Short Communication

Characteristics of Shiga toxin-producing *Escherichia coli* from meat and milk products of different origins and association with food producing animals as main contamination sources

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A B S T R A C T

Shiga toxin-producing strains of *Escherichia coli* (STEC) cause diarrhoea and haemorrhagic colitis in humans. Most human infections are attributed to consumption of STEC contaminated foodstuff. Food producing animals constitute important reservoirs of STEC and serve as source of food contamination. In this study, we have analyzed 593 foodborne STEC strains for their serotypes and for nine virulence genes (*stx1, stx1c, stx1d*, *stx2, stx2b, stx2e, stx2g, E-hly* and *eae*). The 593 STEC strains grouped into 215 serotypes, and 123 serotypes (57.2%) were represented each by only one STEC isolate. Fifteen serotypes (7.0%) were attributed to 198 (33.3%) of the 593 STEC strains. The foodborne STEC were grouped into different categories in relation to the species of the food producing animal (cattle, pigs, sheep, goats, red deer, wild boar and hare). Univariate and multivariate statistical analyses revealed significant similarities between the animal origin of the food and the virulence markers of foodborne STEC. Significant associations (p < 0.001) were found for *stx1* and for *stx2* with bovine meat and milk products. The *stx2e* gene was significantly (p < 0.001) associated with STEC from pork and wild boar meat. *Stx1c* and *stx2b* genes were significantly (p < 0.001) more frequent in STEC from deer meat, as well as from meat and milk products derived from sheep and goats. Using logistic regression models we detected significant (p < 0.01) combinations between *stx1*, *stx2* and *E-hly* genes and STEC from bovine meat. The combination of *stx1c* and *stx2b* genes was significant (p < 0.001) for STEC derived from red deer, sheep and goat products. The properties of foodborne STEC were compared with published data on faecal STEC from food producing animals. Virulence profiles and serotypes of STEC from food showed remarkable similarities to those of faecal STEC that were from the same animal species. The findings from our study clearly indicate that the food producing animals represent the most important source for the entry of STEC in the food chain. Sound hygiene measures implemented at critical stages of food production (milking, slaughtering, and evisceration) should be most effective in reducing the frequency of STEC contamination of food derived from domestic and wildlife animals.

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1. Introduction

Shiga toxin-producing *Escherichia coli* (STEC) are recognised globally as pathogens that cause diarrhoea, haemorrhagic colitis (HC) and haemolytic uremic syndrome (HUS) in humans. STEC are frequently shed in the faeces of healthy slaughter age meat-producing animal species and are not considered to be pathogens of ruminant species except when infections occur in young (pre-weaned) animals (Hornitzky et al., 2005; Wieler et al., 1996).

In 2007, the incidence of O157 and non-O157 STEC infections in the United States was 1.19 and 0.59 per 100,000 people, respectively (Centers for Disease Control and Prevention, 2009). The incidence of STEC infections in the European Union in 2006 and 2007 was 1.1 and 0.6 per 100,000 respectively (European Food Safety Authority (EFSA), 2009b).

About 70% of cases with human STEC infection in the U.S. and 50% in the E.U. were attributed to STEC O157 (European Food Safety Authority (EFSA), 2009b; Mead et al., 1999). Besides the O157 serotype, in 2005 about 400 serotypes of STEC were known to be associated with illness in humans as agents of diarrhoea, HC and HUS (Scheutz and Stockbine, 2005).
More than 85% of cases of illness caused by STEC in the U.S. were associated with consumption of contaminated food (Mead et al., 1999). A survey performed in member states of the E.U. (2005–2007) revealed dairy and meat products as most frequently contaminated with STEC. Food contamination rates varied between 0.1 and 2.4% in different E.U. member states (European Food Safety Authority (EFSA), 2009b).

In Germany, 4818 food samples of animal origin were investigated for STEC in 2006 (Hartung, 2007). STEC positives were frequent among meat samples from sheep (11.1%), wild game (9.9%), and cattle (4.5%) and less frequent in pork (0.68%). Between 0.6 and 1.8% of dairy products contained STEC (Hartung, 2007). Furthermore, the importance of food as a potential source of human infection is indicated by the fact that more than 60% of STEC from food in Germany showed the same serotype as STEC from human patients (Beutin et al., 2007; Miko et al., 2009; Werber et al., 2008).

