



Circulation of influenza D virus in Ukraine: A multi-species serological study

Alessandro Falsini^a , Aurora Fiori^a, Emanuele Montomoli^{a,b}, Nataliia Muzyka^c,
Denys Muzyka^{c,d,1}, Claudia Maria Trombetta^{a,*,1}

^a Department of Molecular and Developmental Medicine, University of Siena, Siena, Italy

^b VisMederi srl, Siena, Italy

^c Department of Avian Diseases and Molecular Diagnostics, National Scientific Center Institute of Experimental and Clinical Veterinary Medicine, Kharkiv, Ukraine

^d Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden

ARTICLE INFO

Keywords:

Influenza D virus
D/660 and D/OK lineage
Ukraine
domestic animals
pet animals
wild animals

ABSTRACT

Influenza viruses infect a wide range of animal species and continue to pose a significant threat to global health. Influenza D virus (IDV), first identified in 2011, has emerged as a new pathogen with a broad host range and remains poorly understood. This seroepidemiological study aimed to investigate the circulation of IDVs in Ukraine by analysing serum samples from domestic, wild and pet animals collected between 2021 and 2024. All samples tested negative for influenza A viruses. The highest seroprevalence for the D/660 lineage was detected in horses (57%), followed by swine (10%), with sporadic positivity observed in wild and companion animals. Positivity for the D/OK lineage was lower across all species. Overall, these findings provide evidence of the circulation and predominance of the D/660 lineage as the major IDV circulating in Ukraine and underscore the importance of coordinated surveillance in livestock, wildlife, and at-risk human populations to fully evaluate the public health implications of this emerging pathogen.

Emerging viral diseases represent a major challenge to global health, food security, and biodiversity. Zoonotic pathogens account for >60 % of all human infectious diseases and approximately 75 % of emerging pathogens originate from animal sources (Jones et al., 2008; Taylor et al., 2001). Understanding host range and serological responses across different animal species is therefore important for identifying potential reservoirs and developing appropriate surveillance and control strategies (Woolhouse and Gowtage-Sequeria, 2005).

Influenza viruses are currently infecting humans, horses, birds and pigs, posing a significant threat to both animal and human health (Cauldwell et al., 2014) and are still unpredictable pathogens. One of the most remarkable examples highlighting the importance of influenza viruses is the worsening global epizootic situation caused by avian influenza virus, particularly highly pathogenic avian influenza (HPAI) A, H5Nx, and its ability to cross the interspecies barrier. HPAI viruses (H5Nx) have infected domestic and wild carnivorous mammals, including cats, dogs, foxes, fur-bearing animals, in many European countries (such as Poland and Finland) in 2022–2024 (Domańska-Blicharz et al., 2023; Lindh et al., 2023; Tammiranta et al.,

2023), as well as cattle in the United States (Burki, 2024; Eisfeld et al., 2024).

Domestic animals are recognized as important hosts in the ecology of influenza A viruses (IAVs). Swine are considered as “mixing vessels” for both avian and human influenza viruses, enabling the emergence of novel viruses with pandemic potential (Kida et al., 1994; Ma et al., 2008; Murcia et al., 2011). It is also important to note that new types of influenza viruses continue to emerge, and their potential impact as dangerous pathogen for human health is still unclear. For instance, a new type of influenza virus is the influenza D virus (IDV), which has recently been detected in various farm animals, including cattle, pigs, and horses in different parts of the world (Nedland et al., 2018; Skelton and Huber, 2022; Yu et al., 2021). The virus, first identified in swine in 2011, has emerged as a pathogen with a broad host range including multiple animal species (Ducatez et al., 2015; Gao et al., 2025; Hause et al., 2013; Lanave et al., 2024; Trombetta et al., 2024). Evidence of high prevalence rates in cattle supports their role as the primary reservoir of IDV (Falsini et al., 2025; Kwasnik et al., 2023; Zhai et al., 2017). More recently, serological studies have detected IDV in domestic

* Corresponding author.

E-mail address: trombetta@unisi.it (C.M. Trombetta).

