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The common grass snake (*Natrix natrix*) on Sylt: human-mediated colonization of a North Sea island

Harald Ahnelt[1,2], Tatyana Romanova[3], Andreas Klinge[4], Wolfgang Böhme[5], Uwe Fritz[6] & Marika Asztalos[6]

[1)] Department of Evolutionary Biology, University of Vienna, Althanstr. 14, 1090 Vienna, Austria

[2)] First Zoological Department, Natural History Museum in Vienna, Burgring 7, 1010 Vienna, Austria

[3)] Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Coastal Ecology Section, Wadden Sea Station Sylt, Hafenstr. 43, 25992 List, Germany

[4)] Faunistisch-Ökologische Arbeitsgemeinschaft e.V., Olshausenstr. 40, c/o Institut für Natur- und Ressourcenschutz der Uni Kiel, 24098 Kiel, Germany

[5)] Zoologisches Forschungsmuseum Alexander Koenig, Leibniz Institute for Biodiversity of Animals, Herpetology Section, Adenauerallee 160, 53113 Bonn, Germany

[6)] Museum of Zoology (Museum für Tierkunde), Senckenberg Dresden, A. B. Meyer Building, 01109 Dresden, Germany

Corresponding author: Harald Ahnelt, e-mail: harald.ahnelt@univie.ac.at

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During the last decades citizen science, the public participation in scientific work, proved to be a valuable tool for quickly obtaining distributional information for individual species (e.g., Johnston et al. 2018). In the present study we combine information from citizen scientists with genetic evidence to elucidate the colonization of Sylt by common grass snakes, *Natrix natrix* (Linnaeus, 1758). Sylt is a North Sea island naturally void of any snakes (Harbst 2005, Böhme & Grell 2013), and the first records for *N. natrix* on Sylt were published only for the year 2007 (Böhme & Grell 2013; Fig. 1, Table 1).

While two herpetological surveys recorded no additional grass snakes on Sylt (Grosse et al. 2006, 2015), repeated recent sightings suggest that a local population established. Several records were recently spread over social media, and some grass snakes were documented by roadkills (Fig. 2, Table 1). During 2020, the number of records reached a peak with thirteen photographed or sighted snakes and two additional roadkills, including several juveniles or hatchlings. The coloration of all grass snakes for which information is available conformed to expectations for northern Central European populations of *N. natrix*, except for one voucher specimen in the collection of the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZMFK 93780, see below).

Until now, the origin of the snakes on Sylt is unclear. Multiple recent introductions, e.g., with fascine material and/or reed bundles, seem to be the most likely explanation, as already reported by Böhme & Grell (2013) for the records of 2007. Nevertheless, natural colonization cannot be fully excluded, especially in the light of records of possibly native grass snakes on the neighbouring island of Rømø (Böhme & Grell 2013, Fugle og natur 2014). The semiaquatic grass snake is known to cross marine waters (Kabisch 1999, Baker 2015), and the population on the island of Gotland (Baltic Sea) results evidently from multiple overseas dispersals (Kindler et al. 2014). Also, released or escaped pet snakes cannot be excluded as an explanation for the occurrence of grass snakes on Sylt.

The recent sightings (Table 1), in particular the record of hatchlings and juveniles at List, strongly suggest that a population established in the north of Sylt. Suitable habitat is there the 'Lister Koog,' a grass and shrub land of 96 ha with ditches and small ponds surrounded by reed, immediately west of List. The 'Koog' itself and its vicinity are inhabited by frogs and toads and the ponds by fishes (Grosse et al. 2006, Kuschereitz 2016), all preferred prey items of the grass snake (Kabisch 1999). Most records of grass snakes from List are close to this 'Koog,' suggestive of a restricted distribution.

