



ALMA MATER STUDIORUM
UNIVERSITÀ DI BOLOGNA

ARCHIVIO ISTITUZIONALE
DELLA RICERCA

Alma Mater Studiorum Università di Bologna Archivio istituzionale della ricerca

A review of potential risk factors linked to shiga toxin-producing *Escherichia coli* (STEC) in wild deer populations and the practices affecting the microbial contamination of wild deer carcasses with enteric bacteria

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version:

Soare, C., McNeilly, T.N., Seguino, A. (2021). A review of potential risk factors linked to shiga toxin-producing *Escherichia coli* (STEC) in wild deer populations and the practices affecting the microbial contamination of wild deer carcasses with enteric bacteria. *FOOD CONTROL*, 127, 1-9 [10.1016/j.foodcont.2021.108128].

Availability:

This version is available at: <https://hdl.handle.net/11585/964767> since: 2024-03-01

Published:

DOI: <http://doi.org/10.1016/j.foodcont.2021.108128>

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>).
When citing, please refer to the published version.

(Article begins on next page)

1 **A review of potential risk factors linked to Shiga toxin-producing *Escherichia coli***
2 **(STEC) in wild deer populations and the practices affecting the microbial**
3 **contamination of wild deer carcasses with enteric bacteria**

4 **Cristina Soare**

5 The Royal (Dick) School of Veterinary Studies and Roslin Institute, Edinburgh University,
6 Easter Bush Campus, Roslin, Midlothian, EH25 9RG

7 **Tom N McNeilly**

8 Moredun Research Institute, Pentlands Science Park, Bush Loan, Penicuik, Midlothian,
9 EH26 0PZ

10 **Alessandro Seguíno**

11 The Royal (Dick) School of Veterinary Studies and Roslin Institute, Edinburgh University,
12 Easter Bush Campus, Roslin, Midlothian, EH25 9RG

13
14 **Abstract**

15 In modern food industry settings, pathogenic microorganisms such as Shiga-toxin producing
16 *Escherichia coli* (STEC) cause global public health concerns. Foodborne infections with STEC are
17 common, and sporadically linked to venison consumption. This article reviews the scientific literature
18 on wild deer culled for human consumption, to outline the factors that influence the carriage of STEC
19 in the intestines of wild deer species and the practices that lead to venison contamination. It
20 discusses the potential risk factors, from culling on the hill to final packaging, linked to this pathogen.
21 The review found important variables influencing the presence of STEC in deer carcasses and
22 venison. Many of these were unrelated to human intervention, being generally linked to the condition
23 of the live animal and the probability of bacterial shedding. Other factors influencing STEC presence
24 related to the management of the environment and dressing hygiene practices, both of which can be
25 optimised to reduce the risk of contamination. We also highlight gaps in the current understanding of
26 the risk related to parts of the wild venison chain that could impact on the microbial quality of food
27 products derived from wild deer carcasses. An industry approach that considers integrating the
28 scientific evidence collated in this review into the traditional knowledge of the hill-to-fork chain would
29 assist in adapting the businesses' food safety management system to better mitigate the possibility of
30 STEC contamination in venison products intended for human consumption.

31 **Keywords**

32 Deer, wild ruminant, venison, food safety, *E. coli*

33 **Highlights**

- 34 • Warm ambient temperatures are associated with higher STEC shedding in wild deer
- 35 • High deer population density, exposure to other ruminants increase STEC shedding
- 36 • Abdominal wounding and intestinal tears increase the risk of STEC transfer to meat
- 37 • Contamination may be more difficult to avoid in larger, male wild deer carcasses
- 38 • Contamination from the terminal rectum may have greater food safety implications

39 **Abbreviations**

40 AGHE: approved game-handling establishment

41 GI: gastrointestinal

42 HACCP: Hazard Analysis and Critical Control Points

43 STEC: Shiga toxin-producing *Escherichia coli*

44 Stx: Shiga toxin

45 **1. Introduction**

46 *Escherichia coli* are commensals of the intestinal microbiota of healthy animals (Tenailon,
47 Skurnik, Picard, & Denamur, 2010). Most of these bacteria are harmless to humans (Kaper,
48 Nataro, & Mobley, 2004); however, some *E. coli* strains, referred as Shiga toxin-producing *E*
49 *coli* (STEC), are able to produce one or multiple subtypes of Shiga-like toxins (Stx),
50 properties that influence their ability to become hazardous to humans (Buvens et al., 2012).
51 Clinical manifestations vary from mild diarrhoea to haemorrhagic gastrointestinal disease or
52 life-threatening haemolytic uraemic syndrome, particularly in children and older people
53 (Thorpe, 2004; WHO, 2017).

54 The STEC serogroup responsible for most human cases is O157 (Majowicz et al., 2014),
55 although in recent years, outbreaks associated with non-O157 STEC serogroups have been
56 increasing in North America (Gould et al., 2013). Similar trends were observed in Europe
57 following a large outbreak of *E. coli* O104:H4 (Buchholz et al., 2011), which prompted the
58 European Food Safety Authority (EFSA) to review the surveillance systems and their ability
59 to detect non-O157 STEC (EFSA, 2013).

60 The global incidence of STEC infections is estimated to be around 2.5 million acute illnesses
61 annually (Majowicz et al., 2014), of which around 50% are attributable to food consumption,
62 excluding water, which causes around 10% of illnesses (Hald et al., 2016). Contaminated
63 beef is the major source of STEC transmission globally, except for South Asia, where the
64 meat of small ruminants is the main food source (Hoffmann et al., 2017). Cattle can be
65 colonised at the recto-anal junction without manifesting clinical disease (Naylor et al., 2003).
66 Small ruminants and deer may also be colonised with STEC (Ferens & Hovde, 2011).

67 Wild deer can excrete in faeces both O157 (Díaz-Sánchez et al., 2013; García-Sánchez et
68 al., 2007; Synge, 2006) and non-O157 STEC types, all of which are potentially pathogenic
69 for humans (Dias, Caetano, Torres, Fonseca, & Mendo, 2019; Díaz-Sánchez et al., 2013;
70 Franklin et al., 2013; Mora et al., 2012; Szczerba-Turek et al., 2020). The implication is that
71 meat of colonised deer could accidentally become contaminated with STEC during slaughter
72 or processing. The safety of wild venison, as of other meats, therefore depends, among
73 other factors, on control of visual contamination at harvest and during production (Heuvelink,
74 Roessink, Bosboom, & de Boer, 2001).

75 Wild deer meat is increasingly appreciated as an environmentally sustainable source of food
76 (Serrano et al., 2020). While it is highly nutritious (Bureš, Bartoň, Kotrba, & Hakl, 2015),
77 occasional contamination of wild venison with STEC has been observed (Díaz-Sánchez et
78 al., 2012; Martin & Beutin, 2011; Miko et al., 2009). A significant risk for acquiring STEC
79 infection is consumption of either raw, undercooked or cured/cold meat cuts (Mughini-Gras
80 et al., 2018); thus, consumer habits may play a role. Several foodborne outbreaks have been
81 linked to the handling of raw meat or the consumption of undercooked wild deer cuts
82 contaminated with STEC O157:H7 (Ahn et al., 2009; Rabatsky-Ehr et al., 2002) or STEC
83 non-O157 (Rounds et al., 2012). A more recent outbreak occurred in Scotland, and was
84 linked to the consumption and handling of raw wild venison contaminated with *E coli* O157
85 (Smith-Palmer et al., 2018). Different from previously observed STEC outbreaks, which
86 tended to be smaller and related to individually prepared deer carcasses, the Scottish
87 outbreak was notable, with 12 patients affected, due to the implicated product being
88 commercially produced and widely distributed via the retail chain.

89 The role of wild deer as a reservoir, and the recent outbreaks warrant public health
90 concerns. Wild venison intended for human consumption is the product of hunting activities

91 and of the welfare necessity to control wild deer population density (Ramanzin et al., 2010).
92 While conforming to hygiene requirements, the processing of deer carcasses undergoes
93 different procedures than for livestock (Casoli, Duranti, Cambiotti, & Avellini, 2005). The
94 differences in the wild game food chain, along with deer host biological characteristics,
95 create some gaps in the current understanding of the factors that contribute to STEC
96 contamination of wild venison. Further to this, the aforementioned Scottish outbreak also
97 identified a lack of knowledge on the microbial risks for wild deer carcasses processed
98 commercially and sold via the retail chain. This prompted a literature review to identify where
99 the highest chance(s) of cross contamination might occur for wild deer carcasses and
100 venison thereof. The objective of this scoping review was therefore to identify risk factors
101 that could influence STEC shedding in live deer. A second aim was to evaluate the steps
102 involved in wild deer processing to discuss the variables influencing microbial contamination
103 with STEC and other enteric bacteria of carcasses and meat.

104

105 **2. Method**

106

107 We searched our institutional electronic library, which is linked to the scientific publication
108 databases PubMed, Scopus, Web of Science, Directory of Open Access Journals, Science
109 Direct and JSTOR. The search terms were: game, deer, wild ruminant*, wild cervid*,
110 venison, food handling, processing, hygiene, carcass, contamination, shiga, verotoxin,
111 STEC, VTEC, *E. coli*. The search strings were constructed with the Boolean operator 'OR'
112 between synonymous terms representing the species, and connected with 'AND' between
113 further key areas of the venison food chain. The first step of the literature review used a
114 short string built with the Boolean operator 'AND' between the synonymous words of the
115 species concerned, in combination with one other keyword added to the string with the
116 Boolean operator 'OR'. The selected time interval was from January 2006, which was the
117 date of the European Hygiene legislation entering into force, to January 2020. All results
118 were reviewed by title, and where the title indicated the publication was relevant for the
119 search, the abstract was also reviewed. Further review included the bibliographies of
120 selected publications.

121 The findings were linked to the following areas of the venison food production chain: (1) the
122 condition of live deer; (2) hunting practices; (3) transportation and extraction of the
123 carcasses; and (4) hygiene practices during further processing of carcasses and meat. Each
124 of these factors will now be discussed in detail.