¹ These authors share senior authorship

animals, specifically in dogs in Italy, cats in China (Gao et al., 2025; Trombetta et al., 2024) and dogs and cats in Ukraine (Trombetta et al., 2026). Experimental infections have further confirmed that IDV can cause mild to moderate respiratory disease in cattle and pigs, while small ruminants and other species may act as spillover hosts (Ferguson et al., 2015). The serological status of wild and exotic animals, however, remains underexplored, although their role in viral ecology is increasingly recognized (Kuiken et al., 2006).

Ukraine is one of the biggest European countries, with a substantial farming industry and considerable wildlife diversity. However, the situation regarding the circulation of influenza viruses in Ukraine remains unclear. To date, only the natural circulation of IAVs in wild birds has been studied in detail (Muzyka et al., 2019, 2016b, 2016a, 2012). Several recent reports have documented the circulation of IAVs in domestic and wild mammals in Ukraine. Most of these studies are based on serological surveys, reporting seroprevalence rates of 10–80 % in domestic horses in 2021–2024, 66.6 % in wild horses (Rula et al., 2024) and 20–100 % in domestic swine (Stegniy, B. T., et al., 2023).

In this seroepidemiological study, we aimed to investigate the circulation of IDVs in Ukraine by analysing serum samples from multiple animal species.

A total of 363 serum samples from different animal species were collected in 2021, 2023 and 2024 in Ukraine, as shown in Table 1. The sample set includes serum samples from clinically healthy domestic animals (pigs and horses), wild animals (mouflon, deer, saiga) and pet animals (guinea pig, rabbit, chinchilla, ferret) collected in different region of Ukraine, as described in Table 1 and further illustrated in the map of Ukraine (Fig. 1). All serum samples were initially tested for the presence of antibodies to IAV using two commercial ELISA kits: IDEXX AI Multi-Screen Ab Test (The Netherlands) and ID Screen® Influenza A Antibody Competition Multi-species (ID Vet, France) and only IAV negative serum samples were included in this study. All serum samples were then screened in duplicate by the hemagglutination inhibition (HI) assay, as previously described (Falsini et al., 2025; Lanave et al., 2024; Trombetta et al., 2022, 2019), using two IDV strains from two viral lineages: D/bovine/Oklahoma/660/2013 virus (D/660 lineage, here referred to as D/660), kindly provided by Prof. Feng Li, University of Kentucky, and influenza D/swine/Italy/199724–3/2015 virus (D/OK lineage, here referred to as D/OK), obtained from the European Virus Archive (EVAg). All serum samples, including both positive and negative controls, were pre-treated with receptor-destroying enzyme (RDE) from *Vibrio cholerae* (Denka, Tokyo, Japan) at a ratio of 1:4 for 18 h at 37 °C in a water bath, followed by heat inactivation at 56 °C for 1 hour. Samples were re-treated with 15 % turkey red blood cells (RBCs) at a 1:1 ratio, resulting in a final serum dilution of 1:10. All serum sample were then tested by HI assay using turkey RBCs adjusted to a final concentration of 0.35 %. Antibody titres were defined as the reciprocal of the highest

serum dilution that completely inhibited agglutination. Since the initial dilution was 1:10, titres below the detection limit were conventionally assigned a value of 5 (half of the lowest detectable titre) for calculation purposes. Serum samples with an average antibody titre ≥ 10 were considered HI positive. The percentages of positive and negative samples were reported along with their corresponding 95 % confidence intervals (CI).

Regarding swine samples, 10 % (19/183) tested positive for D/660 (titres ≥ 10), only 5 % (10/183) showed titres ≥ 10 for D/OK and 2 % (4/183) were positive for both IDV lineages. In contrast, 57 % (79/138) of horse samples tested positive for D/660 with one of these also positive for D/OK. All mouflon samples, included among wild ungulates, resulted negative for both IDV lineages. The remaining animals listed in Table 1 were grouped into an “other animals” category due to small individual sample sizes. Overall, 41 % (9/22) showed titres ≥ 10 to D/660, while only 10 % (1/22) were positive for D/OK. Specifically, three deer samples were positive for D/660, with one of these also positive for D/OK; two saiga antelopes were positive for D/660; two guinea pig were positive for D/660; one rabbit sample was positive for D/660; and the one chinchilla was positive for D/660. The only ferret sample was negative for both IDV lineages (Table 2).