Animals, in particular ruminant species are regarded as a major natural reservoir of STEC, and they excrete these pathogens with their faeces (Caprioli et al., 2005). As a consequence, STEC are found in the environment and in different kinds of foodstuffs for human consumption (Caprioli et al., 2005). Food can become contaminated with STEC at all stages of food production and retail (Hussein, 2007; Hussein and Sakuma, 2005). How STEC enter the food chain is often not known. Evisceration during slaughtering and defeathering during milking are critical events where STEC are likely to enter food products destined for human consumption. To our knowledge, the importance of food producing animals as a source of STEC in foodstuffs has not been statistically assessed.

The finding that some STEC serotypes and Shiga-toxin (Stx)-types are closely associated with certain animal host species makes it possible to search for these in food derived from animals of different species. Toxin subtypes stx1c and stx2b (the latter was formerly called stx2−O111 or stx2D non-activatable) are frequent in STEC from sheep, goats and deer (Brett et al., 2003a; Ishii et al., 2007; Oliveira et al., 2007; Vu-Khac and Cornick, 2008). The stx1 and stx2 genotypes were found associated with STEC from cattle (Brett et al., 2003b; Nakamura et al., 2008; Oliveira et al., 2007; Vu-Khac and Cornick, 2008; Zheng et al., 2008) and stx2e with STEC from healthy and diseased pigs (Beutin et al., 2008; Fratamico et al., 2004; Zweifel et al., 2006). Some STEC serotypes that occur frequently as food isolates (Beutin et al., 2007, 2008; Werber et al., 2008) were previously shown to be common in faeces of domestic and wildlife animals (Brett et al., 2003a, b; Hussein and Bollinger, 2005; Ishii et al., 2007; Oliveira et al., 2007; Zweifel et al., 2006).

In this study, we have analyzed 593 STEC strains derived from food for their serotypes and virulence properties. Using statistical analysis we have explored the relationship between STEC types present in food and the animal food source.

2. Materials and methods

2.1. Characterization of STEC from food samples

The 593 STEC isolates from food samples were sent from 28 public health laboratories for control of food safety in Germany (550 samples), Switzerland (28 samples) and France (15 samples) over a period from March 2005 to October 2009. Serotyping and analysis of virulence genes was performed as described previously (Beutin et al., 2007). Only one isolate per food sample was included in the statistical analyses to avoid evaluation of double or multiple isolates. The properties of 219 STEC from food have been described previously (Beutin et al., 2007, 2008; Miko et al., 2009) The remaining 374 STEC strains were investigated in this study. All 593 strains were investigated for their O:H serotypes, and for Shiga toxin genes stx1, stx1c, stx1d, stx2, stx2b, stx2e, stx2g, as well as for E-hly (EHEC-hemolysin) and eae (intimin) genes. The updated nomenclature for designation of stx- genotypes was used (Persson et al., 2007; Scheutz and Stockbleine, 2005). Closely related Shiga toxin 2 types such as stx2a, stx2c and stx2d-(activatable) (Persson et al., 2007) were not distinguished and are summarized as stx2 in this study.

2.2. Statistical analysis

At first, possible associations between the food categories (food-stuff derived from cattle, pigs, wild boar, goats, sheep, hares and red deer) and the virulence characteristics of the corresponding STEC isolates were analyzed. Proportions of samples with detected STEC virulence genes were calculated with exact 95% confidence interval (95% CI) (Collett, 1999) for each of the food categories (Fig. 1). We compared proportions using the $\chi^2$ test or Fisher exact test when appropriate. The statistical analyses were 2-tailed, and p values $<0.05$ were considered significant.

For interpretation of the results of $\chi^2$ test or Fisher exact test we calculated standardized residuals. A standardized residual of $\leq 2$ indicates that the observed frequency of a given virulence gene is significantly lower than the expected frequency. A residual of $\geq 2$ indicates that the observed frequency is significantly higher than the expected frequency (Bühl, 2008).

