	0	large, manmade pond, Setermyran	722 617	4 dead frogs		2010	JS				
33	0	Skagedam	711 616	6 clutches, 7 dead frogs		2010	JS				
34	0	roadside puddle SE of Valavatnet	708 617	6 clutches		2010	JS				
34	0			8 clutches		2011	JS				
35	0	bog pond W of Valavatnet	704 617	21 clutches		2010	JS	2.3 km		14	0.2
35	0			> 20 clutches		2011	JS				
36	0	drainage ditch NE of Skagavatnet	712 618	1 clutch		2010	JS				
54	0	long pond (of four in a row), Kvisten	734 641	1 clutch		2010	JS				
57	0	brook in roadside, Setermyran	721 618	2 clutches, dead frogs		2010	JS				
113	0	brook NW of Kystavatnet	714 628	ca 20 clutches		2011	JS				
133	0	Kvernhusbekken, large pond (N)	699 622	10 clutches		2011	JS				
133	0			ca 80 clutches		2013	JS				
133	0			ca 110 clutches		2015	JS				
133b	0	Kvernhusbekken, N of large pond (N)	698 624	1 clutch		2015	JS				
133c	0	Kvernhusbekken S of Kvernvatnet	700 619	ca 34 clutches		2015	JS				
134	0	Kvernhusbekken, small pond (S)	699 620	ca. 70 clutches		2011	JS				
134	0			60 clutches		2014	JS				
134	0			16 clutches		2015	JS				
135	0			17 clutches		2014	JS				

Table 1. Continued.

Loc. no.	Release/observ.	Loc. name/ area	UTM 32V MR east	UTM 32V MR north	Number, life stage	Donor place	Year	Released by/ observed by	Information by	Distance (km) from release loc.	No. of years	No. of km/yr
149	O	lakelet S of Sjøstua	704	628	ca. 16 clutches		2011	JS				
174	O	meander SW of Smauna, Kverva	763	634	3 clutches		2011	JS				
187	O	pond NE of Katuglejtjørna	7847	6251	3 clutches		2011	JS				
187	O				7 clutches		2012	JS				
187	O				28 clutches		2013	DD, JT				
187	O				39 clutches		2014	JS				
187	O				16 clutches		2015	JS				
188	O	deep pool/brook bend, Merradalen	7868	6350	1 clutch		2011	JS				
188b	O	brook, Merradalen	782	634	2 clutches, frogs in ampl.		2014	JS				
189	O	Merradalen, E pond	7793	6344	ca. 150 clutches		2011	JS				
189	O				ca. 159 clutches		2012	JS				
189	O				ca. 150 clutches		2013	JS				
189	O				200 clutches		2013	DD, JS, ET, JT				
189	O				70-80 clutches		2014	JS				
189	O				ca. 108 clutches		2015	JS				
190	O	Merradalen, W pond	7782	6343	ca. 36 clutches		2011	JS		6.1 km	15	0.4
190	O				28 clutches		2012	JS				
190	O				ca. 60 clutches		2014	JS				
190	O				ca. 62 clutches		2015	JS				
191	O	bog puddle, Merradalen	789	634	3 clutches		2011	JS				
206	O				35 clutches		2014	JS				
206	O				ca. 83 clutches		2015	JS				
207	O	pond E of Stortjørna, Titran	666	606	1 clutch		2012	JS				
207	O				25 clutches		2014	JS				
222	O	pond N of Dalsvikvatnet, Vettan	688	608	9 clutches		2012	JS				
246	O	Smauna	765	635	1 clutch		2012	JS				
206	O	Stortjørna, Titran	664	604	18 clutches		2012	JS		6.7 km	16	0.4
267b	O	pond, Godvikheia NW	766	627	8 clutches		2012	JS				
339	O	Ytter Røsvatnet, at lakelet S of.	807	631	1 terr. juv. 2+		2013	JS, ET		8.2 km	17	0.5

Table 1. Continued.