This study provides novel serological evidence of IDV circulation among various domestic and wild animal species in Ukraine. By analysing HI titres against two IDV lineages (D/660 and D/OK), we detected positive samples across different animal species. Our results confirm swine and equine as hosts for IDV, consistent with previous reports from Europe, Asia, and North America (Ducatez et al., 2015; Falsini et al., 2025; Murakami et al., 2016; Salem et al., 2017). While pigs are well established as reservoirs for IAVs due to their susceptibility to both avian and human viruses (Ma et al., 2008), their role in IDV ecology appears to be secondary. Experimental studies suggest that swine can sustain replication but are not the primary maintenance host (Ferguson et al., 2016; Hause et al., 2013). Nonetheless, seroprevalence studies show varying rates: 1.6 % positivity in swine samples from France (Gorin et al., 2019), 11.7 % in Northern Italy in 2015 and 2016 (Foni et al., 2017), and an increase to 31 % for D/660 and 29 % for D/OK in Southern Italy in 2021 (Falsini et al., 2025). Our findings align with this trend, demonstrating IDV circulation in Ukrainian swine populations. In contrast, horses from Ukraine showed a remarkably high seroprevalence (57 %) for D/660, providing the first evidence of virus circulation in the country. This finding is particularly notable because a high IDV seroprevalence was detected in horses that tested negative for IAV. In Ukraine, overall IAV seroprevalence in horses has also been reported to be high (10–80 %, depending on the region) (Rula et al., 2024). At this preliminary stage of the study, it is difficult to explain the high level of IDV seropositivity and the potential sources of exposure, as only serological methods were applied. Nevertheless, the serological data support the likelihood of IDV circulation among horses in Ukraine. These findings highlight the need for more comprehensive future studies, including molecular (PCR) and/or virological investigations, to better understand the ecology of IDV, potential sources of exposure, and its epidemiological role in equine populations. Notably, the seroprevalence observed in Ukraine is substantially higher than that reported in a previous study from the Midwestern United States, which analysed samples collected in 2015 and reported seroprevalence rates of only 11 % for D/660 and 12 % for D/OK (Nedland et al., 2018). Similarly, horse samples collected in Italy showed even lower rates, with 5 % positive for D/660 and 1 % for D/OK (Falsini et al., 2025). These results suggest that horses may serve as underappreciated sentinels of viral circulation, with potential infection dynamics varying across regions. Among wild ungulates, deer and saiga antelopes exhibited some samples were positive to D/660. Although the sample size was limited, these findings align with previous studies reporting IDV detection in ungulates, especially wild boars. In France, 0.5 % of wild boar samples collected in 2009 and 2018 tested positive for IDV (Gorin et al., 2019), whereas in Italy, much higher positivity rates were observed, with 80 % of serum samples

Table 1
Summary of the animal species included in this study. Number of samples collected, their geographic origins (as detailed in the map), and the year of collection.

Animal Species	Number of samples	Region	Year
Horse	138	See map (Fig. 1)	2023 (1 sample 2021)
Swine	183	See map (Fig. 1)	2023 and 2021
Mouflon	20	Askania – Nova Kherson	2024
Deer	8	Askania – Nova Kherson	2021
Saiga	7	Askania – Nova Kherson	2021
Guinea Pig	3	Kharkiv	2023
Rabbit	2	Kharkiv	2023
Chinchilla	1	Kharkiv	2023
Ferret	1	Kharkiv	2023



Fig. 1. Representative map of Ukraine. The map shows the sampling regions; different colours indicate the animal species collected from each region.

Table 2

HI prevalence of animal samples. The HI prevalence was described as follows: negative (≤ 5) and positive (≥ 10), with each category reported alongside with the corresponding 95 % confidence interval (CI). The “other animals” category includes deer, saiga, guinea pig, rabbit, chinchilla and ferret, for a total of 22 samples.