Potential interactions between STEC virulence factors and the food categories as STEC source were calculated using multivariable logistic regression models. Strain-specific combinations of stx-subtypes and other virulence genes can thus be identified. These specific combinations are employed as genetic signatures to analyze the association between certain STEC types and their food origin.

Because the dependent variable is dichotomous (food category: yes/no), it is convenient to use binary logistic regression. The independent variables were indicators (presence/absence) for the virulence genes and their interactions. For each of the food categories (Table 1) one regression model with backward elimination approaches was calculated. Hares as food source were excluded from multivariate analyses due to the small sample size. We considered second and third order interactions among virulence factors. Statistical significance was tested using a Likelihood ratio test (Backhaus et al., 2003). The strength of the association between food categories and virulence factors is shown by the odds ratio (OR) with corresponding 95% confidence interval (Table 2). All analyses were performed with SPSS version 17 and Excel 2003.

The data on virulence genes and serotypes of foodborne STEC obtained from this study were used for detecting similarities to STEC strains that were isolated from faeces of food producing animals. Information about characteristic serotypes and virulence properties of faecal STEC from food animals of the six species (cattle, pigs, wild boar, deer, hare, goats and sheep) was obtained from the published literature.

3. Results

3.1. Frequencies and properties of STEC isolated from food produced from different animals

We analyzed 593 STEC strains isolated from food derived from different species of animals (cattle, red deer, pigs; wild boar, hares and sheep and goats) (Table 1). All STEC strains were examined for their serotypes, stx-subtypes and the virulence genes eae and E-hly as previously described (Beutin et al., 2007; Miko et al., 2009). The 593 STEC strains belonged to 215 different serotypes (Supplementary data Table A). In summary, 19.7% the STEC isolates carried only Stx1 group genes (stx1, stx1c, and stx1d). 58.3% only Stx2 group genes (stx2, stx2b, stx2e, and stx2g) and 20.6% carried both Stx1 and Stx2 group genes. Only 2.2% of the STEC carried the eae-gene and 37.9% were positive for the E-hly gene (data not shown).
3.2. Distribution of STEC serotypes in food derived from different animal species

The frequency and food category origin of the 215 serotypes found among the 593 STEC strains is described in Supplementary data Table A. One hundred twenty-three serotypes (57.2%) were only represented each by one STEC isolate. On the other hand, only fifteen (7.0%) serotypes could be attributed to 198 (33.3%) of the STEC strains. The fifteen serotypes and their distribution within the different food categories are illustrated in Fig. 1.

Six (O113:H21, O22:H8, O174:H21, O178:H19, O113:H4 and O91:H14) among the most frequently detected STEC serotypes encompassed 28.6% of strains from bovine meat and products. Serotypes O2:H27, O171:H25 and O91:H21 (total 14.5%) were most frequently found in STEC from bovine milk and dairy products.

Only two (O8:H9 and O100:H30) of a total of 40 serotypes accounted for 22.9% of the STEC from meat and meat products of domestic pigs. STEC of serotypes O100:H30, O146:H28 and ONT:H19 were most frequently isolated from wild boar meat and products (16.2% of total).

Four (O21:H21, O146:H28, O128:H2 and O146:H21) of 64 serotypes of STEC isolated from deer meat accounted for 29.1% of the isolates. STEC O128:H2 was most frequently associated with STEC from lamb (15.2%). Serotypes O76:H19, ONT:H10, O146:H21 and O38:

Table 1
Food category and STEC isolates.