If Sylt was colonized naturally, it is expected that the grass snakes belong to the same subspecies as in the adjacent Jutland peninsula and northern Germany. In this region occurs the nominotypical subspecies of *N. natrix*

(Kindler et al. 2017, 2018, Fritz & Schmidtler 2020). However, one of the first two documented grass snakes on Sylt was found in a reed bundle from Hungary that was transported to the island as construction material for building the traditional thatched roofs. Also, the coloration of this snake matched Hungarian grass snakes. The second grass snake, however, corresponded to other northern German specimens, and it was assumed that it was transported to Sylt with local material for fascines (Böhme & Grell 2013). Both specimens are preserved in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK 93780, 93781), and were available for genetic investigation (see below). In addition, a third grass snake collected at Keitum in 2013 (ZFMK 95280), also found among reed from Hungary, and two roadkills from List, now in the collection of the Museum of Zoology (Museum für Tierkunde), Senckenberg Dresden (MTD D 49957, 49958), were studied genetically. Hungarian grass snakes represent another, genetically distinct, subspecies (*N. n. vulgaris* Laurenti, 1758), so that we would expect that the 'reed bundle specimens' genetically match this subspecies,

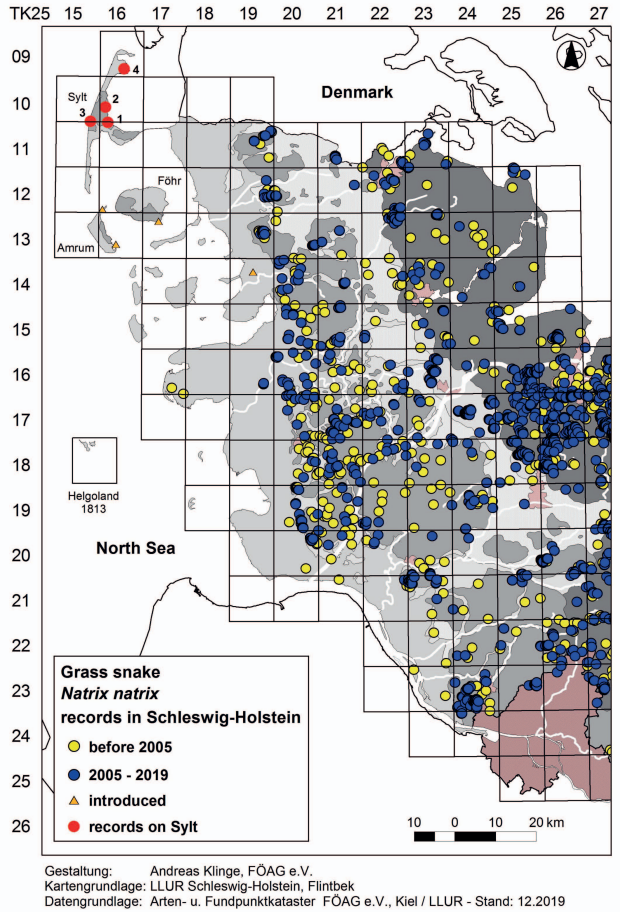

Figure 1. Schematic map showing records of the common grass snake (*Natrix natrix*) in Schleswig-Holstein (Germany). Note the lack of records in the northwestern marshland (medium grey) and the offshore island Sylt. 1–4: documented records from Sylt. 1 – Keitum, 2 – Braderup, 3 – Westerland, 4 – List.

whereas the other specimens should represent the nominotypical subspecies, if they originate from the mainland.

To elucidate the geographic origin of the five grass snakes from Sylt, we compared them genetically with data for twenty samples from previous studies (Table 2). For this purpose served ten pure specimens each of *N. n. natrix* and *N. n. vulgaris*. The latter subspecies was only recently formally recognized (Fritz & Schmidtler 2020) and corresponds to the so-called 'red mtDNA lineage' (clade 4) and 'red microsatellite cluster' of Kindler et al. (2013, 2017). The nominotypical subspecies matches the so-called 'yellow mtDNA lineage' (clade 3) and 'yellow microsatellite cluster' (Fritz & Schmidtler 2020).

For genetic characterization, the samples from Sylt were genotyped at the same thirteen microsatellite loci and the same two mitochondrial DNA fragments (cyt *b*; ND4+tRNAs) were sequenced as in previous studies on grass snakes (e.g., Kindler et al. 2013, 2017, 2018, Schultze et al. 2019, Asztalos et al. 2020). Haplotypes were determined in exploratory network analyses using TCS 1.21 (Clement et al. 2000) in which all published haplotypes were included (results not shown). Microsatellite data were examined with unsupervised Bayesian cluster analyses as implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000) following the approach described in Asztalos et al. (2020). The hybrid threshold was determined using HYBRIDLAB 1.0 (Nielsen et al. 2006) and all the twenty pure genotypes of *N. n. natrix* and *N. n. vulgaris* from the earlier studies.