125

126 **3. Literature review findings**

127 **3.1. Live deer**

128 It is beyond the scope of this literature review to expand on aspects of the pathophysiology
129 of deer; however, some key traits that might affect the health status of the animals will be
130 discussed, since they could influence STEC colonisation of the intestinal tract and shedding
131 of STEC in faeces.

132 The ability of deer to shed STEC in faeces is discussed from the perspective of transmission
133 rates between animals due to increased environmental faecal contamination, as well as a
134 possibility of carcass contamination during the slaughter process via accidental faecal
135 contamination, although the latter is likely to be influenced more directly by levels of STEC
136 within the intestinal tract.

137 3.1.1 Body condition and co-infection

138 In cattle, stress or the negative energy balance subsequent to lactation may result in higher
139 STEC shedding (Venegas-Vargas et al., 2016). Wild deer, particularly red deer, are known
140 to experience cold stress (Simpson, Webster, Smith, & Simpson, 1978). They enter a period
141 of a metabolic slowdown in winter, mobilising most of the body fat towards the energy
142 production needed to regulate core temperature (Turbill, Ruf, Mang, & Arnold, 2011). This is
143 thought to have a negative impact on the optimal allocation of energy devoted to mount
144 effective immune responses (Houston, McNamara, Barta, & Klasing, 2007), which can
145 predispose animals to infections (Smith, 2007). In support of this concept, it was shown that
146 wild bovids with inadequate diet, particularly reduced protein intake, have higher
147 gastrointestinal (GI) parasite burdens (Ezenwa, 2004). Conversely, extensive research in a
148 wild sheep population has found that animals in good body condition are able to invest in
149 improved immune defence, as reflected by reduced GI parasite burdens and increased
150 levels of circulating natural antibodies (Nussey et al., 2014).

151 Specific research looking at the impact of the host's body condition, health status and
152 immune suppression on STEC infections in deer is lacking. However, in cattle co-infection
153 with *Fasciola hepatica*, a parasitic trematode with the capacity to modulate the host's
154 immune response, has been linked with increased risk of shedding STEC O157 (Howell et
155 al., 2018). All deer species, red deer in particular, are well adapted hosts for *Fasciola*
156 *hepatica* throughout mainland Europe (Alasaad et al., 2007; Arias et al., 2012) and the UK
157 (French et al., 2016), with these infections often occurring simultaneously with other helminth
158 infections (Albery et al., 2018; O'Toole et al., 2014). Although red deer may not express
159 overt clinical signs of parasitism, an association has been observed between poorer body
160 conditions and relatively low levels of GI parasites (Irvine, Corbishley, Pilkington, & Albon,
161 2006).

162 While this review could not retrieve evidence from the literature of a direct link between body
163 condition, co-infection and STEC shedding in deer, the cumulative evidence presented here
164 indicates that further research in this area is warranted. In accordance with the European
165 Regulation No. 853/2004, people who hunt wild game for human consumption must acquire
166 sufficient knowledge for an initial examination by undertaking formal training that covers
167 normal as well as abnormal anatomy, physiology, behaviour and pathological changes in
168 wild game due to diseases. The trained hunter plays an important role by carefully selecting
169 for human consumption only deer that display normal anatomy, physiology and behaviour.
170 Therefore, if the health status of deer is a risk factor for STEC shedding, it may already be
171 well controlled by the rejection of weak, emaciated or heavily parasitised animals from the
172 food chain.

173 3.1.2 Shared ecosystems

174 Common origin or ruminant interspecies spread of genetically similar *E. coli* O157:H7 have
175 been initially shown by Sánchez and others (2010). The transmission of STEC between
176 domestic and wild ruminants has further been demonstrated through the isolation of STEC
177 with highly similar genetic profiles from both cattle and deer (Mora et al., 2012; Singh et al.,
178 2015) as well as from sheep and deer (Sánchez et al., 2012).

179 Interaction between domestic and wild ruminants influences the prevalence of STEC in the
180 respective species. Faecal shedding of STEC in deer was observed to be significantly higher
181 in areas with an overabundance of game and domestic large ruminants (Díaz-Sánchez et
182 al., 2013). Equally, two beef herds showed higher likelihoods of STEC carriage when in
183 frequent contact with wild deer and other wildlife (Venegas-Vargas et al., 2016), suggesting
184 that circulation of STEC is bidirectional between ruminant species.

185 STEC can survive from days to months, in various substrates such as faeces, soil and
186 pooling water (Ogden et al., 2002). Drinking contaminated water and foraging in green
187 spaces irrigated with untreated water can thus enable transmission (Franklin et al., 2013). It
188 is apparent from this literature search that both wild deer and domestic ruminants act as
189 reservoir species (Díaz-Sánchez et al., 2013), enabling the maintenance of the bacteria in
190 environments and contributing to horizontal transmission in a shared habitat via grazing
191 territories.

192 3.1.3. Wild deer population density

193 Similar to other species, deer being in close proximity, such as may occur due to crowding at
194 feeding sites, has been suggested to increase horizontal transmission of STEC via the oral
195 ingestion of food contaminated with faeces. This hypothesis is supported by the isolation of
196 identical STEC strains from the tonsils and faeces of both the same and different deer
197 sharing feeding spaces (Eggert et al., 2013). STEC occurrence has been linked to a
198 population density of above 15 wild deer per square kilometre (Díaz-Sánchez et al., 2013).
199 Higher STEC intestinal colonisation due to population density pressure is also suggested by
200 Laaksonen and colleagues (2017), who observed lower STEC prevalence in areas with low
201 reindeer population density. These observations are likely to reflect environmental
202 contamination with STEC.

203 3.1.4 Seasonality

204 A positive relationship between STEC shedding and warmer ambient temperature has been
205 observed in deer, similarly to research carried out in cattle (Henry et al., 2017; Oliver, 2014)
206 and sheep (Evans et al., 2011). Higher STEC shedding was observed in the faeces of elk
207 during warm summer months (Franklin et al., 2013) and white-tailed deer (Singh et al.,
208 2015).

209 The association with summer season is thought to be a function of higher shedding rates,
210 likely due to changes to the diet composition (Delgado et al., 2017) and increased pathogen
211 proliferation in the environment at warmer ambient temperatures (Franklin et al., 2013).
212 While these findings offer some understanding of the climate and ecology of deer species in
213 North America, it cannot assert whether roe and red deer – the main species entering the
214 European food chain (Schulp, Thuiller, & Verburg, 2014) – follow the same ecology.
215 Research in this area would be beneficial.

216 3.1.5 Species

217 It has been unclear to date whether certain deer species are more likely to shed STEC.
218 Several authors observed no significant differences in the faecal prevalence of STEC
219 between red and roe deer (Bardiau et al., 2010; Eggert et al., 2013; Obwegeser, Stephan,
220 Hofer, & Zweifel, 2012). Other studies have reported a higher prevalence of STEC in red
221 deer than roe deer (Dias et al., 2019; Sánchez et al., 2009), although this lack of consistency
222 could also be due to the low roe deer sample sizes used. A larger study detected STEC
223 O157 in more rectal swabs from red deer than roe deer (Szczerba-Turek et al., 2020).

224 Obwegeser and colleagues (2012) observed that red deer isolates were more commonly
225 encoding Shiga toxin type 2 (*Stx2*), which is generally more pathogenic than *Stx1* (Buvens et
226 al., 2012). One of the *Stx2*-positive isolates was also positive for the *eae* gene, an important
227 virulence factor involved in bacterial attachment to the intestinal epithelium (Brooks et al.,
228 2005). *Stx2* genes were also found in all four isolates from red deer but only in one of the
229 two isolates from roe deer, although these were subtype *stx2b*, commonly associated with
230 mild human disease, and subtype *stx2g*, which has not been associated with human disease
231 (Dias et al., 2019). Work by Szczerba-Turek and others (2020) found two STEC strains,

232 isolated from one roe and one red deer, that were positive for both *stx2a* and *eae*, a
233 virulence profile associated with more severe forms of human disease (FAO, WHO, 2018).
234 These findings suggest that both red deer and roe deer carry STEC strains potentially
235 pathogenic to humans. The available research data are insufficient to conclude whether one
236 of these species carries higher levels or more harmful STEC than the other. Few studies
237 report isolates of STEC in the faeces of fallow deer (Sánchez et al., 2009; Szczerba-Turek et
238 al., 2020), suggesting that this species carries STEC, but the limited sample sizes do not
239 allow a meaningful comparison with red and roe deer.

240 3.1.6 Sex

241 Sex was suggested to be a factor affecting the intestinal microbiota of wild-tailed deer due to
242 differences in the movement range and feeding behaviour between males and females.
243 However, the study investigating this relationship showed that there was no significant
244 difference in gut content associated with sex (Delgado et al., 2017). By comparing the sexes
245 in red and roe deer, Eggert and colleagues (2013) observed that *Stx* genes were detected
246 more frequently in *E. coli* isolated from the faecal samples of male red deer (8/10; 80%) than
247 of females (13/20; 65%). In roe deer the *Stx* gene was detected more frequently in faeces
248 collected from females (9/10; 90%) than males (7/10; 70%), but these sex differences were
249 not significantly different (Eggert et al., 2013). Similarly, other studies have consistently
250 failed to identify any differences in the proportion of *Stx*-positive faecal samples between
251 male and female deer. Bardiau and colleagues (2010) found no significant difference in the
252 proportion of *Stx*-positive faecal samples in male (9/58; 15.5%) and female (11/75; 14.7%)
253 deer, irrespective of species, and Díaz-Sánchez and others (2013) also reported no
254 statistical significance in *Stx* carriage between red male deer (50/120; 41.7%) and female
255 red deer (32/67; 47.8%).

256 Cumulatively, these data suggest that there is little evidence that sex influences the
257 shedding of STEC, although most studies used relatively small sample sizes; further
258 research in this area is thus required.

259 **3.2 Hunting practices**

260 Hunting methods vary, depending on terrain, traditions and the deer species. The driven
261 hunts, particularly those using dog packs, where wild deer are actively pursued, is discussed
262 to increase ante-mortem stress, which may favour the translocation of STEC from the
263 colonised gut to sterile organs and muscles. A similar translocation effect is thought to occur
264 when deer are only wounded initially due to increased pain and stress (Bartels & Bülte,
265 2011).