<table>
<thead>
<tr>
<th>Food category</th>
<th>Nos. of STEC isolates (%)</th>
<th>Nos. of STEC serotypes (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cattle (28.8)</td>
<td>171 (100)</td>
<td>84 (23.9)</td>
</tr>
<tr>
<td>Minced beef</td>
<td>116 (67.8)</td>
<td></td>
</tr>
<tr>
<td>Meat</td>
<td>53 (31.0)</td>
<td></td>
</tr>
<tr>
<td>Sausage</td>
<td>2 (1.2)</td>
<td></td>
</tr>
<tr>
<td>Cattle (22.1)</td>
<td>131 (100.0)</td>
<td>78 (22.2)</td>
</tr>
<tr>
<td>Raw milk</td>
<td>88 (67.2)</td>
<td></td>
</tr>
<tr>
<td>Cheese</td>
<td>43 (32.8)</td>
<td></td>
</tr>
<tr>
<td>Deer (19.7)</td>
<td>117 (100.0)</td>
<td>64 (18.2)</td>
</tr>
<tr>
<td>Red deer meat</td>
<td>46 (39.3)</td>
<td></td>
</tr>
<tr>
<td>Roe deer meat</td>
<td>65 (55.6)</td>
<td></td>
</tr>
<tr>
<td>Other (e.g. reindeer meat)</td>
<td>6 (5.1)</td>
<td></td>
</tr>
<tr>
<td>Pigs (14.0)</td>
<td>83 (100.0)</td>
<td>40 (11.4)</td>
</tr>
<tr>
<td>Minced pork</td>
<td>39 (47.0)</td>
<td></td>
</tr>
<tr>
<td>Sausage</td>
<td>36 (43.4)</td>
<td></td>
</tr>
<tr>
<td>Pork meat</td>
<td>8 (9.6)</td>
<td></td>
</tr>
<tr>
<td>Wild boar (6.2)</td>
<td>37 (100.0)</td>
<td>33 (9.4)</td>
</tr>
<tr>
<td>Meat (e.g. goulash)</td>
<td>37 (100.0)</td>
<td></td>
</tr>
<tr>
<td>Goats and sheep (5.6)</td>
<td>33 (100.0)</td>
<td>22 (6.3)</td>
</tr>
<tr>
<td>Goats (raw milk and cheese)</td>
<td>8 (24.2)</td>
<td></td>
</tr>
<tr>
<td>Lamb meat</td>
<td>24 (72.7)</td>
<td></td>
</tr>
<tr>
<td>Sheep (raw milk)</td>
<td>1 (3.0)</td>
<td></td>
</tr>
<tr>
<td>Hare (3.5)</td>
<td>21 (100.0)</td>
<td>18 (5.1)</td>
</tr>
<tr>
<td>Meat (leg and saddle)</td>
<td>21 (100.0)</td>
<td></td>
</tr>
<tr>
<td>Total (100.0)</td>
<td>593 (100.0)</td>
<td>352* (100.0)</td>
</tr>
</tbody>
</table>

* Some of the STEC serotypes occurred in two or more of the seven food categories. 215 different serotypes were detected among the 593 food-borne STEC strains.

Table 2
Association between virulence factors and STEC isolated from different animal food categories estimated by logistic regression models.

<table>
<thead>
<tr>
<th>STEC from food categories (nos.)</th>
<th>Virulence gene(s)</th>
<th>ORb</th>
<th>95% CIc</th>
<th>pd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cattle milk and products (131)</td>
<td>stx1</td>
<td>4.0</td>
<td>2.0–8.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>stx2</td>
<td>4.0</td>
<td>2.2–7.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>E-hly</td>
<td>1.7</td>
<td>1.1–2.8</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Cattle meat and products (171)</td>
<td>stx1 + stx2 + E-hly</td>
<td>2.3</td>
<td>1.3–4.1</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>stx2e</td>
<td>54.2</td>
<td>28.8–102.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wild boar meat and products (37)</td>
<td>stx2e</td>
<td>4.09</td>
<td>1.64–10.23</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>E-hly</td>
<td>2.43</td>
<td>1.06–5.57</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Red deer meat and products (117)</td>
<td>E-hly</td>
<td>3.4</td>
<td>1.5–8.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Goats and sheep meat, milk and products (33)</td>
<td>stx1e + stx2b</td>
<td>4.4</td>
<td>1.9–9.9</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>stx1e + stx2b</td>
<td>18.9</td>
<td>7.3–49.4</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

a) Final results of significant terms in logistic regression models fitted to each of the food categories. Interaction terms are indicated in boldface. b) OR = odds ratio; The OR value (>1) indicates the strength of the relationship between the virulence factors and their corresponding food category. c) 95% CI: 95% confidence for OR. d) p: from likelihood ratio test.
H26 represented 33.3% of STEC isolated from meat, milk and their products derived from sheep and goats.