Loc. no.	Release/observ.	Loc. name/ area	UTM 32V MR east	UTM 32V MR north	Number, life stage	Donor place	Year	Released by/ observed by	Information by	Distance (km) from release loc.	No. of years	No. of km/yr
410	O	N. Kavledalsstjern, Kavledalen	794	624	1 clutch, 1 frog		2014	JS		6.9 km	18	0.4
411	O	S. Kavledalsstjern, Kavledalen	794	623	2 clutches		2013	DD, JT		6.9 km	17	0.4
	O	N of Omnheia, Hallaren	812	611	terr. juv. frog		2010	Alf Sagmo	Morten Sagmo 2013	9.0 km	14	0.6
	O	Stutvassdalen	85	64	frog or toad seen		?	Kenneth Wærø	Kenneth Wærø 2013			
	O	Bessevassheia	872	653	terr. ad.		2012	Frank Robert Lyngvær	Artsdatabanken: Artskart 2015			
310	R	Huseya, Uttian	9416	7093	eggs or tadpoles	Hallsset, Trondheim	ca. 1970	X	Jon Oddbjørn Mathisen 2011			
310	O				frogs seen every year				Jon Oddbjørn Mathisen 2011			
310	O	Huseya, Uttian			ca. 50 clutches		2013	DD, JS, ET		0	43	
	R	Ørndalen, pond NE of Storheia, Midisian, Sistranda	910	666	tadpoles	Trondheim	ca. 1970 ±	Margareth (Midisian) Larsson	Trygve Smalø 2013, Lars Gunnar Larsson 2015,			
250	O	Ørndalen, Hammervatnet	904	666	frog or toad		ca. 1980-84	Hallgeir Bakken	Hallgeir Bakken 2013			
250	O	Ørndalen and Hammervatnet (Ørndalsbukta)			several adults and egg clutches		2002-2012	Ola Vie	Ola Vie 2013			
250	O	Hammervatnet at Ørndalen (Ørndalsbukta)			adults (< 2012), egg clutches (2012)		< 2012, 2012	Eskil Sandvik + daughter	Eskil Sandvik 2013			
250	O	Hammervatnet (Ørndalsbukta)	904	666	1 clutch		2013	DD, JS, ET				
251	O	Litvatnet	903	669	several frogs + clutches		2013	DD, JS, ET				
251	O				ca. 22 clutches		2015	JS				
253	O	deep-pool/brook N of Litvatnet	902	674	1 clutch		2012	JS				
275	R	Omnheia, Hallaren; pond at house	814	610	frog spawn/tadpoles	Haukvatnet, Trondheim	2010-2011-2012		Morten Sagmo 2013			
	R	Smaløya, Bogøyvær	782	827	frog spawn	Trondheim	ca. 1988	Anton X	Maria Nordheim 2013			
	O	Smaløya, Bogøyvær	782	827	lots of frogs in 5-6 ponds		2013 and before	Maria Nordheim	Maria Nordheim 2013			

Table 2. Reported releases (R), and observations (O) of the common toad *Bufo bufo*. Locality numbers refer to our field protocol. Coordinates with 2x2 digits may not be fully correct, and the record may belong to a neighbouring square. DD = Dag Dolmen, JS = Jan Seland, ET = Eva Tilsteth, JT = Jan Troan.