266 In the European community, the same hygiene provisions as for domestic livestock regulate
267 the culling of wild ungulates, namely Regulation (EC) No 852/2004, on general requirements
268 for production of food of animal origin and Regulation (EC) No 853/2004 outlining specific
269 hygiene rules for food of animal origin. There are additional guidelines produced by the
270 industry on appropriate harvesting methods.

271 The small body of research that offers some understanding of the effects of hunting
272 operations and primary dressing is synthesised below, highlighting the steps that appear
273 more critical concerning the risk of STEC contamination of the deer carcass in field
274 conditions.

275 3.2.1 Wounding accuracy

276 Recommended shooting procedures aim to achieve a rapid death, minimising the suffering
277 of deer, which in turn facilitates the easy retrieval of game (Casoli et al., 2005; Laaksonen &
278 Paulsen, 2015).

279 Abdominal shots are discouraged (Gill, 2007; Ramanzin et al., 2010) due to welfare
280 concerns and a significant risk of carcass contamination. Shooting to any position posterior
281 to the sixth rib will, in most cases, cause visible contamination of the carcass (Urquhart &
282 McKendrick, 2006), jeopardising hygiene through the spread of the endogenous gut
283 microflora, including potentially pathogenic microorganisms such as STEC (Bartels & Bülte,
284 2011).

285 It is generally accepted that the muscles and deep tissues of healthy animals are sterile (Gill
286 & Penney, 1977). It is also thought that the bullet might become a fomite, introducing
287 pathogens from the hide (Paulsen, 2011), or from the gastrointestinal tract if the shooting
288 lacerates the intestines (Gill, 2007).

289 Deer carcasses with abdominal wounds were shown to have 0.2–0.6 cfu/cm² higher
290 Enterobacteriaceae counts than those with no abdominal wounds (Atanassova, Apelt, Reich,
291 & Klein, 2008). On assessing the microflora of over 300 wild deer carcasses, Obwegeser
292 and colleagues (2012) found Enterobacteriaceae in 90% of samples. The authors suggested
293 these results were partly linked to the difficulty of hygienic evisceration in the field, especially
294 if the shooting affected the integrity of the gastrointestinal tract. Abdominal shooting was also
295 recently shown to be statistically associated with high *E. coli* counts in moose and white-
296 tailed deer (Sauvala et al., 2019). As *E. coli* and STEC are part of the Enterobacteriaceae
297 family (Paton & Paton, 1998), these observations offer indirect evidence that STEC might
298 contaminate deer carcasses via abdominal wounding. In a STEC outbreak linked to venison
299 consumption, abdominal shot was thought to be the cause of wild venison contamination
300 (Rabatsky-Ehr et al., 2002b), which further supports evidence of STEC risk.

301 3.2.2 Evisceration

302 For food safety purposes, the evisceration of deer, or gralloching, is carried out at the place
303 of cull, with the aim of removing viscera that may cause contamination and deterioration if
304 left within the carcass, particularly if the gastrointestinal tract was damaged, and with the
305 scope of lowering the carcass temperature.

306 3.2.2.1 Delayed evisceration

307 Several publications describe delayed evisceration as an opportunity for increased carcass
308 microbiological contamination (Casoli et al., 2005; Gill, 2007). One of the concerns is that
309 digestive flora will continue to ferment, resulting in a bloated digestive tract and an increased
310 possibility of faecal contamination during evisceration, through inadvertent puncture of the
311 intestinal tract.

312 The observations of Atanassova and colleagues (2008) suggest that the evisceration of
313 “expertly shot” deer within 90 minutes results in carcasses of superior microbiological quality.
314 The European Hygiene Regulation (EC) No 853/2004 requires wild large game to be
315 eviscerated “as soon as possible”, enabling member countries to establish an appropriate
316 timeframe. Other intervals recommended for hygienic evisceration include a maximum of two
317 hours after shooting (Deutz & Fötschl, 2014), or no longer than one hour (Laaksonen &
318 Paulsen, 2015). The outdoor temperature during the culling process is important since mild
319 or warm environments are likely to speed up microbial multiplication, necessitating prompt
320 evisceration.

321 One of the concerns around delayed evisceration is that intestinal bacteria may penetrate
322 the gut lining and contaminate muscle tissue after a few hours from killing (Ramanzin et al.,

323 2010). This concern might not be substantiated, as suggested by the study of Gill and
324 colleagues (1978), which showed bacteria do not leave the intestinal lumen until there is a
325 form of tissue disruption or breakdown produced by proteolytic enzymes, which occurs at
326 least 24 hours post-mortem.

327 3.2.2.2 Gastrointestinal perforation

328 Microbiological testing of wild deer carcasses (Avagnina et al., 2012; Obwegeser et al.,
329 2012) suggests that handling practices during harvesting play an important role in
330 determining initial enteric microbial counts, including of *E. coli*, on carcasses, impacting on
331 the safety of meat, a concept also reinforced by Gill (2007), and Ramanzin and colleagues
332 (2010). The microbial contamination was significantly associated with improper evisceration
333 procedures (Avagnina et al., 2012) that lead to faecal contamination (Obwegeser et al.,
334 2012). Based on personal observations of multiple gralloching techniques, it can be seen
335 that spillage of gastrointestinal contents can also occur, due to hunter-independent reasons,
336 such as distended forestomach with excessive food content or juvenile deer having tissues
337 that tear more easily.

338 In deer, *E. coli* are primarily found in the microbiota of the colon (Li et al., 2014). It is not yet
339 known whether STEC O157 in deer, similar to cattle, mainly colonise the mucosal epithelium
340 at the recto-anal junction (Naylor et al., 2003) and whether this is associated with high ($>10^3$
341 CFU/g faeces) shedding of STEC O157, as is seen in cattle (Chase-Topping, Gally, Low,
342 Matthews, & Woolhouse, 2008). However, if colonisation of STEC O157 is similar between
343 deer and cattle, it would be expected that the main risk of contamination came from spillage
344 of the colon or rectal contents during gralloching. Thus, great care should be taken to
345 minimise contamination of the carcass from gut contents arising from the lower intestinal
346 tract.

347 To rectify contamination, some hunters are committed to old traditions such as washing
348 carcasses with water from streams or canals (Avagnina et al., 2012). However, these
349 practices might lead to further contamination spread on the carcass (Anderson, Marshall, &
350 Dickson, 1991), or the water can become an additional source of nonvisual contamination, if
351 polluted with pathogens from local deer or other ruminants (Probert, Miller, & Ledin, 2017).

352 According to European Hygiene Regulation 853/2004, the carcasses of wild ungulates
353 intended to be marketed for human consumption must be subjected to an initial examination
354 by a person who has undergone training with regards to hygiene techniques applicable to
355 handling, transportation, evisceration as well as training to recognise environmental
356 contamination, and other factors that might affect human health after consumption. To this
357 extent the trained hunter can ascertain through the provision of a 'hunter declaration' which
358 accompanies the carcass of wild ungulate, that it does not present environmental
359 contamination or abnormalities that might affect human health after consumption. Article 5 of
360 Regulation (EC) 852/2004 on the hygiene of foodstuffs requires that food business operators
361 of the AGHEs must identify and control food hazards, including pathogenic bacteria that
362 might originate from faecal contamination, through the implementation of Hazard Analysis
363 and Critical Control System (HACCP). Therefore, any light contamination with
364 gastrointestinal contents must be removed by prompt trimming of the contaminated area with
365 a clean knife, making sure that a wide margin of uncontaminated tissues is also removed..
366 The principles of the HACCP dictate that wild deer carcasses extensively contaminated with
367 gastrointestinal contents must be rejected for human consumption (Food Standards Agency,
368 2008).

369 **3.3 Extraction and transport along the food chain**

370 Due to the terrain where wild deer thrive, it is not always possible to immediately load the
371 eviscerated carcasses into a vehicle. In Europe, smaller roe deer can be dragged into a
372 “drag bag”, or carried in a “roe sac”. Larger, heavier deer are extracted either by manual
373 dragging, or, in rare instances, in countries such as Scotland, by loading them onto a pony.

374 3.3.1 The influence of extraction practices

375 To the extent of this literature search, there were no specific risk factors linked to STEC
376 contamination during extraction and transport. However, dragging of freshly gralloched
377 carcasses could present a risk of contamination with environmental materials such as soil
378 and vegetation (Laaksonen & Paulsen, 2015). Consequently, if the environment contains
379 ruminant faeces, dragging could result in STEC contamination.

380 Stacking of deer carcasses is prohibited by the European Hygiene Regulation 853/2004,
381 given that this practice has an insulating effect, particularly for carcasses in the middle of the
382 heap. Equally, this practice promotes cross-contamination during transport. Vehicles should
383 therefore enable hygienic extraction such that wild deer carcasses do not touch and air can
384 freely circulate to enable cooling (Bekker, Hoffman, & Jooste, 2011).

385 3.3.2 Temperature controls

386 In wild game settings, active chilling begins at the collection centre or approved game-
387 handling establishment (AGHE). The time elapsed from hunting to chilling largely depends
388 on the remoteness of the hunting place and its proximity to the collection centre or AGHE.
389 Hygiene Regulation (EC) No. 853/2004 states: “where climatic conditions so permit, active
390 chilling is not necessary”. When the deer-hunting season coincides with colder ambient
391 temperatures, below the recommended chilling temperature for red meat (7°C), the effect of
392 the outdoors is less concerning. In turn, it was observed that during summer months,
393 ambient temperatures of 17.8±1.2°C significantly influenced the growth of
394 Enterobacteriaceae on the surface of game carcasses lacking visual contamination (Paulsen
395 & Winkelmayr, 2004). Subsequent cooling of carcasses at near-freezing temperatures (e.g.
396 0.4°C) prevented additional bacterial growth for four days, but the counts that accompanied
397 the carcasses going into storage persisted (Paulsen, 2011; Paulsen & Winkelmayr, 2004).
398 Therefore, a key hygiene factor is establishing a cold chain as soon as practicably possible
399 to maintain lower microbiological counts. Once established, an uninterrupted cold chain must
400 be kept to prevent bacterial growth (EFSA, 2014).