Only two (08:H19 and ONT:H21) of 19 serotypes accounted for 23.8% of all STEC isolated from hare meat.

3.3. Association between STEC virulence genes and food source

A summary of the findings is presented in Fig. 2 and in detail in Supplementary data, Table B. Significant (p<0.001) associations were found for the presence of the stx2 (55.7%) gene with STEC from bovine milk and dairy products. Bovine meat and products were significantly (p<0.001) more frequently associated with STEC carrying stx1 (43.3%) and stx2 genes (68.4%).

The presence of the stx2e gene was significantly (p<0.001) more frequently associated with STEC from pork (75.9%) and from wild boar meat (32.4%). In contrast, the E-hly gene was significantly less frequent in STEC from pork (13.3% positive) (p<0.001) compared to STEC from other food categories (36.4–71.4%).

stx1c (24.8%) and stx2b (55.6%) genes were significantly more frequently (p<0.001) carried by STEC isolated from deer meat, as well as STEC from food products derived from sheep and goats (69.7% stx1c and 36.4% stx2b positive). Significant associations between STEC virulence genes and meat and products derived from hares were not detected (Fig. 1).

3.4. Interactions between STEC virulence factors and their food origin

The results of the logistic regression models are presented in Table 2. A significant interaction (p<0.01) was detected between the presence of stx1c and stx2b genes and bovine meat and products.

Another significant interaction was detected between the presence of stx1c and stx2b genes and STEC from red deer meat and products (p<0.001). The same interaction was found for STEC from food derived from sheep and goats (p<0.001) (Table 2). Univariate and multivariate analyses revealed a significant association between STEC from pork (p<0.001) and wild boar meat (p<0.01) with the stx2e gene. The proportion of stx2e strains was substantially higher in STEC from pork (75.9%, OR=54.2) than in STEC from wild boar meat (32.4%, OR=4.09) (Fig. 1 and Table 2).

4. Discussion

STEC infections in humans are primarily regarded as food-borne, and numerous outbreaks have been attributed to consumption of STEC contaminated foodstuffs (European Food Safety Authority (EFSA), 2009a; Mead et al., 1999; Rangel et al., 2005). Food may become contaminated with STEC at all stages of production and retail but in most cases the source of STEC in foodstuffs remains unknown (Centers for Disease Control and Prevention, 2009; European Food Safety Authority (EFSA), 2009a; Mead et al., 1999). Livestock is regarded as important source of food contamination (Fratamico et al., 2004; Hussein, 2007; Hussein and Sakuma, 2005) but its impact has not yet been statistically assessed.

In this study, we have analyzed statistically the relationship between nine different virulence markers of STEC strains and their food origin. Domestic and wildlife animals are frequently colonized by STEC. These STEC strains are characterized by certain serotypes, stx-subtypes and other virulence markers which can indicate their origin from distinct species of animals (see below). We were interested to analyze the role of the food producing animals in contamination of their respective food products with STEC. For investigation, we have assigned the 593 food-borne STEC strains to different food categories on the basis of species of the producer animals (Table 1). We wanted to examine whether the occurrence of the virulence factors is

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**Fig. 2.** Proportion of virulence factors identified in different food categories. The statistical analysis refers to the occurrence of single virulence factors in STEC from seven food categories. The virulence markers tested for strains from each of the seven food categories are listed on the X-axis of the bar diagram. The Y-axis shows the percentage of STEC isolates positive for a given virulence marker. For each bar, the upper and lower limits of the 95% confidence interval are shown by a vertical line. The true (but unknown) percentage of positive strains is between these two limits (95% probability). Significant results from χ² test or Fisher’s exact test are labelled with * (for p<0.05) or with ** (for p<0.001). “p<0.05 + standard residual of +2 or more.” “p<0.001 + standard residual of +2 (−2) or more (or less).” Fisher’s exact test was used to calculate the significance of stx2g in STEC from milk and dairy products from cattle.
independent of the food categories (null hypothesis). The analysis revealed that STEC derived from bovine, ovine/caprine, hare, red deer and porcine food sources differed from each other in their stx-subtypes and their serotypes.