Animal Species	D/660		D/OK		D/660 – D/OK
	Negative (≤ 5)	Positive (≥ 10)	Negative (≤ 5)	Positive (≥ 10)	Positive (≥ 10)
Swine	90 % (164/183) 95 %CI 84,2–93,63 %	10 % (19/183) 95 %CI 6,37–15,74 %	95 % (173/183) 95 %CI 90,18–97,35 %	5 % (10/183) 95 %CI 2,65–9,82 %	2 % (4/183) 95 %CI 0,60–5,50 %
Horse	43 % (59/138) 95 %CI 34,37–51,45 %	57 % (79/138) 95 %CI 48,55–65,63 %	99 % (137/138) 95 %CI 96,03–99,98 %	1 % (1/138) 95 %CI 0,02–3,97 %	1 % (1/138) 95 %CI 0,02–3,97 %
Mouflon	100 % (20/20) 95 %CI 83,16–100 %	0 % (0/20) 95 %CI 0–16,84 %	100 % (20/20) 95 %CI 83,16–100 %	0 % (0/20) 95 %CI 0–16,84 %	0 % (0/20) 95 %CI 0–16,84 %
Other Animals	59 % (13/22) 95 %CI 36,35–79,29 %	41 % (9/22) 95 %CI 20,71–63,65 %	95 % (21/22) 95 %CI 77,16–99,98 %	5 % (1/22) 95 %CI 0,12–22,84 %	5 % (1/22) 95 %CI 0,12–22,84 %

collected in 2020–2021 testing positive for D/660 and 56 % for D/OK. In contrast, all mouflon samples were uniformly negative. The detection of IDV antibodies in ruminants has been sporadically reported in America and Asia (Luo et al., 2017; Zhai et al., 2017). Given that cattle are considered the primary reservoir (Ferguson et al., 2016; Zhai et al., 2017), spillover into sympatric wildlife likely occurs in areas where domestic and wild ruminants share pastures or water sources. The absence of detectable antibodies in mouflons may reflect the small sample size, distinct ecological niches, or lower intrinsic susceptibility. Further longitudinal studies are needed to clarify the role of wild ruminants in sustaining or amplifying IDV transmission cycles. Small mammals in our survey, including guinea pigs, rabbits, and chinchillas, demonstrated occasional seropositivity to D/660, whereas the ferret tested negative. These findings are intriguing because rodents and lagomorphs are not typically considered as natural hosts of influenza viruses, although have been extensively used as laboratory models (Bouvier and Lowen, 2010). The detection of antibodies in naturally exposed individuals suggests that these species may be susceptible to spillover under field conditions. While the epidemiological significance of such infections remains unclear, their occurrence underscores the broad host range of IDV. This adaptability raises concerns regarding viral persistence in multi-host ecosystems and the possibility of

recombination or reassortment events. However, the interpretation of these findings is limited by the small sample size, only three guinea pigs, two rabbits, and one each of chinchilla and ferret were tested.

Taken together, our results confirm the circulation and predominance of the D/660 lineage as the main circulating IDV in Ukraine as well, highlighting the progressive replacement of D/OK lineage, consistent with trends reported in other parts of Europe. This trend underscores the dynamic evolution of IDV and its potential to generate new antigenic variants (Gaudino et al., 2022).

This study has some limitations. First, the sample sizes for some species (e.g., deer, saiga, guinea pig, chinchilla, ferret, rabbits) were small, which limits statistical power and generalizability of our findings. In addition, the cross-sectional design of our sampling precludes temporal inference, and longitudinal surveillance would be required to evaluate seasonal dynamics and viral persistence. No information was available regarding the age of the wild animals.

In conclusion, our study highlights the predominance of the D/660 lineage in swine, equine, wild ungulates and small mammals in Ukraine providing a valuable comparative framework for IDV serology across a diverse array of species in Eastern Europe. By documenting exposure in both domestic and wild animal exposure, we provide evidence for the broad ecological plasticity of IDV. These findings underscore the

importance of coordinated monitoring of livestock, wildlife, and at-risk human populations to fully assess the public health significance of this emerging orthomyxovirus. Ultimately, elucidating the diversity of serological responses across multiple animal species is essential for a “One Health” approach to infectious disease research, integrating human, animal, and ecosystem health (Destoumieux-Garzón et al., 2018). Comparative serology across species can inform public health authorities, veterinarians, and wildlife managers, supporting the development of evidence-based strategies to mitigate the risk of viral emergence and strengthen preparedness against future pandemics.