401 Countries such as Austria have developed procedures where chilling should start a
402 maximum 12 hours from culling (Paulsen, 2011). In South Africa, the Meat Safety Act No. 40
403 requires partially dressed carcasses to undergo chilling within 12 hours of hunting, to a
404 temperature not exceeding 7°C.

405 Another hygiene risk might arise when new carcasses are brought into the collection centre,
406 and warm bodies are hung close to already chilled ones, particularly in facilities with
407 insufficient ventilation, as the dampness from the warm body increases the humidity and so
408 moisture on the surface of the chilled carcasses. An experimental study has shown that
409 fluctuating temperatures and fluctuating water activity result in a growth response translating
410 into an increase in *E. coli* culturable cell numbers (Mellefont, Kocharunchitt, & Ross, 2015).
411 An alternative to avoiding moisture on carcasses is to combine a short pre-cooling phase, at
412 temperatures of around 10°C, with the use of professional cooling facilities, which enable
413 effective ventilation and dehumidification (Paulsen, 2011).

414 Cumulatively, this information suggests that contamination of wild game carcasses with
415 enteric bacteria is more likely to occur in summer, which is also the season associated with
416 increased STEC faecal shedding (Franklin et al., 2013; Singh et al., 2015). Stricter hygiene
417 and faster cooling should thus be sought to prevent contamination.

418

419 **3.4 Hygiene practices along the food chain**

420 The procedures applicable to venison differ depending on whether the carcasses are
421 intended for higher-throughput facilities or are sold on the small-throughput, local market,
422 which is exempt from the European Hygiene Regulations, allowing the resulting small
423 quantities of wild deer carcasses and venison to be sold locally without passing through
424 AGHEs (FSA & FSS, 2018). In line with the aims of this review, this section refers to the wild
425 deer food chain that falls under the European legislation since this represents the wild game
426 meat sold widely for human consumption via large retailers or the export market.

427 3.4.1 Length of time for primary storage of carcasses

428 The storage of skin-on carcasses is an accepted practice, as part of the maturation and the
429 development of characteristic game flavour (Soriano et al., 2016). The time in storage of
430 unskinned carcasses may vary. While storage intervals of 1–4 days for maturation purposes
431 have been described (Soriano et al., 2016), up to 20-day intervals have also been observed
432 (Gill, 2007; Laaksonen & Paulsen, 2015). Recently, Sauvala and colleagues (2019) showed
433 that the storage time (0–9 days) was statistically associated with *E. coli* counts on white
434 tailed deer carcasses.

435 It is generally accepted that the muscle surface remains protected by the skin, if stored
436 hygienically, but it should be considered that STEC are able to withstand chilling (Mann &
437 Brashears, 2006). Evidence from studies of *E. coli* on beef carcasses suggests that the
438 reductions of *E. coli* growth following effective chilling conditions can be temporary and that
439 after around 40 hours, bacterial growth can start to increase as the bacteria adapt to the new
440 environmental conditions (King, Kocharunchitt, Gobius, Bowman, & Ross, 2016; Mellefont et
441 al., 2015). Therefore, it is expected that some STEC will survive during storage, more so if
442 not all the contamination is rectified by generous trimming on arrival and if there are
443 breaches in the cold chain.

444 3.4.2 Skinning

445 Removal of the skin occurs at the AGHE before the carcass undergoes further trimming and
446 final veterinary inspection. Skinning has been discussed repeatedly as an important step in
447 ensuring the hygiene of wild game carcasses (Atanassova et al., 2008; Avagnina et al.,
448 2012; Casoli et al., 2005; Gill, 2007; van Schalkwyk, Hoffman, & Laubscher, 2011). Some
449 evidence that skinning can result in *E. coli* contamination of game carcasses comes from the
450 study of Gouws and colleagues (2017). Swabs taken from the incision line immediately after
451 evisceration were negative for *E. coli* but, following skinning, up to 42% of carcasses
452 displayed *E. coli* contamination, suggesting that improper execution of the skinning can
453 result in carcass contamination with *E. coli*.

454 In cattle, a number of studies have examined the influence of visual cleanliness on carcass
455 microbial load, including Enterobacteriaceae, generic *E. coli* and STEC O157 (Antic et al.,
456 2010; Blagojevic, Antic, Ducic, & Buncic, 2011, 2012). Using a four-category visual
457 cleanliness scoring scheme, based on an adaptation of the UK Clean Livestock Policy,
458 Blagojevic and colleagues (2012) showed that category 4 (very dirty) cattle presented
459 significantly higher Enterobacteriaceae compared with cleaner categories (1–3), and a
460 greater proportion of the category 4 carcasses were *E. coli* O157-positive. The observations
461 on slaughtering of cattle suggest that soiling or dry debris on the hide increase the risk of
462 presence of STEC on the carcass (Blagojevic et al., 2012).

463 Another study exploring the ability of contaminated cattle hides to transfer bacteria to meat *in*
464 *vivo* found hide-to-meat transmission of generic *E. coli* occurred in 10% of contacts,

465 suggesting the transfer of about 1% of the total *E. coli* population on the hide to the meat
466 (Antic et al., 2010).

467 Specific procedures that have been described as influencing the transfer of pathogens from
468 the hide to the carcass include the pressure with which the hide is pulled during skinning
469 (Antic et al., 2010). Sudden pressure may produce aerosols that are likely to be taken up by
470 the freshly exposed, moist meat. A compounding problem is that deer skins are removed
471 from cold, set carcasses, which makes the process more forceful compared with working on
472 warm carcasses, due to rigor mortis and harder subcutaneous fat as a result of chilling.
473 Depending on the hunting season, which might overlap with moulting, skin removal can lead
474 more readily to hair contamination (Casoli et al., 2005).

475 3.4.3 Further dressing and processing

476 In other species, there has been an emphasis on the role of faecal contamination, and zero
477 tolerance has been proposed as a tool in the control of STEC (Heuvelink et al., 2001).
478 Considering the type of dressing that wild venison undergo, it might not be possible to
479 achieve the same criteria as for livestock, yet minimal contamination should be aimed for.
480 Microbiological analysis in game carcasses, including roe and red deer, confirms that visible
481 faecal contamination on the body cavities was associated with significantly higher (median
482 0.97 log₁₀ cfu/cm²) counts of Enterobacteriaceae, compared with visually clean body cavities
483 (Paulsen & Winkelmayr, 2004). Similarly, Paulsen (2011) reports that Enterobacteriaceae
484 counts on visually contaminated abdominal cavities were an average of 1.6 log₁₀ cfu/cm²
485 higher in roe deer carcasses.

486 Regarding STEC, there is very limited evidence on its prevalence in deer carcasses. STEC
487 O157 was found in the faeces of red deer (4/264, 1.5%); however, no STEC O157 was
488 isolated from the carcasses sampled (Díaz-Sánchez et al., 2013). In contrast, this same
489 study found a higher faecal prevalence of non-O157 STEC (89/264, 34%) and a
490 correspondingly higher carcass prevalence of non-O157 STEC (19/271, 7%). The authors
491 concluded that the higher detection rate of non-O157 STEC on carcasses was a result of
492 faecal cross-contamination during carcass processing (Díaz-Sánchez et al., 2013). The
493 mechanisms of meat contamination during processing operations are similar for enteric
494 pathogens in all meat animal species (Nørrung & Buncic, 2008). Once operatives' hands, the
495 processing environment or the equipment become contaminated, this can contribute to the
496 spread of enteric pathogens, including STEC, during storage, boning or processing.

497 To the authors' knowledge, no studies have assessed in detail the hygiene practices during
498 venison dressing and cutting. Work in Switzerland identified that the processing
499 establishment was associated with Enterobacteriaceae contamination (Obwegeser et al.,
500 2012). A Finnish study confirmed that Enterobacteriaceae on the carcasses were associated
501 with the smaller facilities having only one room, although this was not statistically significant
502 for *E. coli* (Sauvala et al., 2019). Sauvala and colleagues (2019) also found that male wild
503 deer carcasses were significantly more often contaminated with *E. coli* than female
504 carcasses, which could be a consequence of the more difficult hygiene handling of male
505 carcasses, which are typically larger and heavier than females. In cattle, higher *E. coli*
506 counts have been interpreted as possibly resulting from cross-contamination of meat cuts by
507 meat handlers (Nel, Lues, Buys, & Venter, 2004). Increased handling of the beef product,
508 particularly if gloves are not worn or are made of fabric (Gill & Jones, 2002) may be a
509 contamination risk. An additional food safety concern is that naturally occurring pathogens
510 such as *E. coli* can persist on contact surfaces even after routine sanitation, particularly on
511 surfaces that are more difficult to access for debris removal and are less exposed to air
512 drying (Yang, Wang, He, & Tran, 2017).

513 **4. Conclusions**

514 This review highlights a complex journey between the hill source and the consumer's plate,
515 where food safety risks may exist at every step. The risk factors for STEC contamination in
516 venison are directly linked to the ability of the live animal to harbour these pathogens and,
517 further, to multifactorial steps related to dressing practices in field conditions, handling of the
518 venison during extraction, chilling and further cutting, as well as to the environment through
519 which wild deer carcasses pass. The available evidence suggests that STEC risk can be
520 most efficiently managed through interventions applied at the primary production combined
521 with later optimisation of the dressing and butchering hygiene. To efficiently control
522 foodborne pathogens such as STEC, a robust, continuous hill-to-fork food safety
523 management system should be in place. The risk consideration should not stop at the
524 hygiene possibilities along the food chain covered by this work, but should ultimately
525 consider consumers' attitudes and behaviours, which were not included in this review.

526 Although delivering pathogen-free carcasses to AGHEs might not be a realistic target under
527 the wild conditions of deer hunting, there are many factors that could be managed to deliver
528 minimally contaminated game to the game processors. The findings in the literature reinforce
529 the importance of accurate shooting, prompt evisceration, generous trimming of lightly
530 contaminated parts if contamination accidentally occurs, avoidance of excessive handling,
531 strict adherence to the cold chain, fast processing of venison carcasses and clean and dry
532 processing environments to control the occurrence of STEC during culling and processing.