Our findings indicate that most STEC found as food contaminants can be traced back to the food producing animal as a specific source, rather than to an entry from environmental or human sources along the food chain. In the latter case, we would expect the virulence genes and serotypes to be randomly distributed across STEC isolates from all food categories.

To determine the relevance of the food producing animals as sources of STEC in foodstuff, we analyzed published data on serotypes, stx-types and other virulence attributes of faecal STEC from food animals of different species. These were compared with our data from foodborne STEC. In most cases, we found similarities between the STEC strains derived from the same animal species regardless of whether they were from faeces or from food products. As an example, stx1 and stx2 genes were reported to be typical for STEC as colonizers of cattle (Brett et al., 2003a; Vu-Khac and Cornick, 2008), and in the current study, there was a significant association (p < 0.001) of these genes with bovine meat and milk products. Similar findings were made for the occurrence of stx1c and stx2b genes. These are frequently found in STEC from sheep, goats and deer (Brett et al., 2003a; Ishii et al., 2007; Koch et al., 2001; Ramachandran et al., 2001; Vu-Khac and Cornick, 2008) and in this study, they were significantly associated (p < 0.001) with food products derived from these animal species. Another association was found between the occurrence of the stx2e gene with STEC from pigs (Fratamico et al., 2004; Zweifel et al., 2006). Correspondingly, the stx2e gene predominated significantly in STEC from pork (p < 0.001) and wild boar meat (p < 0.01). Similar findings were made by comparing the serotypes of STEC strains that were isolated from food and from animal faeces. Because of the serotype diversity (n = 215), associations with food source or virulence genes could not be calculated statistically. However, the fifteen most commonly isolated STEC serotypes were found unequally distributed between the different food categories (Fig. 1).

The most frequently isolated STEC serotypes from food of bovine origin in this study (O113:H21, O22:H8, O174:H21, O178:H19, O113:H4 and O91:H14) have been described as the most frequent colonizers of cattle worldwide (Beutin et al., 1993; Hussein and Sakuma, 2005; Irino et al., 2005; Pradel et al., 2000; Sandhu et al., 1996; Zweifel et al., 2005). STEC serotypes that were shown to be closely associated with pigs (O8:H9, O8:H19, and O100:H30), sheep (O128:H2 and O146:H21), goats (O76:H19) and deer (O21:H2, O174:H8, and O146:H28) (Djordjevic et al., 2004; Beutin et al., 1993; Blanco et al., 2003; Beutin et al., 2008; Fratamico et al., 2004; Ishii et al., 2007; Lehmann et al., 2006; Zweifel et al., 2004) were also found frequently in food products derived from these animals (Fig. 1, Supplementary data Table A).

The Shiga toxin genotype was previously shown to have an influence on the clinical picture of STEC infected patients. Infections with STEC carrying a stx2 (including stx2a, stx2c and stx2d) gene were associated with severe clinical outcomes (Friedrich et al., 2002; Jelacic et al., 2003). STEC carrying stx1c and stx2b genes were mainly associated with uncomplicated diarrhoeal disease (Friedrich et al., 2002, 2003) and stx2e was not implicated in human illness (Beutin et al., 2008; Friedrich et al., 2002). In our study, the stx2e gene was found closely associated with STEC from bovine meat (68.4%) and milk (55.7%) products and with meat from hare (61.9%). STEC contaminated food derived from cattle and hare may thus bear an increased risk for the human consumer compared to products derived from other animals.

The findings of our study indicate that the food producing animal represents the most important source for the entry of STEC in the food chain. Sound hygiene measures implemented at critical stages of food production (milking, slaughtering, and evisceration) should be most effective in reducing the frequency of STEC contamination of food derived from domestic and wildlife animals.

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