Loc. no.	Release/observ.	Loc. name/ area	UTM 32V MR		Number, lifestage	Donor place	Year	Released by/ observed by	Information by
			east	north					
R		Norddal, Sandvika	843	686	20-30 ads released in large brook at the farm Norddal	Hitra	ca. 1995	Roger Lyngvær	Roger Lyngvær 2013
O		Norddal, Sandvika			terr. toads often seen at the farm, in 2015 also toadlets		≤ 2015		Roger Lyngvær 2013, 2015
193	O	Tungvågvatnet	844	681	ads, remains, eggs		2010-13	Eskil Sandvik	Eskil Sandvik 2013
196	O	Tungvågvatnet, N part	848	683	many tadpoles		2011	JS	
196	O				remains		2013	JS	
196	O				remains		2014	JS	
196	O	at Tungvågvatnet, on the road			dead toad on the road		2015	Roger Lyngvær	Roger Lyngvær 2015
302c	O	at lakelet N of Brattstieha?	855	691	?croaking on land		2013	JS	
R?		?						?	
174	O	meander SW of Smauna, Solli, Kverva	763	634	egg strings (dead?)		2011	JS	
251	R	Litvatnet, Sistranda	903	669	20-30 adults ("2 buckets")	Storvatnet at Strom, Hitra	1990-91	Roger Ervik	Roger Ervik 2013
O		Sistranda	91	66					Hitra-Frøya 26.09. 2000
O		Ørndalen, Sistranda	90	66	1 ad (photo)		2001	Björg Stoen	Björg Stoen 2001
250	O	Hammervatnet (Sistranda)	90	66	several ads, juvs, tadpoles			cottage owners, daughter	Björg Stoen 2001
250	O	Ørndalen - Ørndalsbukta of Hammervatnet, Sistranda	904	666	several adults, egg strings, tadpoles		2002-2012	Ola Vie	Ola Vie 2013
O		Lyngåsv. W of Nordli, S of Hammervatnet	903	645	terr. ad. on the road		2008	Ola Wergeland-Krog	Artsdatabanken: Artskart 2015
O		Ytersian, upper part (Sistranda)	910	675	several terr. toads		2012	Kenneth Wæro	Kenneth Wæro 2013
250c	O	brook deep-pool S of Litvatnet (Sistranda)	902	668	toad? remains		2012	JS	
251	O	Litvatnet, Sistranda	903	669	several ads + remains		2013	DD, JS, ET, JT	
251	O				egg strings + remains		2015	JS	
321	O	Hammervatnet, bay in SW (Hammervika)	901	647	several toads (30-40)		2013	DD	
R		Outlet from Ervikvatnet	9156	6869	adults	Smågevatn, Hitra	1960+	X	Kenneth Wæro 2013
O		Ervikvatnet, at the pump house	910	681	3 dead toads or frogs on the road		2012	Kenneth Wæro	Kenneth Wæro 2013
O		Ervikvatnet, at	914	686	common			Roger Ervik	Roger Ervik 2013
R		Skardsvågen, brook	83	61	2 toads released (not for introduction)	Fillan, Hitra	ca. 1954	Oddbjørn Bakken	Oddbjørn Bakken 2013

## RESULTS

### New reported records and information on frog releases

The article in Hitra–Frøya on 26 September 2000 (Støen 2000) mentioned above (see also Anon. 2000) included a photograph of an adult common frog; three frogs had been observed at Daløya, about 3 km west of Singstad (the first known locality). This was now the second “official” record of the common frog on Frøya. According to the same article, frogs were also rumoured to have been seen at Sistranda and tadpoles in Ervikvatnet, both situated on the eastern side of the island, as much as 20 km away.

Already on the day after the publication of the newspaper, D. Dolmen received a telephone call from an informant (Anon., pers. comm. 2000) that explained the frogs at Singstad. Around 1996, two boys (aged 8 and 5 years) from Trondheim had collected frog spawn in a pond in Trondheim and hatched and reared tadpoles at home. Since they spent their summer holidays on Frøya, they brought about 30 tadpoles from Trondheim and released them into the pond they called “Anne-Britt-tjørna” on the western part of the island. This was exactly the same locality (Singstad) where Dolmen had recorded frog spawn in 2000.

During the years from 2000 onwards, the newspaper article, interviews and communication with zoologists and other people well acquainted with the island resulted in new, interesting pieces of information (see Table 1). In western Frøya, by 2009 and 2010, respectively, frogs were reported from Kverva and Nordskaget, 5.7 and 5.9 km east of Singstad (Anon. 2009).

However, frogs had been introduced as early as around 1970 in the Sistranda area, on the eastern side of Frøya (see above). Several tadpoles collected in Trondheim were released in a small pond northeast of Storheia, between Ørndalen and Midsian. The pond was later filled in, but several observations of frogs have been made in the same area (Ørndalen – Hammervatnet) since then (ca. 1980–2013).

In addition, according to the informants, frogs had been introduced from Trondheim to Husøya, on the southern part of the small island of Uttian (eastern part of Frøya), also around 1970, and they have been observed there every year since then.

A fourth introduction of frogs took place about 1988 to the small island of Smaløya at Bogøyvær, north of “mainland” Frøya, and they now breed in at least 5 or 6 ponds there.

We have heard a couple more stories about introductions of frogs to eastern Frøya, but they are probably only less precise versions of the first-mentioned one above.