Funding

In Ukraine the research was supported by a grant from the National Research Foundation of Ukraine (Grant n. #2021.01/0006).

Ethical approval

The animal study was reviewed and approved by the Institutional Animal Care and Use Committee of the National Scientific Center Institute of Experimental and Clinical Veterinary Medicine (protocol #1–23, 19.04.2023).

CRediT authorship contribution statement

Alessandro Falsini: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Aurora Fiori:** Investigation. **Emanuele Montomoli:** Resources. **Nataliia Muzyka:** Resources. **Denys Muzyka:** Writing – review & editing, Resources, Conceptualization. **Claudia Maria Trombetta:** Writing – review & editing, Supervision, Resources, Project administration.

Declaration of competing interest

EM is founder and Chief Scientific Officer of VisMederi srl. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgement

This publication was supported by the European Virus Archive GLOBAL project that received funding from the European Union’s Horizon 2020 research and innovation program (grant agreement No 871029).

Data availability

Data will be made available on request.

References

- Bouvier, N.M., Lowen, A.C., 2010. Animal models for influenza virus pathogenesis and transmission. *Viruses* 2, 1530–1563. <https://doi.org/10.3390/v20801530>.
- Burki, T., 2024. Avian influenza in cattle in the USA. *Lancet Infect. Dis.* 24, e424–e425. [https://doi.org/10.1016/S1473-3099\(24\)00369-4](https://doi.org/10.1016/S1473-3099(24)00369-4).
- Cauldwell, A.V., Long, J.S., Moncorgé, O., Barclay, W.S., 2014. Viral determinants of influenza A virus host range. *J. Gen. Virol.* 95, 1193–1210. <https://doi.org/10.1099/vir.0.062836-0>.
- Destoumieux-Garzón, D., Mavingui, P., Boetsch, G., Boissier, J., Darriet, F., Duboz, P., Fritsch, C., Giraudoux, P., Le Roux, F., Morand, S., Paillard, C., Pontier, D., Sueur, C., Voituron, Y., 2018. The one health concept: 10 years old and a long road ahead. *Front. Vet. Sci.* 5, 14. <https://doi.org/10.3389/fvets.2018.00014>.
- Domańska-Blicharz, K., Świętoń, E., Świątalska, A., Monne, I., Fusaro, A., Tarasiuk, K., Wyrstek, K., Stys-Fijol, N., Giza, A., Pietruk, M., Zecchin, B., Pastori, A., Adaszek, L., Pomorska-Mól, M., Tomczyk, G., Terregino, C., Winiarczyk, S., 2023. Outbreak of highly pathogenic avian influenza A(H5N1) clade 2.3.4.4b virus in cats. *June to July 2023 Euro Surveill.* 28, 2300366. <https://doi.org/10.2807/1560-7917.ES.2023.28.31.2300366>.
- Ducatez, M.F., Pelletier, C., Meyer, G., 2015. Influenza D virus in cattle, France, 2011–2014. *Emerg. Infect. Dis.* 21, 368–371. <https://doi.org/10.3201/eid2102.141449>.
- Eisfeld, A.J., Biswas, A., Guan, L., Gu, C., Maemura, T., Trifkovic, S., Wang, T., Babujee, L., Dahn, R., Halfmann, P.J., Barnhardt, T., Neumann, G., Suzuki, Y., Thompson, A., Swinford, A.K., Dimitrov, K.M., Poulsen, K., Kawaoka, Y., 2024. Pathogenicity and transmissibility of bovine H5N1 influenza virus. *Nature* 633, 426–432. <https://doi.org/10.1038/s41586-024-07766-6>.