533 Gaps identified in the literature include the lack of information on the role of extraction
534 practices on the microbiology of the carcasses. Further gaps result from a scarcity of data
535 regarding STEC carriage on deer carcasses, which would have offered a better baseline
536 understanding of the risks related to handling procedures influencing the STEC
537 contamination specifically. The great majority of the studies retrieved assessed the microbial
538 condition of deer carcasses by looking at other enteric bacteria, and focused more on the
539 impact of primary production in field conditions, thus offering less opportunity for discussion
540 of the factors linked to good manufacturing practices at collection centres and AGHEs.

541 In cattle, several studies have shown that the condition of the hide influences the condition of
542 the carcass. There are no studies to date, however, reporting the prevalence of STEC on
543 deer skins, and fieldwork in this area would be necessary to better understand whether
544 skinning processes have a role in contaminating deer carcasses with STEC. Following up
545 from these findings, a holistic research study that considers the risk of STEC contamination
546 from the primary source, and examines the handling practices along the food chain, from hill
547 to fork, would promote a better understanding of which of the above factors have a
548 significant impact on the STEC contamination of wild deer carcasses. These risk factors
549 should be considered in local circumstances, as applicable to the ecology and the species of
550 deer that are harvested for human consumption. This would assist the research community
551 and venison sector to work towards adapting food safety management systems to
552 contemporary changes, and improving consumer protection.

553

554 **Funding**

555 This work has been funded by Food Standards Scotland and the Scottish Government as
556 part of objective three of the project, 'The risk of STEC (Shiga toxin-producing *E. coli*)
557 contamination in wild venison', grant number CR/2016/26.

558 **Acknowledgements**

559 Many thanks go to Dr. Marianne James of Food Standards Scotland for her scientific
560 comments on the draft and for enabling us to undertake this work. The authors would like to
561 thank Mr. Richard Playfair for sharing his knowledge of the venison sector. Finally, thanks to
562 the independent editor Markus MacGill for reviewing the manuscript for clarity.

563

564 References

- 565 Ahn, C. K., Russo, A. J., Howell, K. R., Holt, N. J., Sellenriek, P. L., Rothbaum, R. J., ...
566 Tarr, P. I. (2009). Deer Sausage: A Newly Identified Vehicle of Transmission of
567 Escherichia coli O157:H7. *The Journal of Pediatrics*, 155(4), 587–589.
568 <https://doi.org/10.1016/j.jpeds.2009.02.051>
- 569 Alasaad, S., Huang, C. Q., Li, Q. Y., Granados, J. E., García-Romero, C., Pérez, J. M., &
570 Zhu, X. Q. (2007). Characterization of Fasciola samples from different host species and
571 geographical localities in Spain by sequences of internal transcribed spacers of rDNA.
572 *Parasitology Research*, 101(5), 1245–1250. <https://doi.org/10.1007/s00436-007-0628-2>
- 573 Albery, G. F., Kenyon, F., Morris, A., Morris, S., Nussey, D. H., & Pemberton, J. M. (2018).
574 Seasonality of helminth infection in wild red deer varies between individuals and
575 between parasite taxa. *Parasitology*, 145(11), 1410–1420.
576 <https://doi.org/10.1017/S0031182018000185>
- 577 Anderson, M. E., Marshall, R. T., & Dickson, J. S. (1991). Estimating depths of bacterial
578 penetration into post rigor carcass tissue during washing. *Journal of Food Safety*, 12(3),
579 191–198. <https://doi.org/10.1111/j.1745-4565.1991.tb00078.x>
- 580 Antic, D., Blagojevic, B., Ducic, M., Nastasijevic, I., Mitrovic, R., & Buncic, S. (2010).
581 Distribution of microflora on cattle hides and its transmission to meat via direct contact.
582 *Food Control*, 21(7), 1025–1029. <https://doi.org/10.1016/J.FOODCONT.2009.12.022>
- 583 Arias, M. S., Martínez-Carrasco, C., León-Vizcaíno, L., Paz-Silva, A., Díez-Baños, P.,
584 Morrondo, P., & Alonso, F. (2012). Detection of Antibodies In Wild Ruminants To
585 Evaluate Exposure To Liver Trematodes. *Journal of Parasitology*, 98(4), 754–759.
586 <https://doi.org/10.1645/ge-2804.1>
- 587 Atanassova, V., Apelt, J., Reich, F., & Klein, G. (2008). Microbiological quality of freshly shot
588 game in Germany. *Meat Science*, 78(4), 414–419.
589 <https://doi.org/10.1016/j.meatsci.2007.07.004>
- 590 Avagnina, A., Nucera, D., Grassi, M. A., Ferroglio, E., Dalmaso, A., & Civera, T. (2012).
591 The microbiological conditions of carcasses from large game animals in Italy. *MESC*,
592 91, 266–271. <https://doi.org/10.1016/j.meatsci.2012.01.025>
- 593 Bardiau, M., Grégoire, F., Muylaert, A., Nahayo, A., Duprez, J.-N., Mainil, J., & Linden, A.
594 (2010). Enteropathogenic (EPEC), enterohaemorrhagic (EHEC) and verotoxigenic
595 (VTEC) Escherichia coli in wild cervids. *Journal of Applied Microbiology*, 109(6), 2214–
596 2222. <https://doi.org/10.1111/j.1365-2672.2010.04855.x>
- 597 Bartels A, C., & Bülte M. (2011). Verotoxigenic Escherichia Coli (VTEC) in wild ruminants in
598 Germany. In A. S. F. J. . Paulsen Peter., Bauer A., Vodnansky M., Winkelmeier R.
599 (Ed.), *Game Meat Hygiene in Focus- microbiology, Epidemiology, Risk analysis and*
600 *quality assurance* (pp. 107–110). Wageningen, the Netherlands.
- 601 Bekker, J. L., Hoffman, L. C., & Jooste, P. J. (2011). Essential food safety management
602 points in the supply chain of game meat in South Africa. In *Game meat hygiene in focus*
603 (pp. 39–65). https://doi.org/10.3920/978-90-8686-723-3_2

- 604 Blagojevic, B., Antic, D., Ducic, M., & Buncic, S. (2011). Ratio between carcass-and skin-
605 microflora as an abattoir process hygiene indicator. *Food Control*, 22(2), 186–190.
606 <https://doi.org/10.1016/J.FOODCONT.2010.06.017>
- 607 Blagojevic, B., Antic, D., Ducic, M., & Buncic, S. (2012). Visual cleanliness scores of cattle at
608 slaughter and microbial loads on the hides and the carcasses. *Veterinary Record*,
609 (170(22)), 563. <https://doi.org/10.1136/vr.100477>
- 610 Brooks, J. T., Sowers, E. G., Wells, J. G., Greene, K. D., Griffin, P. M., Hoekstra, R. M., &
611 Strockbine, N. A. (2005). Non-O157 Shiga Toxin–Producing *Escherichia coli* Infections
612 in the United States, 1983–2002. *The Journal of Infectious Diseases*, 192(8), 1422–
613 1429. <https://doi.org/10.1086/466536>
- 614 Browning, L., Hawkins, G., Allison, L., & Bruce, R. (2016). *National Outbreak of Escherichia*
615 *coli* O157 Phage Type 32 in Scotland. Retrieved from
616 <http://www.hps.scot.nhs.uk/resourcedocument.aspx?id=2987>
- 617 Buchholz, U., Bernard, H., Werber, D., Böhmer, M. M., Remschmidt, C., Wilking, H., ...
618 Kühne, M. (2011). German outbreak of *Escherichia coli* O104:H4 associated with
619 sprouts. *New England Journal of Medicine*, 365(19), 1763–1770.
620 <https://doi.org/10.1056/NEJMoa1106482>
- 621 Bureš, D., Bartoň, L., Kotrba, R., & Haki, J. (2015). Quality attributes and composition of
622 meat from red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and Aberdeen Angus
623 and Holstein cattle (*Bos taurus*). *Journal of the Science of Food and Agriculture*, 95(11),
624 2299–2306. <https://doi.org/10.1002/jsfa.6950>
- 625 Buvens, G., De Gheldre, Y., Dediste, A., De Moreau, A. I., Mascart, G., Simon, A., ...
626 Piérard, D. (2012). Incidence and virulence determinants of verocytotoxin-producing
627 *Escherichia coli* infections in the Brussels-Capital Region, Belgium, in 2008-2010.
628 *Journal of Clinical Microbiology*, 50(4), 1336–1345. [https://doi.org/10.1128/JCM.05317-](https://doi.org/10.1128/JCM.05317-11)
629 11
- 630 Caprioli, A., Morabito, S., Brugère, H., & Oswald, E. (2005). Enterohaemorrhagic
631 *Escherichia coli*: emerging issues on virulence and modes of transmission. *Veterinary*
632 *Research*, 36(3), 289–311. <https://doi.org/10.1051/vetres:2005002>
- 633 Casoli, C., Duranti, E., Cambiotti, F., & Avellini, P. (2005). Wild ungulate slaughtering and
634 meat inspection. In *Veterinary research communications*.
635 <https://doi.org/10.1007/s11259-005-0028-y>
- 636 Chase-Topping, M., Gally, D., Low, C., Matthews, L., & Woolhouse, M. (2008). Super-
637 shedding and the link between human infection and livestock carriage of *Escherichia*
638 *coli* O157. *Nature Reviews Microbiology*, 6(12), 904–912.
639 <https://doi.org/10.1038/nrmicro2029>
- 640 Delgado, M. L., Singh, P., Funk, J. A., Moore, J. A., Cannell, E. M., Kanefsky, J., ...
641 Scribner, K. T. (2017). Intestinal Microbial Community Dynamics of White-Tailed Deer
642 (*Odocoileus virginianus*) in an Agroecosystem. *Microbial Ecology*, 74(2), 496–506.
643 <https://doi.org/10.1007/s00248-017-0961-7>
- 644 Deutz, A., & Fötschl, H. (2014). 18. Game meat hygiene under Alpine conditions. In P. P., B.
645 A., & S. F.J.M. (Eds.), *Trends in game meat hygiene* (pp. 211–222).
646 https://doi.org/10.3920/978-90-8686-238-2_18
- 647 Dias, D., Caetano, T., Torres, R. T., Fonseca, C., & Mendo, S. (2019). Shiga toxin-producing
648 *Escherichia coli* in wild ungulates. *Science of the Total Environment*, 651, 203–209.
649 <https://doi.org/10.1016/j.scitotenv.2018.09.162>