However, a more recent introduction has also been made. Frog tadpoles from Trondheim were introduced to a small pond at Omnheia, Hallaren, on southern Frøya in 2010, and also later. Moreover, in 2012, 11 smooth newts *Lissotriton vulgaris* from Flatåsen, Trondheim, were released in the same pond. Both frogs and newts have later reproduced there. The five known introductions of the common frog on Frøya and its archipelago are shown in Figure 1.

### Discoveries during the fieldwork

On our visit on 27 April 2010, about 93 egg clutches were counted from all parts of the pond at Singstad. On the same trip, we also investigated another 14 ponds and lakelets in the same area, up to approximately 2 km from Singstad, and recorded frog spawn in as many as 11 of them. J. Seland’s fieldwork in 2010, 2011 and 2012 resulted in additional records. Table 1 gives an overview of all records of *R. temporaria* on Frøya up to now. During 2010–2015, we have discovered or verified 50 breeding localities of the common frog in the western distribution area and 7 in other parts of Frøya, including the small islands. In addition, there have been a few observations of terrestrial frogs, by us or by others, which could not be associated with any breeding pond or lake. Frogs have thus been recorded in most 1x1 km squares as far as Titran in the west, a distance of 6.7 km. In the east, frog spawn has been found as far as Kavldalen, south of Steinsvatnet, a distance of 6.9 km. Single, juvenile animals were detected at Ytter Røsvatnet, east of Steinsvatnet, about 8.2 km from the dispersal centre at Singstad, and at Omnheia, at Hallaren on southern Frøya. This distance is approximately 9.0 km (Table 1).

We also carried out fieldwork in eastern Frøya, and at Sistranda we confirmed good populations of frogs and toads in two lakes, Litlvatnet and Hammervatnet, but not in ponds and lakelets we investigated in the hills around these two lakes. (In Litlvatnet, a male and a female toad that we caught in amplexus measured 5.2 and 8.5 cm snout–vent length, respectively, while a male and a female frog in amplexus measured as much as 9.2 and 11.0 cm.)

Likewise, we found about 50 hatching egg clutches of frogs on Husøya, in the pond where frogs had been introduced, but not in any of the other 16 ponds investigated on the small island. Husøya is connected to the larger island of Uttian via a narrow isthmus, but no frogs were found in the around 25 ponds visited on Uttian, at least some of which seemed suitable for frogs.

We have also received information about two records of terrestrial frogs in central Frøya (Table 1). One is from the area around Stutvassdalen, about 6 km east of Kavldalen (see above) and 5 km west of Hammervatnet. The other, at Besselvassheia, is closer to Hammervatnet, about 2.8 km. Figure 2 gives an overview of all known frog localities on Frøya.

### The common toad

We know of only a few common toad localities on Frøya. The species has been observed by us or by others in four areas: Sistranda and Ervika in the east, Sandvika in the north-central part and Kverva in the west-central part of the island (Table 2). The occurrences in the first three areas coincide with known releases of toads, but we do not have information about any introductions at the fourth place (Kverva).

The first known introduction of the common toad to Frøya was in the 1960s when an unknown number of adult toads were collected from Hitra, and released in the outlet stream from Ervikvatnet on Frøya. Today, toads are still reported from the