- Falsini, A., Coppola, C., Fiori, A., Buonavoglia, D., Marchi, S., Montomoli, E., Pellegrini, F., Lanave, G., Martella, V., Camero, M., Trombetta, C.M., 2025. Influenza D virus circulation among bovines, swine, equines, and wild boars in Italy: a sero-epidemiological study. *Pathogens* 14, 891. <https://doi.org/10.3390/pathogens14090891>.
- Ferguson, L., Eckard, L., Epperson, W.B., Long, L.-P., Smith, D., Huston, C., Genova, S., Webby, R., Wan, X.-F., 2015. Influenza D virus infection in Mississippi beef cattle. *Virology* 486, 28–34. <https://doi.org/10.1016/j.virol.2015.08.030>.
- Ferguson, L., Eckard, L., Epperson, W.B., 2016. Influenza D virus infection in Mississippi beef cattle. *Virology* 486, 28–34. <https://doi.org/10.1016/j.virol.2015.08.030>.
- Foni, E., Chiapponi, C., Baioni, L., Zanni, I., Merenda, M., Rosignoli, C., Kyriakis, C.S., Luini, M.V., Mandola, M.L., Bolzoni, L., Nigrelli, A.D., Faccini, S., 2017. Influenza D in Italy: towards a better understanding of an emerging viral infection in swine. *Sci. Rep.* 7, 11660. <https://doi.org/10.1038/s41598-017-12012-3>.
- Gao, H., Sun, W., Lu, P., Dong, Z., Wu, J., Li, Y., Wan, W., Feng, Y., Qian, B., Zhang, M., Wu, Y., Dong, C., Shen, B., Wang, T., Xia, X., Zhang, J., Cao, W., Gao, Y., 2025. Efficient airborne transmission of influenza D virus in ferret models and serological evidence of human exposure in Northeast China. *Emerg. Microbes. Infect.* 14, 2564308. <https://doi.org/10.1080/22221751.2025.2564308>.
- Gaudino, M., Chiapponi, C., Moreno, A., Zohari, S., O'Donovan, T., Quinless, E., Sausy, A., Oliva, J., Salem, E., Fusade-Boyer, M., Meyer, G., Hübschen, J.M., Saegerman, C., Ducatez, M.F., Snoeck, C.J., 2022. Evolutionary and temporal dynamics of emerging influenza D virus in Europe (2009–22). *Virus. Evol.* 8, veac081. <https://doi.org/10.1093/ve/veac081>.
- Gorin, S., Fablet, C., Quéguiner, S., Barbier, N., Paboeuf, F., Hervé, S., Rose, N., Simon, G., 2019. Assessment of Influenza D virus in domestic pigs and wild boars in France: apparent limited spread within swine populations despite serological evidence of breeding sow exposure. *Viruses* 12, 25. <https://doi.org/10.3390/v12010025>.
- Hause, B.M., Ducatez, M., Collin, E.A., 2013. Isolation of a novel swine influenza virus from Oklahoma in 2011 which is distantly related to human influenza C viruses. *PLoS. Pathog.* 9, e1003176. <https://doi.org/10.1371/journal.ppat.1003176>.
- Jones, K.E., Patel, N.G., Levy, M.A., Storeygard, A., Balk, D., Gittleman, J.L., Daszak, P., 2008. Global trends in emerging infectious diseases. *Nature* 451, 990–993. <https://doi.org/10.1038/nature06536>.
- Kida, H., Ito, T., Yasuda, J., Shimizu, Y., Itakura, C., Shortridge, K.F., Kawaoka, Y., Webster, R.G., 1994. Potential for transmission of avian influenza viruses to pigs. *J. Gen. Virol.* 75 (Pt 9), 2183–2188. <https://doi.org/10.1099/0022-1317-75-9-2183>.