The two 'reed bundle snakes' from Keitum (ZFMK 93780, 95280) held haplotypes of the red mtDNA lineage as expected for *N. n. vulgaris* (Fig. 3, Table 2). ZFMK 95280 yielded a new haplotype for the mtDNA fragment coding for ND4+tRNAs (haplotype r38, ENA accession number LR983952) that differs by one mutation step from the previously identified haplotype r3. All three grass snakes from List represented the yellow mtDNA lineage, as expected for the nominotypical subspecies. However, with respect to their nuclear genomic identity, none of the five grass snakes from Sylt was a pure *N. n. natrix*. The two individuals with 'red haplotypes' were identified by our microsatellite analyses as pure representatives of *N. n. vulgaris*, and the three snakes with 'yellow haplotypes' were genotypically admixed with very high percentages of *N. n. vulgaris* ancestry. This indicates that they originated from later hybrid generations and/or backcrossing involving *N. n. natrix* and *N. n. vulgaris* (Table 2). There are two possible explanations for the observed genetic pattern: (1) Either grass snakes (*N. n. natrix*) from the mainland reached naturally or facilitated by humans Sylt and hybridized there with grass snakes imported with reed bundles or fascine material from the distribution range of *N. n. vulgaris*, or (2) the snakes that arrived with reed or fascine material originated in a region within the wide hybrid zone between the nominotypical subspecies of *N. natrix* and *N. n. vulgaris*.

Both hypotheses are equally likely. It is known that material for fascines is imported from Germany, Poland, and the Netherlands (K. Uekermann, pers. comm.); reed imported to Sylt originates mainly in Romania, Hungary, Po-