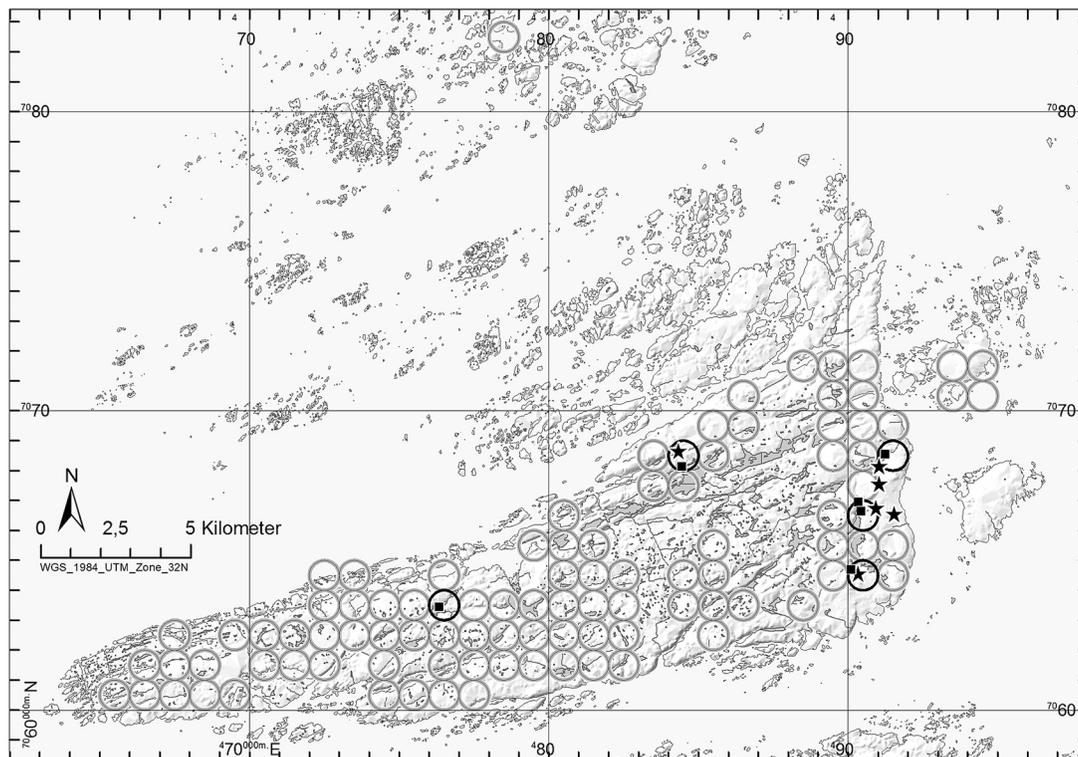


Figure 3. The known distribution of the common toad (*Bufo bufo*) on Frøya. Large grey circles show 1x1 km UTM squares where investigations have taken place (with the addition of Bogøyvær) and black circles where common toads were also found. Small squares show the toad breeding localities more precisely, while small stars denote terrestrial individuals.

area around Ervikvatnet and tadpoles in the lake, although we were unable to find any there.

Around 1990–91, “two buckets” of toads (probably 20–30 individuals) were collected from Hitra, and released in Litlvatnet at Sistranda. Toads had never been seen in Litlvatnet before. Since then, however, toads have been reported from the area on several occasions, and we observed a number of breeding toads in Litlvatnet in 2012–2015. There were also toads in Hammervatnet, further south, including a large number of breeding individuals in a bay in the southwest. However, toads were not found in the surrounding lakes.

Toads were introduced from Hitra to a stream at Sandvika about 1995, and breeding toads, egg strings or remains (skin, viscerals etc.) have been seen by us and others in nearby lakes in 2010–2014. In the fourth area, further west, at Kverva, one 3 m long egg string (possibly dead) of the common toad was discovered in 2011 by J. Seland. The three known introductions of the common toad on Frøya are shown in Figure 1.

An incident worth mentioning is that, as far back as about 1954, in order to play a trick on someone, two common toads had been picked up on Hitra, and eventually released at Skardsvågen, in the southern part of Frøya. This story may explain a little bit about people’s attitude to the common toad and its “popularity” on the islands.

During the years we have undertaken investigations, we

have discovered five (or possibly six) breeding localities of the common toad. Figure 3 shows all the known toad localities on Frøya.

## DISCUSSION

### The introduction of frogs and toads to Frøya

There is full conformity between the distribution of the common frog on Frøya and previous releases of frogs on the island. Moreover, the species has never been found on the large island of Hitra, between Frøya and the mainland. We therefore conclude that the occurrence of the common frog on Frøya is of anthropogenic origin. There is also a very high degree of conformity between the distribution of the common toad and known releases on Frøya. We therefore think that the toad is also of anthropogenic origin there, even though the species is very common on Hitra. The introduction of frogs on islands along the Norwegian coast is a very widespread practice, as shown by Nilssen et al. (1994) for islands in northern Norway. In the present study, we show that it has taken place at least five times in different parts of Frøya and the archipelago since 1970: Ørndalen, Uttian, Bogøyvær, Singstad and Hallaren. All the donor places were in Trondheim, and the frogs (spawn or tadpoles) were usually released by people with connections to

Trondheim, on holiday on Frøya.

The common toad has been deliberately introduced to Frøya at least three times since 1960, to Ervika, Sistranda and Sandvika, and two toads were released more fortuitously around 1954 (Skardsvågen). The donor places were all on Hitra, and the toads (adults) were released by people living on Frøya.