- Kuiken, T., Holmes, E.C., McCauley, J., Rimmelzwaan, G.F., Williams, C.S., Grenfell, B. T., 2006. Host species barriers to influenza virus infections. *Science* (1979) 312, 394–397. <https://doi.org/10.1126/science.1122818>.
- Kwasnik, M., Rola, J., Rozek, W., 2023. Influenza D in domestic and wild animals. *Viruses* 15, 2433. <https://doi.org/10.3390/v15122433>.
- Lanave, G., Camero, M., Coppola, C., 2024. Serological evidence for circulation of influenza D virus in the ovine population in Italy. *Pathogens* 13, 162.
- Lindh, E., Lounela, H., Ikonen, N., Kantala, T., Savolainen-Kopra, C., Kauppinen, A., Österlund, P., Kareinen, L., Katz, A., Nokireki, T., Jalava, J., London, L., Pitkäpaasi, M., Vuolle, J., Punto-Luoma, A.-L., Kaarto, R., Voutilainen, L., Holopainen, R., Kalin-Mänttari, L., Laaksonen, T., Kiviranta, H., Pennanen, A., Helve, O., Laamanen, I., Melin, M., Tamminen, N., Rimhanen-Finne, R., Gadd, T., Salminen, M., 2023. Highly pathogenic avian influenza A(H5N1) virus infection on multiple fur farms in the South and Central Ostrobothnia regions of Finland. *July 2023 Euro Surveill.* 28, 2300400. <https://doi.org/10.2807/1560-7917.ES.2023.28.31.2300400>.
- Luo, J., Ferguson, L., Smith, D.R., Woolums, A.R., Epperson, W.B., Wan, X.-F., 2017. Serological evidence for high prevalence of Influenza D Viruses in Cattle, Nebraska, United States, 2003–2004. *Virology* 501, 88–91. <https://doi.org/10.1016/j.virol.2016.11.004>.
- Ma, W., Kahn, R.E., Richt, J.A., 2008. The pig as a mixing vessel for influenza viruses: human and veterinary implications. *J. Mol. Genet. Med.* 3, 158–166.
- Murakami, S., Endoh, M., Kobayashi, T., 2016. Influenza D virus infection in herd of cattle. *Japan. Emerg. Infect. Dis.* 22, 1517–1519. <https://doi.org/10.3201/eid2208.160123>.
- Murcia, P.R., Wood, J.L.N., Holmes, E.C., 2011. Genome-scale evolution and phylogenetics of equine H3N8 influenza A virus. *J. Virol.* 85, 5312–5322. <https://doi.org/10.1128/JVI.02619-10>.
- Muzyka, D., Pantin-Jackwood, M., Spackman, E., Smith, D., Rula, O., Muzyka, N., Stegny, B., 2016a. Isolation and genetic characterization of avian influenza viruses isolated from wild birds in the Azov-Black Sea region of Ukraine (2001–2012). *Avian Dis.* 60, 365–377. <https://doi.org/10.1637/11114-050115-Reg>.
- Muzyka, D., Pantin-Jackwood, M., Spackman, E., Stegny, B., Rula, O., Shutchenko, P., 2012. Avian influenza virus wild bird surveillance in the Azov and Black Sea regions of Ukraine (2010–2011). *Avian Dis.* 56, 1010–1016. <https://doi.org/10.1637/10157-040912-ResNote.1>.
- Muzyka, D., Pantin-Jackwood, M., Starick, E., Fereidouni, S., 2016b. Evidence for genetic variation of Eurasian avian influenza viruses of subtype H15: the first report of an H15N7 virus. *Arch. Virol.* 161, 605–612. <https://doi.org/10.1007/s00705-015-2629-2>.