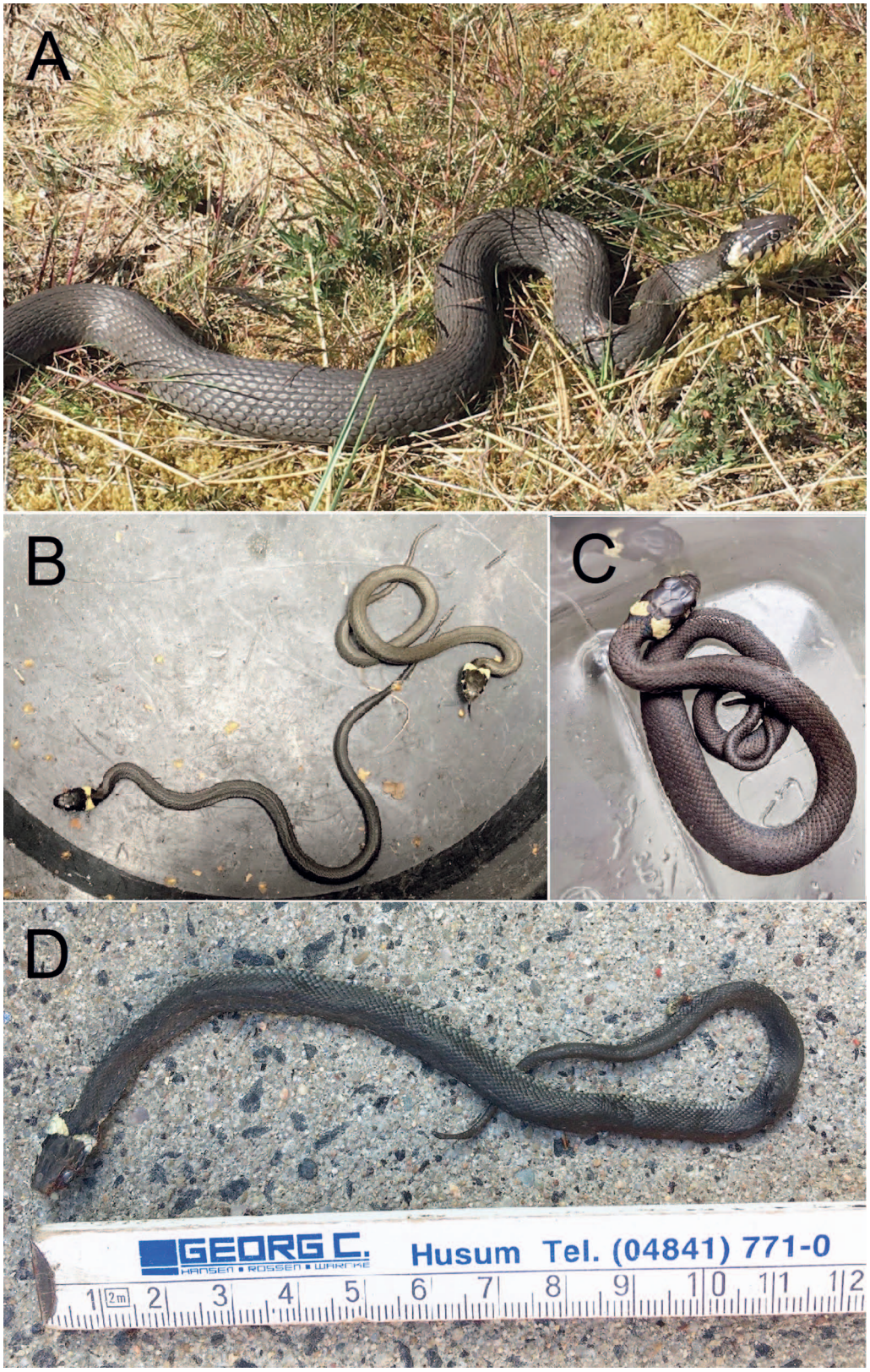

Figure 2. *Natrix natrix* from List/Sylt, Germany. (A) adult individual, 13 May 2020, photo by Margot Böhm; (B, C) recently hatched individuals, total length approximately 15–20 cm; (B) 30 September 2018, photo by Jan Böll; (C) 6 October 2020, photo by Tim Kress; (D) roadkill, June 2020, photo by Tatyana Romanova.

Table 1. Records of *Natrix natrix* on Sylt, in chronological order for vouchered records and sightings. Geographic coordinates of Keitum and List only indicate the villages, as the exact collection sites are unknown (Böhme & Grell 2013). † First documented records for Sylt (dead specimens; Böhme & Grell 2013), * originally reported as from Keitum (Böhme & Grell 2013), however, the snake was collected at List (R. Klockenhoff pers. comm.), ** first record of a life grass snake, + records from social media. Abbreviations: AWI – Alfred-Wegener Institut, Wattenmeerstation Sylt, MTD D – Museum of Zoology (Museum für Tierkunde), Senckenberg Dresden (Herpetological Collection), ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn.

Date	n	Voucher	Age/size	Locality	Coordinates
2007†	1	ZFMK 93780	Subadult	Keitum	54°53'24"N, 8°22'24"E
2007†	1	ZMFK 93781	Adult	List*	55°01'12"N, 8°25'40"E
?/09/2013	1	ZMFK 95280	Juvenile	Keitum	54°53'24"N, 8°22'24"E
30/09/2018**	2	Photo	Juvenile	List, Alte Dorfstraße	55°01'16"N, 8°26'00"E
07/04/2020	1+	Photo	Adult	List, near Mövenbergdeich	55°01'29"N, 8°25'49"E
12/04/2020	1+	Photo	Adult	List, Alte Dorfstraße	55°01'14"N, 8°25'53"E
13/05/2020	1+	Photo	Adult	List, near Mövenbergdeich	55°01'24"N, 8°25'56"E
19/05/2020	1+	Photo	Adult	List, 'Am Brünk'	55°01'22"N, 8°25'41"E
31/05/2020	1	Photo	Juvenile	List, 'Am Loo'	55°01'26"N, 8°25'10"E
?/06/2020	1	MTD D 49957	Subadult	List, Mövengrund	55°00'38"N, 8°24'56"E
17/06/2020	1+	Photo	Subadult	List, south of ferry terminal	55°00'56"N, 8°26'12"E
23/06/2020	1+	Photo	Adult	Westerland, town hall square	54°54'33"N, 8°18'24"E
04/07/2020	1+	Photo	Adult	List, west of "Am Brünk"	55°01'27"N, 8°25'43"E
08/07/2020	1+	Photo/video	Adult	List, 'Landwehrdeich'	55°01'21"N, 8°25'30"E
21/09/2020	1	MTD D 49958	Juvenile	List, 'Am Loo'	55°01'26"N, 8°25'12"E
06/10/2020	1	Photo	Juvenile, 15–17 cm	List, AWI	55°01'16"N, 8°26'15"E
Sightings					
2006	1	–	?	List	?
2011	1	–	Adult	Wenningstedt-Braderup	?
18/07/2011	1	–	Adult	List, Frischwassertal	55°00'41"N, 8°25'28"E
05/07/2012	1	–	Adult	Wennigstedt-Braderup	54°55'58"N, 8°21'27"E
04/06/2019	1	–	Juvenile, ~17 cm	List, 'Am Buttgraben'	55°01'26"N, 8°25'22"E
07/2019	1+	–	Adult	List, near Mövenbergdeich	55°01'29"N, 8°25'49"E
05/2020	1+	–	Adult (roadkill)	List, 'Alte Dorfstraße'	55°01'14"N, 8°26'00"E
01/09/2020	1+	–	Subadult, 30–40 cm	List, near 'Alte Dorfstraße'	55°01'19"N, 8°25'55"E
22/09/2020	1	–	Juvenile, 20–25 cm	List, near AWI	55°01'22"N, 8°26'08"E