The introductions of common frogs and common toads to Frøya have been very successful. The species have become established at all the known release sites and have viable or even very large populations. We have not heard of attempts to introduce frogs and toads to Frøya that were unsuccessful. This shows that the landscape, climate and many biotopes on Frøya are suitable for the species.

### Distribution and dispersal of the common frog on western Frøya

The dispersal of the common frog and the large area it now occupies on western Frøya are most striking (Table 1). Within 16 years or less from the release of tadpoles at Singstad, the species had reached and bred at the western end of the island in 2012 (Titran is 6.7 km from Singstad). In the east, it took no more than 15 years (2011) to reach Merradalen (6.1 km from Singstad) on the border of a probable brackish-water barrier, Steinsvatnet. Common frogs were also found breeding further southeast, at Kavledalen (6.9 km from Singstad), in 2013, and this was recorded after 17 years. (A few dead frogs, but no egg clutches, had been observed in the same lakelet two years earlier.) Single frogs have reached even farther eastwards (see Results), but the most eastern recorded animals may have migrated there from the eastern distribution area. However, the average speed of population dispersal, both westwards and eastwards, has been at least 0.4 km/yr. (Table 1). Seland (2014) found that the number of frog-breeding pools per area unit was very large in the central part of the distribution area (near Singstad); almost all potential breeding localities there were occupied by the common frog. Furthermore, the numbers of egg clutches in each locality were for the most part increasing every year; some pools could have more than 100 egg clutches. The density of localities and the number of egg clutches were much smaller in the periphery of the distribution. This is also what could be expected for an expanding population.

An anecdote from an island further north on the Norwegian coast (Myken, Rødøy, in the county of Nordland) can similarly illustrate how the common frog may have a tremendous population growth and potential impact on the natural ecosystem once it has been introduced to a new area. D. Dolmen got a telephone call from a person resident on the small island (Gro Bygdevoll, pers. comm. 1997). She said that common frog tadpoles had been released on the island about 15 years earlier, and the lack of natural predators had resulted in an enormous growth of the frog population. Consequently, lots of frogs were run over by cars, especially in the evenings. The same informant (or another?) also described how, in the hay-making season, frogs were accidentally killed all over the island by the

mowing machines, and in spring people had a hard time finding drinking water that was not filled up with frog spawn.

The speed of dispersal and the distances mentioned above refer to the expansion of the amphibian populations. An individual's yearly migration distance or the distance travelled over more years, for instance by juveniles, is another matter. We have no data to draw conclusions on the latter topic. However, from the literature, we see that up to about 1 km is mentioned for the migration of the common frog (Baker & Halliday 1999).

### The common frog on eastern Frøya and Bogøyvær

The frogs introduced to the eastern part of Frøya have not had the same degree of dispersal success as the western population. Even though the populations are viable, they have not expanded their borders very much. This is most clear at Sistranda, where frogs have existed since about 1970. There is no doubt that the frogs thrive. If their body size can be used as an indication of adaptation, the frogs at Litlvatnet seem well adapted. We caught some that were far above average size, the largest being a female whose snout-vent length was 11.0 cm, the largest common frog reported from Norway (Dolmen 2008) and possibly the maximum the species can achieve in Scandinavia (Fog et al. 1997). The relatively steep hillsides towards the west hardly pose a strong physical obstruction for the expansion of the distribution area. A few lone terrestrial frogs have actually also been recorded west of Litlvatnet and Hammervatnet (Stutvassdalen and Besselvassheia). However, we think that the hilly area may act as an ecological barrier with a lack of suitable limnetic and terrestrial habitats for the common frog. Whereas the lowland lakes, Ervikvatnet, Litlvatnet and Hammervatnet, all situated below 25 m a.s.l., have sheltered areas with bogbean *Menyanthes trifoliata*, common reed *Phragmites australis* and/or sedges *Carex* spp., vascular plants are much more scarce in ponds and lakes in the hills. The terrestrial habitat is also quite exposed to the wind and lacks sheltering vegetation.