- Muzyka, D., Rula, O., Tkachenko, S., Muzyka, N., Köthe, S., Pishchanskyi, O., Stegny, B., Pantin-Jackwood, M., Beer, M., 2019. Highly pathogenic and low pathogenic avian influenza H5 subtype viruses in wild birds in Ukraine. *Avian Dis.* 63, 219–229. <https://doi.org/10.1637/11879-042718-ResNote.1>.
- Nedland, H., Wollman, J., Sreenivasan, C., Quast, M., Singrey, A., Fawcett, L., Christopher-Hennings, J., Nelson, E., Kaushik, R.S., Wang, D., Li, F., 2018. Serological evidence for the co-circulation of two lineages of influenza D viruses in equine populations of the Midwest United States. *Zoonoses. Public Health* 65, e148–e154. <https://doi.org/10.1111/zph.12423>.
- Rula, O.M., Muzyka, N.M., Drozhzhe, Zh.M., Pishchanskyi, O.V., Stegny, B.T., Muzyka, D.V., 2024. Serological monitoring of Influenza A among wild and domestic ungulates in Ukraine. *J. Vet. Med. Biotechnol. Biosafety* 10, 29–36. <https://doi.org/10.36016/JVMBBS-2024-10-3-5>.
- Salem, E., Cook, E.A.J., Lbacha, H.A., Oliva, J., Awoume, F., Aplogan, G.L., Hymann, E. C., Muloi, D., Deem, S.L., Alali, S., Zouagui, Z., Fèvre, E.M., Meyer, G., Ducatez, M.F., 2017. Serologic evidence for Influenza C and D virus among ruminants and Camelids, Africa, 1991–2015. *Emerg. Infect. Dis.* 23, 1556–1559. <https://doi.org/10.3201/eid2309.170342>.
- Skelton, R.M., Huber, V.C., 2022. Comparing influenza virus biology for understanding influenza D virus. *Viruses* 14, 1036. <https://doi.org/10.3390/v14051036>.
- Stegny, B.T., Rula, O.M., Muzyka, N.M., Dunaiev, Yu.K., Busol, V.O., Kolchik, O.V., Muzyka, D.V., 2023. Risk of Swine influenza for veterinary medicine and human health in Ukraine. *J. Veterin. Med., Biotechnol. Biosafety* 33–41. <https://doi.org/10.36016/JVMBBS-2023-9-3-6>.
- Tammiranta, N., Isomursu, M., Fusaro, A., Nylund, M., Nokireki, T., Giussani, E., Zecchin, B., Terregino, C., Gadd, T., 2023. Highly pathogenic avian influenza A (H5N1) virus infections in wild carnivores connected to mass mortalities of pheasants in Finland. *Infect. Genet. Evol.* 111, 105423. <https://doi.org/10.1016/j.meegid.2023.105423>.
- Taylor, L.H., Latham, S.M., Woolhouse, M.E., 2001. Risk factors for human disease emergence. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 356, 983–989. <https://doi.org/10.1098/rstb.2001.0888>.
- Trombetta, C., Fiori, A., Falsini, A., Pellegrini, F., Poder, S.L., Eichenbaum, A., Cardona, V., Oliva, J., Meyer, G., Muzyka, N., Muzyka, D., Montomoli, E., Martino, B.D., Ducatez, M., Lanave, G., Martella, V., Camero, M., 2026. Serological investigation of influenza D virus in cats and dogs in Europe. <https://doi.org/10.64898/2026.01.03.697426>.
- Trombetta, C.M., Marchi, S., Manini, I., 2019. Influenza D Virus: serological evidence in the Italian population from 2005 to 2017. *Viruses* 12, 30.
- Trombetta, C.M., Marchi, S., Marotta, M.G., Moreno, A., Chiapponi, C., Montomoli, E., Lanave, G., Camero, M., Martella, V., 2024. Detection of Influenza D antibodies in dogs, Apulia Region, Italy, 2016 and 2023. *Emerg. Infect. Dis.* 30, 1045–1047. <https://doi.org/10.3201/eid3005.231401>.
- Trombetta, C.M., Montomoli, E., Di Bartolo, I., 2022. Detection of antibodies against influenza D virus in swine veterinarians in Italy in 2004. *J. Med. Virol.* 94, 2855–2859. <https://doi.org/10.1002/jmv.27466>.
- Woolhouse, M.E.J., Gowtage-Sequeria, S., 2005. Host range and emerging and reemerging pathogens. *Emerg. Infect. Dis.* 11, 1842–1847. <https://doi.org/10.3201/eid1112.050997>.
- Yu, J., Li, F., Wang, D., 2021. The first decade of research advances in influenza D virus. *J. Gen. Virol.* 102, jgv001529. <https://doi.org/10.1099/jgv.0.001529>.
- Zhai, S.L., Zhang, H., Chen, S.N., 2017. Influenza D virus in animal species in Guangdong Province, southern China. *Emerging Infect. Dis.* 23, 1392–1396. <https://doi.org/10.3201/eid2308.161667>.