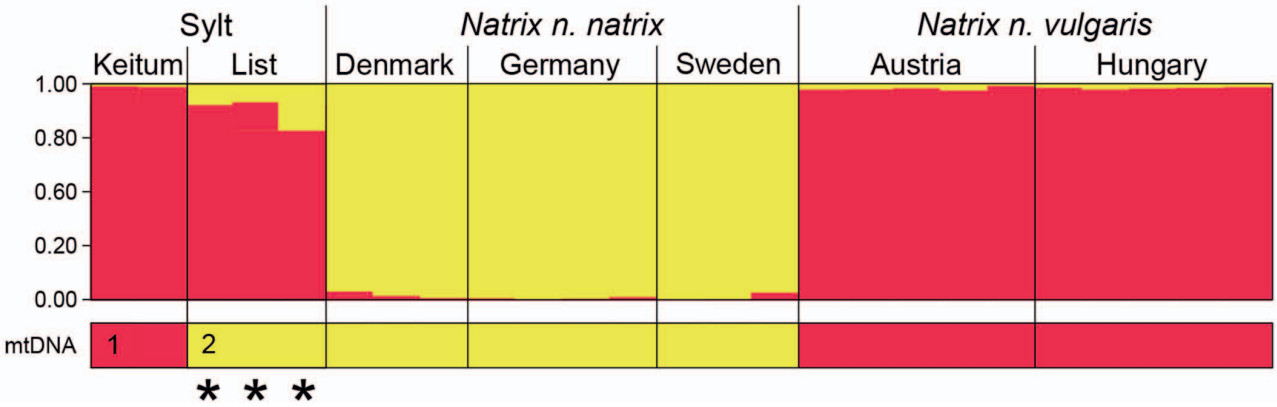

Figure 3. Graphic presentation showing genotypic identity of the studied 25 grass snakes. The mitochondrial lineage of each sample is shown below the STRUCTURE diagram for microsatellite data. Colours correspond to haplotypes of mtDNA lineage 3 (yellow) and mtDNA lineage 4 (red) of *Natrix natrix*. In the STRUCTURE diagram (top), an individual is represented by a vertical segment that reflects its ancestry (yellow = *N. n. natrix*; red = *N. n. vulgaris*). Asterisks highlight admixed snakes from Sylt (Germany). Numbers indicate individuals described in Böhme & Grell (2013): 1 = ZFMK 93780, 2 = ZFMK 93781.

Table 2. *Natrix natrix* samples used in the present study. The hybrid threshold for microsatellites (determined in HYBRIDLAB 1.0) was both for *N. n. natrix* and *N. n. vulgaris* 93%. The vertical sequence in this table matches the horizontal sequence of samples in Figure 3. * Haplotype newly identified in the present study. Abbreviations: MTD D – Museum of Zoology, Senckenberg Dresden (Herpetological Collection), MTD T – Museum of Zoology, Senckenberg Dresden (Tissue Collection), NHMW – Naturhistorisches Museum Wien, ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn, ZMH – Zoologisches Museum Hamburg.