- 650 Díaz-Sánchez, S., Sánchez, S., Herrera-León, S., Porrero, C., Blanco, J., Dahbi, G., ...
651 Vidal, D. (2013). Prevalence of Shiga toxin-producing *Escherichia coli*, *Salmonella* spp.
652 and *Campylobacter* spp. in large game animals intended for consumption: Relationship
653 with management practices and livestock influence. *Veterinary Microbiology*, 163(3–4),
654 274–281. <https://doi.org/10.1016/j.vetmic.2012.12.026>
- 655 Díaz-Sánchez, S., Sánchez, S., Sánchez, M., Herrera-León, S., Hanning, I., & Vidal, D.
656 (2012). Detection and characterization of Shiga toxin-producing *Escherichia coli* in
657 game meat and ready-to-eat meat products. *International Journal of Food Microbiology*,
658 160(2), 179–182. <https://doi.org/10.1016/J.IJFOODMICRO.2012.09.016>
- 659 EFSA. (2013). Scientific Opinion on VTEC-seropathotype and scientific criteria regarding
660 pathogenicity assessment. *EFSA Journal*, 11(4), 3138.
661 <https://doi.org/10.2903/j.efsa.2013.3138>
- 662 EFSA. (2014). Scientific Opinion on the public health risks related to the maintenance of the
663 cold chain during storage and transport of meat. Part 2 (minced meat from all species).
664 *EFSA Journal*, 12(7), 3783. <https://doi.org/10.2903/j.efsa.2014.3783>
- 665 Eggert, M., Stüber, E., Heurich, M., Fredriksson-Ahomaa, M., Burgos, Y., Beutin, L., &
666 Märtilbauer, E. (2013). Detection and characterization of Shiga toxin-producing
667 *Escherichia coli* in faeces and lymphatic tissue of free-ranging deer. *Source:*
668 *Epidemiology and Infection*, 141(2), 251–259.
669 <https://doi.org/10.1017/S0950268812000246>
- 670 Evans, J., Knight, H., McKendrick, I. J., Stevenson, H., Varo Barbudo, A., Gunn, G. J., &
671 Low, J. C. (2011). Prevalence of *Escherichia coli* O157 : H7 and serogroups O26,
672 O103, O111 and O145 in sheep presented for slaughter in Scotland. *Journal of Medical*
673 *Microbiology*, 60(5), 653–660. <https://doi.org/10.1099/jmm.0.028415-0>
- 674 Ezenwa, V. O. (2004). Interactions among host diet, nutritional status and gastrointestinal
675 parasite infection in wild bovids. *International Journal for Parasitology*, 34(4), 535–342.
676 <https://doi.org/10.1016/j.ijpara.2003.11.012>
- 677 FAO, W. (2018). *Shiga toxin-producing Escherichia coli (STEC) and food: attribution,*
678 *characterization, and monitoring. Microbiological Risk Assessment Series 31 Report:*
679 *Shiga toxin-producing Escherichia coli (STEC) and food: attribution, characterisation,*
680 *and monitoring.*
- 681 Ferens, W. A., & Hovde, C. J. (2011). *Escherichia coli* O157:H7: Animal Reservoir and
682 Sources of Human Infection. *Foodborne Pathogens and Disease*, 8(4), 465–487.
683 <https://doi.org/10.1089/fpd.2010.0673>
- 684 Food Standards Agency. (2008). *HACCP guidance for those producing wild game meat for*
685 *human consumption either at an approved game handling establishment or under*
686 *exemption allowed by the food hygiene regulations HACCP.* Retrieved from
687 <https://www.food.gov.uk/sites/default/files/multimedia/pdfs/gamehaccpplan.pdf>
- 688 Frank, E., Bonke, R., Drees, N., Heurich, M., Märtilbauer, E., & Gareis, M. (2019). Shiga
689 toxin-producing *Escherichia coli* (STEC) shedding in a wild roe deer population.
690 *Veterinary Microbiology*, 239. <https://doi.org/10.1016/j.vetmic.2019.108479>
- 691 Franklin, A. B., VerCauteren, K. C., Maguire, H., Cichon, M. K., Fischer, J. W., Lavelle, M. J.,
692 ... Scallan, E. (2013). Wild ungulates as disseminators of Shiga toxin-producing
693 *Escherichia coli* in urban areas. *PLoS ONE*, 8(12).
694 <https://doi.org/10.1371/journal.pone.0081512>
- 695 French, A. S., Zadoks, R. N., Skuce, P. J., Mitchell, G., Gordon-Gibbs, D. K., Craine, A., ...
696 Taggart, M. A. (2016). Prevalence of Liver Fluke (*Fasciola hepatica*) in Wild Red Deer

- 697 (Cervus elaphus): Coproantigen ELISA Is a Practicable Alternative to Faecal Egg
698 Counting for Surveillance in Remote Populations. *PLOS ONE*, 11(9), e0162420.
699 <https://doi.org/10.1371/journal.pone.0162420>
- 700 FSA, & FSS. (2018). The Wild Game Guide. Retrieved from
701 https://www.foodstandards.gov.scot/downloads/The_Wild_Game_Guide_1.pdf
- 702 García-Sánchez, A., Sánchez, S., Rubio, R., Pereira, G., Alonso, J. M., Hermoso de
703 Mendoza, J., & Rey, J. (2007). Presence of Shiga toxin-producing *E. coli* O157:H7 in a
704 survey of wild artiodactyls. *Veterinary Microbiology*, 121(3–4), 373–377.
705 <https://doi.org/10.1016/j.vetmic.2006.12.012>
- 706 Gill, C. O. (2007). Microbiological conditions of meats from large game animals and birds.
707 *Meat Science*, 77(2), 149–160. <https://doi.org/10.1016/j.meatsci.2007.03.007>
- 708 Gill, C. O., & Jones, T. (2002). Effects of wearing knitted or rubber gloves on the transfer of
709 *Escherichia coli* between hands and meat. *Journal of Food Protection*, 65(6), 1045–
710 1048. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12092720>
- 711 Gill, C. O., & Penney, N. (1977). Penetration of bacteria into meat. *Applied and
712 Environmental Microbiology*, 33(6), 1284–1286. Retrieved from
713 <http://www.ncbi.nlm.nih.gov/pubmed/406846>
- 714 Gill, C. O., Penney, N., & Nottingham, P. M. (1978). Tissue sterility in uneviscerated
715 carcasses. *Applied and Environmental Microbiology*, 36(2), 356–359. Retrieved from
716 <http://www.ncbi.nlm.nih.gov/pubmed/29564>
- 717 Gould, L. H., Mody, R. K., Ong, K. L., Clogher, P., Cronquist, A. B., Garman, K. N., ... Griffin,
718 P. M. (2013). Increased recognition of Non-O157 shiga toxin-producing *Escherichia coli*
719 infections in the United States during 2000-2010: Epidemiologic features and
720 comparison with *E. coli* O157 infections. *Foodborne Pathogens and Disease*, 10(5),
721 453–460. <https://doi.org/10.1089/fpd.2012.1401>
- 722 Gouws, P. A., Shange, N., & Hoffman, L. C. (2017). 14. Microbial quality of springbok (
723 *Antidorcas marsupialis*) meat in relation to harvesting and production process. In
724 *Game meat hygiene* (pp. 223–228). https://doi.org/10.3920/978-90-8686-840-7_14
- 725 Hald, T., Aspinall, W., Devleesschauwer, B., Cooke, R., Corrigan, T., Havelaar, A. H., ...
726 Hoffmann, S. (2016). World Health Organization Estimates of the Relative Contributions
727 of Food to the Burden of Disease Due to Selected Foodborne Hazards: A Structured
728 Expert Elicitation. *PLOS ONE*, 11(1), e0145839.
729 <https://doi.org/10.1371/journal.pone.0145839>
- 730 Henry, M. K., Tongue, S. C., Evans, J., Webster, C., Mckendrick, I. J., Morgan, M., ...
731 Chase-Topping, M. E. (2017). British *Escherichia coli* O157 in Cattle Study (BECS) to
732 determine the prevalence of *E. coli* O157 in herds with cattle destined for the food chain
733 Citation for published version: British *Escherichia coli* O157 in Cattle Study (BECS): to
734 determine the preval. *Epidemiology and Infection*, 145(15), 3168–3179.
735 <https://doi.org/10.1017/S0950268817002151>
- 736 Heuvelink, A. E., Roessink, G. L., Bosboom, K., & de Boer, E. (2001). Zero-tolerance for
737 faecal contamination of carcasses as a tool in the control of O157 VTEC infections. In
738 *International journal of food microbiology* (Vol. 66). Retrieved from
739 <http://www.ncbi.nlm.nih.gov/pubmed/11407542>
- 740 Hoffmann, S., Devleesschauwer, B., Aspinall, W., Cooke, R., Corrigan, T., Havelaar, A., ...
741 Hald, T. (2017). Attribution of global foodborne disease to specific foods: Findings from
742 a World Health Organization structured expert elicitation. *PLOS ONE*, 12(9), e0183641.
743 <https://doi.org/10.1371/journal.pone.0183641>