The lack of expansion on the small island of Husøya is easier to explain. The pond where frogs were released around 1970, and where the species still reproduces, is a typical frog pond with shallow parts, a few big stones and to some extent surrounded by grassland. Grass also grows in parts of the pond. All the other ponds on the island seem unsuitable for frogs. Many have too deep edges and are surrounded by heather or overgrown by *Sphagnum* mosses, and a few are brackish. The isthmus to Uttian is narrow (<30 m), very low and probably sometimes overflowed by salty water, at least at extreme high tides. The isthmus may therefore act as a filter route (Udvardy 1969) and a quite effective barrier against migration from Husøya.

We did not visit Bogøyvær. However, our informant explained that since the introduction of frogs on Smaløya in about 1988, they have thrived and now occupy most of the ponds there. In 2012, people counted about 50–60 frogs, and the place is often visited by school classes on a “frog safari”.

As for the frogs and newts newly introduced to Hallaren on

southern Frøya, both species reproduce, and in 2015 as many as 24 egg clutches were seen in the pond. However, it is still too early to see to what degree they will expand their distribution.

### Potential predators

How far local predators have influenced the speed of dispersal is an open question. The landscape is very open, and frogs on the move may easily be detected. Seland (2014) lists the following potential frog predators on Frøya: otter *Lutra lutra*, mink *Neovison vison*, grey heron *Ardea cinerea*, raven *Corvus corax* and hooded crow *C. cornix*. Seagulls *Larus* spp. (Kilpi & Byholm 1995) and birds of prey (Accipitriformes and Strigiformes) may also take their share. Herons, ravens and crows are all known to kill and/or eat common toads in huge numbers on the neighbouring island of Hitra (E. Brennbøe & L.O. Eide, pers. comm. 2013). On Bogøyvær (M. Nordheim, pers. comm. 2013), domestic cats in addition to otters and seagulls have been seen hunting frogs. During our investigations on Frøya, otter tracks were often seen at the edge of frog-breeding pools, and viscerals of frogs and leftovers of egg clumps etc. were found at several such localities.

Potential predators probably learn quickly how to utilise the new food source. G. Bangjord (pers. comm. 2013, 2015) has analysed eagle owl *Bubo bubo* pellets at 16 nests in nine territories on Frøya. In the west-central part of the island, in the area where the common frog was first introduced and where frogs are now abundant, hip bones of small frogs were first found in the pellets in 1995 or 1996 (frog remains were never seen in the pellets in 1984–1994). These periods coincide very well with the year when frogs (tadpoles) were released at Singstad. The number of frog remains and the age (size) of the frogs have increased since then, within the same area or close by, and frog remains in the pellets are now very common. In one territory, frogs make up 65 % of all the prey of the owl. In 2014 and 2015, frog remains were also found in eagle owl pellets on eastern Frøya.

### What about the common toad?

In our fieldwork, we also looked for lakelets which seemed suitable for the common toad just outside its four small distribution areas. The lack of toads in these water bodies is another indication that the common toad does not have a long history on Frøya.

With the possible exception of the Sandvika and Kverva toads in north-central and west-central Frøya (see later), the situation for the common toad on Frøya seems to be similar to that of the common frog on the eastern part of the island, i.e. strong and healthy, but very area-restricted populations. However, we must add that the many small lakes in the north-central area, at Sandvika, have not been thoroughly studied with respect to the toad. Whereas common frogs breed in shallow water, and egg clutches and tadpoles are easy to find, common toads tend to breed in deeper water, and their tadpoles may frequently school in any part of the lake, often making them

difficult to detect.

The climate on Frøya is probably quite suitable for the toad, at least locally, since all reported introductions of toads on Frøya have been successful. The species is, moreover, very widespread and common on the neighbouring island of Hitra, which has only slightly different (colder) climatic conditions. We think the habitat may help to explain the restricted distribution areas of the toad, i.e. the lack of woodland on Frøya, compared to Hitra, which is quite densely forested, for the most part by Scots pine *Pinus sylvestris*. The common frog is a more euryoecious animal; it may thrive in a wide range of biotopes in open landscape (heaths, moors and marshes, rocky places and scantily wooded areas of deciduous trees) and reproduce in large and small water bodies. At least in Western Norway, the common toad, however, seems to prefer – although not necessarily always demand – more coniferous forested areas and cultivated land (Frafjord & Byrkjedal 1994) and, in addition, usually larger breeding localities (Dolmen et al. 2008). Higher vegetation is even more important for the common toad than the common frog (see above), especially plants like common reed, bogbean and marsh cinquefoil *Comarum palustre*, which have large rhizomes where the toads like to lay their egg strings. Litlvetnet and Hammervatnet at Sistranda, Ervikvatnet at Ervika and Tungvågvatnet at Sandvika, meet most of these requirements; to a lesser degree also Smauna at Kverva.