		mtDNA data			Microsatellite data	
Voucher	Locality	Clade	ND4 + tRNAs	cyt *b*	Nuclear genomic identity	Reference
ZFMK 93780	Germany: Schleswig-Holstein: Sylt, Keitum	**4**	r30	r3	*N. n. vulgaris*	This study
ZFMK 95280	Germany: Schleswig-Holstein: Sylt, Keitum	**4**	r38*	r3	*N. n. vulgaris*	This study
ZFMK 93781	Germany: Schleswig-Holstein: Sylt, List	**3**	y1	y1	admixed	This study
MTD D 49957	Germany: Schleswig-Holstein: Sylt, List	**3**	y1	y20	admixed	This study
MTD D 49958	Germany: Schleswig-Holstein: Sylt, List	**3**	y1	y1	admixed	This study
MTD T 9652	Denmark: Funen: NNW Svendborg	**3**	y1	y1	*N. n. natrix*	Kindler et al. (2013)
MTD T 9913	Denmark: Jutland: SE Gammel Rye	**3**	y1	y38	*N. n. natrix*	Kindler et al. (2013)
ZMH R09204	Denmark: Zealand: Fredensborg	**3**	y20	–	*N. n. natrix*	Kindler et al. (2017)
MTD T 14070	Germany: Schleswig-Holstein: Daldorf: Kiebitzholmer Moor	**3**	y1	y20	*N. n. natrix*	Kindler et al. (2017)
ZFMK 85184	Germany: Schleswig-Holstein: Kiel-Elmschenhagen	**3**	y1	y20	*N. n. natrix*	Kindler et al. (2013)
ZMH R09338	Germany: Schleswig-Holstein: Langenhorst	**3**	y1	y19	*N. n. natrix*	Kindler et al. (2017)
MTD T 13936	Germany: Schleswig-Holstein: Lübeck: Schellbruch	**3**	y1	y20	*N. n. natrix*	Kindler et al. (2017)
MTD T 10920	Sweden: Öland: Halltorps Hage	**3**	y36	y17	*N. n. natrix*	Kindler et al. (2014)
MTD T 11579	Sweden: Södermanland: near Nyköping	**3**	y1	y17	*N. n. natrix*	Kindler et al. (2014)
MTD T 14860	Sweden: Västergötland: Vegby	**3**	y1	y1	*N. n. natrix*	Kindler et al. (2017)
NHMW 39266 (2)	Austria: Burgenland: Apetlon	**4**	r3	r18	*N. n. vulgaris*	Kindler et al. (2017)
MTD T 12066	Austria: Lake Neusiedl: Jois	**4**	r4	–	*N. n. vulgaris*	Kindler et al. (2017)
NHMW 40084 (1)	Austria: Lower Austria: Stopfenreuth	**4**	r3	r3	*N. n. vulgaris*	Kindler et al. (2017)
NHMW 36405 (1)	Austria: Upper Austria: St. Ulrich bei Steyr	**4**	r3	r21	*N. n. vulgaris*	Kindler et al. (2017)
MTD T 14562	Austria: Vienna	**4**	r3	r10	*N. n. vulgaris*	Kindler et al. (2017)
ZFMK 61029	Hungary: Győr	**4**	r3	r10	*N. n. vulgaris*	Kindler et al. (2013)
MTD T 12759	Hungary: near Tokaj	**4**	r3	r3	*N. n. vulgaris*	Kindler et al. (2017)
MTD T 12761	Hungary: near Tokaj	**4**	r27	r3	*N. n. vulgaris*	Kindler et al. (2017)
MTD T 12765	Hungary: near Tokaj	**4**	r3	r3	*N. n. vulgaris*	Kindler et al. (2017)
MTD T 12777	Hungary: near Tokaj	**4**	r3	r4	*N. n. vulgaris*	Kindler et al. (2017)

land, and Austria (Anonymus 2020, Hölms 2020). The Netherlands can be ruled out as source region because there occurs another species of grass snake, *N. helvetica* (Lacepède, 1789). However, many of the other regions lie within the hybrid zone of *N. n. natrix* and *N. n. vulgaris* that can reach a width of approximately 700 km (Kindler et al. 2017). Pure populations of *N. n. vulgaris* are currently only known from southern Central Europe, including Hungary and Austria (Kindler et al. 2017, Schultze et al. 2019, Fritz & Schmidtler 2020).

In any case, our results provide unambiguous evidence for the introduction and naturalization of grass snakes on Sylt from founder individuals some of which, at least, originated far away. This highlights that grass snakes can easily disperse across long distances as "stowaways" and are well suited for establishing new populations. This finding poses considerable challenges for nature conservation that aims to maintain native pure populations wherever grass snakes are naturally distributed.

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