- 744 Houston, A. I., McNamara, J. M., Barta, Z., & Klasing, K. C. (2007). The effect of energy
745 reserves and food availability on optimal immune defence. *Proceedings of the Royal*
746 *Society B: Biological Sciences*, 274(1627), 2835–2842.
747 <https://doi.org/10.1098/rspb.2007.0934>
- 748 Howell, A. K., Tongue, S. C., Currie, C., Evans, J., Williams, D. J. L., & Mcneilly, T. N.
749 (2018). *Co-infection with Fasciola hepatica may increase the risk of Escherichia coli*
750 *O157 shedding in British cattle destined for the food chain*.
751 <https://doi.org/10.1016/j.prevetmed.2017.12.007>
- 752 Irvine, R. J., Corbishley, H., Pilkington, J. G., & Albon, S. D. (2006). Low-level parasitic worm
753 burdens may reduce body condition in free-ranging red deer (*Cervus elaphus*).
754 *Parasitology*, 133(4), 465–475. <https://doi.org/10.1017/S0031182006000606>
- 755 Kaper, J. B., Nataro, J. P., & Mobley, H. L. T. (2004). Pathogenic *Escherichia coli*. *Nature*
756 *Reviews Microbiology*, 2(2), 123–140. <https://doi.org/10.1038/nrmicro818>
- 757 King, T., Kocharunchitt, C., Gobius, K., Bowman, J. P., & Ross, T. (2016). Physiological
758 Response of *Escherichia coli* O157:H7 Sakai to Dynamic Changes in Temperature and
759 Water Activity as Experienced during Carcass Chilling. *Molecular & Cellular*
760 *Proteomics : MCP*, 15(11), 3331–3347. <https://doi.org/10.1074/mcp.M116.063065>
- 761 Laaksonen, S., Oksanen, A., Julmi, J., Zweifel, C., Fredriksson-Ahomaa, M., & Stephan, R.
762 (2017). Presence of foodborne pathogens, extended-spectrum β -lactamase -producing
763 Enterobacteriaceae, and methicillin-resistant *Staphylococcus aureus* in slaughtered
764 reindeer in northern Finland and Norway. *Acta Veterinaria Scandinavica*, 59(1).
765 <https://doi.org/10.1186/s13028-016-0272-x>
- 766 Laaksonen, S., & Paulsen, P. (2015). 4. Hunting hygiene. In *Hunting hygiene* (pp. 217–278).
767 https://doi.org/10.3920/978-90-8686-800-1_4
- 768 Li, Z., Zhang, Z., Xu, C., Zhao, J., Liu, H., Fan, Z., ... Li, G. (2014). Bacteria and
769 methanogens differ along the gastrointestinal tract of Chinese roe deer (*Capreolus*
770 *pygargus*). *PLoS ONE*, 9(12). <https://doi.org/10.1371/journal.pone.0114513>
- 771 Majowicz, S. E., Scallan, E., Jones-Bitton, A., Sargeant, J. M., Stapleton, J., Angulo, F. J., ...
772 Kirk, M. D. (2014). Global Incidence of Human Shiga Toxin–Producing *Escherichia coli*
773 Infections and Deaths: A Systematic Review and Knowledge Synthesis. *Foodborne*
774 *Pathogens and Disease*, 11(6), 447–455. <https://doi.org/10.1089/fpd.2013.1704>
- 775 Mann, J. E., & Brashears, M. M. (2006). Validation of time and temperature values as critical
776 limits for the control of *Escherichia coli* O157:H7 during the production of fresh ground
777 beef. *Journal of Food Protection*, 69(8), 1978–1982. Retrieved from
778 <http://www.ncbi.nlm.nih.gov/pubmed/16924927>
- 779 Martin, A., & Beutin, L. (2011). Characteristics of Shiga toxin-producing *Escherichia coli* from
780 meat and milk products of different origins and association with food producing animals
781 as main contamination sources. *International Journal of Food Microbiology*, 146(1), 99–
782 104. <https://doi.org/10.1016/j.ijfoodmicro.2011.01.041>
- 783 Mellefont, L. A., Kocharunchitt, C., & Ross, T. (2015). Combined effect of chilling and
784 desiccation on survival of *Escherichia coli* suggests a transient loss of culturability.
785 *International Journal of Food Microbiology*, 208, 1–10.
786 <https://doi.org/10.1016/j.ijfoodmicro.2015.04.024>
- 787 Miko, A., Pries, K., Haby, S., Steege, K., Albrecht, N., Krause, G., & Beutin, L. (2009).
788 Assessment of Shiga toxin-producing *Escherichia coli* isolates from wildlife meat as
789 potential pathogens for humans. *Applied and Environmental Microbiology*, 75(20),
790 6462–6470. <https://doi.org/10.1128/AEM.00904-09>

- 791 Mora, A., López, C., Dhabi, G., López-Beceiro, A. M., Fidalgo, L. E., Díaz, E. A., ... Blanco,
792 J. (2012). Seropathotypes, Phylogroups, Stx subtypes, and intimin types of wildlife-
793 carried, shiga toxin-producing escherichia coli strains with the same characteristics as
794 human-pathogenic isolates. *Applied and Environmental Microbiology*, 78(8), 2578–
795 2585. <https://doi.org/10.1128/AEM.07520-11>
- 796 Mughini-Gras, L., van Pelt, W., van der Voort, M., Heck, M., Friesema, I., & Franz, E. (2018).
797 Attribution of human infections with Shiga toxin-producing Escherichia coli (STEC) to
798 livestock sources and identification of source-specific risk factors, The Netherlands
799 (2010-2014). *Zoonoses and Public Health*, 65(1), e8–e22.
800 <https://doi.org/10.1111/zph.12403>
- 801 Naylor, S. W., Low, J. C., Besser, T. E., Mahajan, A., Gunn, G. J., Pearce, M. C., ... Gally,
802 D. L. (2003). Lymphoid follicle-dense mucosa at the terminal rectum is the principal site
803 of colonization of enterohemorrhagic Escherichia coli O157:H7 in the bovine host.
804 *Infection and Immunity*, 71(3), 1505–1512. [https://doi.org/10.1128/IAI.71.3.1505-](https://doi.org/10.1128/IAI.71.3.1505-1512.2003)
805 [1512.2003](https://doi.org/10.1128/IAI.71.3.1505-1512.2003)
- 806 Nel, S., Lues, J. F. ., Buys, E. ., & Venter, P. (2004). The personal and general hygiene
807 practices in the deboning room of a high throughput red meat abattoir. *Food Control*,
808 15(7), 571–578. <https://doi.org/10.1016/J.FOODCONT.2003.09.004>
- 809 Nørrung, B., & Buncic, S. (2008). Microbial safety of meat in the European Union. *Meat*
810 *Science*, 78(1–2), 14–24. <https://doi.org/10.1016/j.meatsci.2007.07.032>
- 811 Nussey, D. H., Watt, K. A., Clark, A., Pilkington, J. G., Pemberton, J. M., Graham, A. L., &
812 McNeilly, T. N. (2014). Multivariate immune defences and fitness in the wild: Complex
813 but ecologically important associations among plasma antibodies, health and survival.
814 *Proceedings of the Royal Society B: Biological Sciences*, 281(1779).
815 <https://doi.org/10.1098/rspb.2013.2931>
- 816 O'Toole, A., Browne, J. A., Hogan, S., Bassière, T., DeWaal, T., Mulcahy, G., & Zintl, A.
817 (2014). Identity of rumen fluke in deer. *Parasitology Research*, 113(11), 4097–4103.
818 <https://doi.org/10.1007/s00436-014-4078-3>
- 819 Obwegeser, T., Stephan, R., Hofer, E., & Zweifel, C. (2012). Shedding of foodborne
820 pathogens and microbial carcass contamination of hunted wild ruminants. *Veterinary*
821 *Microbiology*, 159(1–2), 149–154. <https://doi.org/10.1016/J.VETMIC.2012.03.031>
- 822 Ogden, I. D., Hepburn, N. F., MacRae, M., Strachan, N. J. C., Fenlon, D. R., Rusbridge, S.
823 M., & Pennington, T. H. (2002). Long-term survival of Escherichia coli O157 on pasture
824 following an outbreak associated with sheep at a scout camp. *Letters in Applied*
825 *Microbiology*, 34(2), 100–104. Retrieved from
826 <http://www.ncbi.nlm.nih.gov/pubmed/11849503>
- 827 Oliver, D. M. (2014). Seasonal and within-herd variability of *E. coli* concentrations in fresh
828 dairy faeces. *Letters in Applied Microbiology*, 59(1), 86–92.
829 <https://doi.org/10.1111/lam.12248>
- 830 Paton, J. C., & Paton, A. W. (1998). Pathogenesis and diagnosis of Shiga toxin-producing
831 Escherichia coli infections. *Clinical Microbiology Reviews*, 11(3), 450–479. Retrieved
832 from <http://www.ncbi.nlm.nih.gov/pubmed/9665978>
- 833 Paulsen, P. (2011). Hygiene and microbiology of meat from wild game: an Austrian view. In
834 *Game meat hygiene in focus* (pp. 19–37). https://doi.org/10.3920/978-90-8686-723-3_1
- 835 Paulsen, P., & Winkelmayer, R. (2004). Seasonal variation in the microbial contamination of
836 game carcasses in an Austrian hunting area. *European Journal of Wildlife Research*,
837 50(3), 157–159. <https://doi.org/10.1007/s10344-004-0054-z>