The last-mentioned record of the common toad is so far unexplained. Only a 3 m long double egg string (probably dead) was found at Kverva; no adults. The closest known population of toads is Tungvågvatnet, Sandvika, 9 km further east-northeast. However, there are several lowland (<10 m a.s.l.) lakes and lakelets on the stretch westwards from Tungvågvatnet, aligned southwest-northeast and forming an almost continuous waterway towards Kverva. The terrestrial habitat is also quite favourable for toads, in part with sheltered pine woodland mixed with agriculture landscape. Since the common toad is less easy to detect than the common frog, we may have missed possible connecting localities. So, all the lakes on this stretch should be investigated further.

Although quite philopatric, the common toad can carry out long migrations, for instance 3.6 km is mentioned by Smith & Green (2005). A considerable gene flow between ponds less than 2 km apart has also been found for the common toad in England (Scribner et al. 2001). Hence, considering the toad's great ability to travel long distances and to tolerate brackish water (Hagström 1981; see also Wells 2007; Hopkins & Brodie 2015), it is not inconceivable that the egg string found at Kverva stems from toads that had crossed Steinsvatnet from the east side and eventually ended up at this new breeding pool in the west. In that case, they took about 16 years (ca. 1995 to 2011; see Table 2) to disperse from Norddal at Sandvika to the locality at Kverva. The stretch (in a straight line) is 9.5 km, but the dispersal route was probably longer, at least 9.9 km to avoid salty water. This gives a dispersal speed of about 0.6 km/yr.

## Conclusions

When it comes to island faunas, where sea barriers seem impossible to cross, zoogeographers can, nevertheless, sometimes encounter surprising patterns of distribution in animals. Did the species in question really get there by active locomotion or by rafting or other natural dispersal, or did humans bring it there? The common toad was basically thought to be a better disperser in coastal landscapes than the common frog, because of its rougher skin and higher tolerance to salty water (see the Introduction). However, this idea seemed to be seriously wrong when frogs (and no toads, at the time) were discovered on Frøya. We solved the mystery by extensive mapping and requests for information which showed that, in fact, both species had been introduced to the island. The introduction history also became quite clear because we started the mapping in time, i.e. before the distribution picture became too complicated. The main conclusions are as follows.

- The common frog population at Singstad on western Frøya is of anthropogenic origin – as we hypothesised (see the Introduction). Moreover, we have traced as many as five introductions of the common frog and three introductions of the common toad on Frøya.

- Anthropochore dispersal of frogs and toads has been a very important factor and probably necessary for the species' possibility to reach Frøya and for their present distribution on the island. With one possible exception, we have been able to track all known occurrences of the common frog and the common toad on Frøya back to a prior release of the species nearby.

- Amphibians are easy to disperse anthropogenically, and all known introductions of frogs and toads to Frøya have been successful, i.e. the localities have viable populations today. Moreover, the localities where common frogs were released on western Frøya, and possibly where common toads were introduced in north-central Frøya, have later acted as centres for large-scale natural dispersal. However, in most cases (e.g. on eastern Frøya), the amphibians have not dispersed much from where they were released for several decades, probably due to habitat and/or ecological barriers.

- The speed by which the common frog population has expanded its distribution area on western Frøya, estimated from the year when tadpoles were introduced at Singstad to eggs being found in a new water body, is at least up to about 0.4 km/yr. However, single animals have been seen far outside the population distribution border. If our supposition about long-range dispersal westwards from north-central Frøya is correct for the common toad, the corresponding figure is at least about 0.6 km/yr.

- Based on their present distributions, we predict that, in time: 1. The common frog population on western Frøya will fuse with that in the south, and frogs will invade most of the island, but with only a few localities in the central eastern uplands. 2. The common toad will expand its areas to a much lesser extent and be restricted to the most sheltered and wooded areas in the eastern, northern and possibly southern parts of Frøya.

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