- 838 Probert, W. S., Miller, G. M., & Ledin, K. E. (2017, July 1). Contaminated stream water as
839 source for *Escherichia coli* O157 illness in children. *Emerging Infectious Diseases*, Vol.
840 23, pp. 1216–1218. <https://doi.org/10.3201/eid2307.170226>
- 841 Rabatsky-Ehr, T., Dingman, D., Marcus, R., Howard, R., Kinney, A., & Mshar, P. (2002a).
842 Deer meat as the source for a sporadic case of *Escherichia coli* O157:H7 infection,
843 Connecticut. *Emerging Infectious Diseases*, 8(5), 525–527.
844 <https://doi.org/10.3201/eid0805.010373>
- 845 Rabatsky-Ehr, T., Dingman, D., Marcus, R., Howard, R., Kinney, A., & Mshar, P. (2002b).
846 Deer Meat as the Source for a Sporadic Case of *Escherichia coli* O157:H7 Infection,
847 Connecticut1. *Emerging Infectious Diseases*, 8(5), 525–527.
848 <https://doi.org/10.3201/eid0805.010373>
- 849 Ramanzin, M., Amici, A., Casoli, L. E., Paola Lupi, G., Marsico, S. M., Oliviero, O., ...
850 Marinucci, M. T. (2010). Italian journal of animal science : journal and official organ of
851 the Scientific Association of Animal Production (A.S.P.A.). In *Italian Journal Of Animal*
852 *Science* (Vol. 9). Retrieved from [https://discovered.ed.ac.uk/primo-](https://discovered.ed.ac.uk/primo-explore/fulldisplay?docid=TN_wos000284230800009&context=PC&vid=44UOE_VU2&ang=en_US&search_scope=default_scope&adaptor=primo_central_multiple_fe&tab=default_tab&query=any,contains,Meat from wild ungulates: ensuring quality)
853 [explore/fulldisplay?docid=TN_wos000284230800009&context=PC&vid=44UOE_VU2&](https://discovered.ed.ac.uk/primo-explore/fulldisplay?docid=TN_wos000284230800009&context=PC&vid=44UOE_VU2&ang=en_US&search_scope=default_scope&adaptor=primo_central_multiple_fe&tab=default_tab&query=any,contains,Meat from wild ungulates: ensuring quality)
854 [ang=en_US&search_scope=default_scope&adaptor=primo_central_multiple_fe&tab=d](https://discovered.ed.ac.uk/primo-explore/fulldisplay?docid=TN_wos000284230800009&context=PC&vid=44UOE_VU2&ang=en_US&search_scope=default_scope&adaptor=primo_central_multiple_fe&tab=default_tab&query=any,contains,Meat from wild ungulates: ensuring quality)
855 [efault_tab&query=any,contains,Meat from wild ungulates: ensuring quality](https://discovered.ed.ac.uk/primo-explore/fulldisplay?docid=TN_wos000284230800009&context=PC&vid=44UOE_VU2&ang=en_US&search_scope=default_scope&adaptor=primo_central_multiple_fe&tab=default_tab&query=any,contains,Meat from wild ungulates: ensuring quality)
- 856 Regulation (EC) No 852/2004 of the European parliament and of the council of 29 April 2004
857 on the hygiene of foodstuffs. , [https://webarchive.nationalarchives.gov.uk/eu-](https://webarchive.nationalarchives.gov.uk/eu-exit/https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:02004R0852-20090420)
858 [exit/https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:02004R0852-](https://webarchive.nationalarchives.gov.uk/eu-exit/https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:02004R0852-20090420)
859 [20090420](https://webarchive.nationalarchives.gov.uk/eu-exit/https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:02004R0852-20090420) §.
- 860 Regulation (EC) No 853/2004 of the European Parliament and of the Council of 29 April
861 2004 laying down specific hygiene rules for food of animal origin. ,
862 [https://webarchive.nationalarchives.gov.uk/eu-exit/https://eur-lex.europa.eu/legal-](https://webarchive.nationalarchives.gov.uk/eu-exit/https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:02004R0853-20190726)
863 [content/EN/TXT/?uri=CELEX:02004R0853-20190726](https://webarchive.nationalarchives.gov.uk/eu-exit/https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:02004R0853-20190726) §.
- 864 Rounds, J. M., Rigdon, C. E., Muhl, L. J., Forstner, M., Danzeisen, G. T., Koziol, B. S., ...
865 Smith, K. E. (2012). Non-O157 Shiga toxin-producing *Escherichia coli* associated with
866 venison. *Emerging Infectious Diseases*, 18(2), 279–282.
867 <https://doi.org/10.3201/eid1802.110855>
- 868 Sánchez, S., Beristain, X., Martínez, R., García, A., Martín, C., Vidal, D., ... Herrera-León, S.
869 (2012). Subtilase cytotoxin encoding genes are present in human, sheep and deer
870 intimin-negative, Shiga toxin-producing *Escherichia coli* O128:H2. *Veterinary*
871 *Microbiology*, 159(3–4), 531–535. <https://doi.org/10.1016/j.vetmic.2012.04.036>
- 872 Sánchez, S., García-Sánchez, A., Martínez, R., Blanco, J., Blanco, J. E., Blanco, M., ... Rey,
873 J. (2009). Detection and characterisation of Shiga toxin-producing *Escherichia coli*
874 other than *Escherichia coli* O157:H7 in wild ruminants. *Veterinary Journal*, 180(3), 384–
875 388. <https://doi.org/10.1016/j.tvjl.2008.01.011>
- 876 Sánchez, S., Martínez, R., Rey, J., García, A., Blanco, J., Blanco, M., ... Alonso, J. M.
877 (2010). Pheno-genotypic characterisation of *Escherichia coli* O157:H7 isolates from
878 domestic and wild ruminants. *Veterinary Microbiology*, 142(3–4), 445–449.
879 <https://doi.org/10.1016/j.vetmic.2009.10.009>
- 880 Sauvala, M., Laaksonen, S., Laukkanen-Ninios, R., Jalava, K., Stephan, R., & Fredriksson-
881 Ahomaa, M. (2019). Microbial contamination of moose (*Alces alces*) and white-tailed
882 deer (*Odocoileus virginianus*) carcasses harvested by hunters. *Food Microbiology*, 78,
883 82–88. <https://doi.org/10.1016/j.fm.2018.09.011>
- 884 Schulp, C. J. E., Thuiller, W., & Verburg, P. H. (2014). *Analysis Wild food in Europe: A*
885 *synthesis of knowledge and data of terrestrial wild food as an ecosystem service.*

- 886 <https://doi.org/10.1016/j.ecolecon.2014.06.018>
- 887 Serrano, M. P., Maggiolino, A., Landete-Castillejos, T., Pateiro, M., Barbería, J. P., Fierro,
888 Y., ... Lorenzo, J. M. (2020). Quality of main types of hunted red deer meat obtained in
889 Spain compared to farmed venison from New Zealand. *Scientific Reports*, 10(1).
890 <https://doi.org/10.1038/s41598-020-69071-2>
- 891 Simpson, A., Webster, A. J., Smith, J. S., & Simpson, C. (1978). Energy and nitrogen
892 metabolism of red deer (*Cervus elaphus*) in cold environments; a comparison with
893 cattle and sheep. *Comparative Biochemistry and Physiology Part A: Physiology*, 60(3),
894 251–256. [https://doi.org/10.1016/0300-9629\(78\)90243-8](https://doi.org/10.1016/0300-9629(78)90243-8)
- 895 Singh, P., Sha, Q., Lacher, D. W., Del Valle, J., Mosci, R. E., Moore, J. A., ... Manning, S. D.
896 (2015). Characterization of enteropathogenic and Shiga toxin-producing *Escherichia*
897 *coli* in cattle and deer in a shared agroecosystem. *Frontiers in Cellular and Infection*
898 *Microbiology*, 5, 29. <https://doi.org/10.3389/fcimb.2015.00029>
- 899 Smith-Palmer, A., Hawkins, G., Browning, L., Allison, L., Hanson, M., Bruce, R., ... Horne, J.
900 (2018). Outbreak of *Escherichia coli* O157 Phage Type 32 linked to the consumption of
901 venison products. *Epidemiology and Infection*, 146(15), 1922–1927.
902 <https://doi.org/10.1017/S0950268818001784>
- 903 Smith, V. (2007). Host resource supplies influence the dynamics and outcome of infectious
904 disease. *Integrative and Comparative Biology*, 47(2), 310–316.
905 <https://doi.org/10.1093/icb/icm006>
- 906 Soriano, A., Montoro, V., Vicente, J., Sánchez-Migallón, B. F., Benítez, S., Utrilla, M. C., &
907 García Ruiz, A. (2016). Influence of evisceration time and carcass ageing conditions on
908 wild venison quality. Preliminary study. *MESC*, 114, 130–136.
909 <https://doi.org/10.1016/j.meatsci.2015.12.021>
- 910 Synge, B. (2006). *Epidemiological studies of Verocytotoxin-producing Escherichia coli*
911 *infections in animals in Scotland* (Edinburgh University). <https://doi.org/103-104>
- 912 Szczerba-Turek, A., Siemionek, J., Socha, P., Bancercz-Kisiel, A., Platt-Samoraj, A.,
913 Lipczynska-Illczuk, K., & Szweda, W. (2020). Shiga toxin-producing *Escherichia coli*
914 isolates from red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and fallow
915 deer (*Dama dama*) in Poland. *Food Microbiology*.
916 <https://doi.org/10.1016/j.fm.2019.103352>
- 917 Tenailon, O., Skurnik, D., Picard, B., & Denamur, E. (2010). The population genetics of
918 commensal *Escherichia coli*. *Nature Reviews Microbiology*, 8(3), 207–217.
919 <https://doi.org/10.1038/nrmicro2298>
- 920 Thorpe, C. M. (2004). Shiga Toxin--Producing *Escherichia coli* Infection. *Clinical Infectious*
921 *Diseases*, 38(9), 1298–1303. <https://doi.org/10.1086/383473>
- 922 Turbill, C., Ruf, T., Mang, T., & Arnold, W. (2011). Regulation of heart rate and rumen
923 temperature in red deer: effects of season and food intake. *Journal of Experimental*
924 *Biology*, 214(6), 963–970. <https://doi.org/10.1242/jeb.052282>
- 925 Urquhart, K. A., & McKendrick, I. J. (2006). Prevalence of “head shooting” and the
926 characteristics of the wounds in culled wild Scottish red deer. *The Veterinary Record*,
927 159(3), 75–79. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/16844818>
- 928 van Schalkwyk, D. L., Hoffman, L. C., & Laubscher, L. A. (2011). Game harvesting
929 procedures and their effect on meat quality: the Africa experience. In *Game meat*
930 *hygiene in focus* (pp. 67–92). https://doi.org/10.3920/978-90-8686-723-3_3
- 931 Venegas-Vargas, C., Henderson, S., Khare, A., Mosci, R. E., Lehnert, J. D., Singh, P., ...

- 932 Manning, S. D. (2016). Factors Associated with Shiga Toxin-Producing *Escherichia coli*
933 Shedding by Dairy and Beef Cattle. *Applied and Environmental Microbiology*, 82(16),
934 5049–5056. <https://doi.org/10.1128/AEM.00829-16>
- 935 WHO. (2017). WHO | *E. coli*. Retrieved November 21, 2017, from WHO website:
936 <http://www.who.int/mediacentre/factsheets/fs125/en/>
- 937 Yang, X., Wang, H., He, A., & Tran, F. (2017). Microbial efficacy and impact on the
938 population of *Escherichia coli* of a routine sanitation process for the fabrication facility of
939 a beef packing plant. *Food Control*, 71, 353–357.
940 <https://doi.org/10.1016/J.FOODCONT.2016.07.016>
- 941