Gene transfer events and their occurrence in selected environments

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Abbreviations: DNA, deoxyribonucleic acid; DNases, deoxyribonucleases; FDA, Food and Drug Administration; GI, gastrointestinal tract; GM, genetically modified; HC, haemorrhagic colitis HGT, horizontal gene transfer; HUS, haemolytic-uremic syndrome ROAR, reservoirs of antibiotic resistance; STEC, shiga toxin-producing E. coli; Stx, shiga toxin; T-DNA, transferred DNA; U. S., United States; UHT, ultra heat treated; WHO, World Health Organisation;
Abstract

Genes encoding virulence determinants are transferred between species in many different environments. In this review we describe gene transfer events to and from different species of bacteria, from bacteria to plants, and from plants to bacteria. Examples of the setting for these transfer events include: the GI tract, the rumen, the oral cavity, and in food matrixes. As a case study, the flux of virulence factors from E.coli O157:H7 is described as an example of gene flow in the environment.
Introduction

The movement of genes amongst different species occurs in nature, between closely
related organisms via the typical avenues of reproduction, and between different
species via horizontal gene transfer (HGT). An important consideration about the
concept of HGT is not whether genes can move into other organisms but whether
these genes confer enough of an advantage to make keeping them worthwhile. Gene
transfer events in nature have been assessed by three different approaches:
examination of the nucleotide sequences of similar genes in different organisms;
experimental demonstration of gene transfer under laboratory conditions and the
analysis of horizontal transfer events in microcosms and field surveys. These transfer
events have been shown to take place between different bacterial species; between
plants and bacteria; and between animals and plants (Droge et al., 1998). Some of the
evidence relating to these transfer events will be presented below. Gene transfer in
some selected environments will also be described in greater detail. The movement of
virulence factors from Escherichia coli O157:H7 will be presented as an example of
gene flux in the environment.

Transfer of genes between bacterial species

The first documented evidence of in vitro transfer between Gram-negative bacteria
and Gram-positive bacteria was in 1987, when Trieu-Cuot et al. transferred the
plasmid pAT187 from Gram-negative E. coli to the Gram-positive strains:
 Enterococcus faecalis, Streptococcus lactis, Streptococcus agalactiae, Bacillus
 thuringiensis, Listeria monocytogenes and Staphylococcus aureus (Trieu-Cuot et al.,
1987). These transfer events lead to the belief that there could be “inter-Gram”
genetic exchange in natural conditions. In a review by Courvalin, it was proposed that
in nature, there is a bias in the gene flux from Gram-positive cocci to Gram-negative bacteria, because of the barriers to heterologous gene expression that impedes the expression of Gram-positive genes in Gram-negative bacteria and not vice versa (Courvalin, 1994). The ubiquitous transfer mechanism between Gram-positive and Gram-negative bacteria is thought to be conjugation due to the broad host range of transfer and autonomous replication, however, the possibility of transfer via transduction or transformation has not been ruled out between the two Gram type strains. Lactic acid bacteria, including members of the genus *Enterococcus*, *Lactobacillus* and *Lactococcus* have been shown to freely participate in the communications superhighway that is the lateral transfer of genes, particularly antibiotic resistance determining genes. Therefore lactic acid bacteria, like other bacteria, participate in the transfer of antibiotic resistance characteristics across species and genus borders. Identical genes responsible for antibiotic resistance are found in commensal lactic acid bacteria, pathogenic bacteria and opportunistic pathogenic bacteria. This has lead to the suggestion that there are no barriers between these three bacterial groups (Mathur and Singh, 2005).

**Transfer of genes from bacteria to plants**

*Agrobacterium tumefaciens* is a ubiquitous soil bacterium which can transfer DNA to plants in genetic modification studies. This bacterium is responsible for crown gall disease, which induces galls, or tumours, on certain plants. Gall formation is attributable to the integration of bacterial transferred DNA (T-DNA) into the plant chromosome. The advent of biotechnological techniques has enabled the manipulation of T-DNA so as to facilitate the transfer of foreign genes into a wide variety of plants (Broothaerts et al., 2005). *A. tumefaciens* was considered to be the only bacterial
species capable of this transfer, but Broothaerts group managed to obtain various plant transformants using non-\textit{Agrobacterium} strains \textit{Rhizobium} sp., \textit{Sinorhizobium meliloti} and \textit{Mesorhizobium loti}, albeit at a lower frequency rate than with \textit{A. tumefaciens}.

\textbf{Transfer of genes from plants to bacteria}

Genes from transgenic tobacco plants, with transgenes residing on the chloroplast genome, have been shown to be transferred to \textit{Acinetobacter}. In this case the bacterial species housed a plasmid that contained homologous sequences to the chloroplast genome (Kay et al., 2002). Despite the fact that plant nucleases, microbial nucleases and shear forces contribute to the destruction of plant DNA, intact DNA sections can actually be located in the environment. DNA found in the environment can be protected by adsorption to sand and clay particles, making it more resistant to the action of DNases (Davison, 1999, Gay, 2005). Gene transfer between GM plants and bacteria has occurred in a soil environment, where a prerequisite for this transfer was a homology between donor and recipient DNA (Eede et al., 2004). Many GM plants have been developed with antibiotic genes that retain their original bacterial promoter. This is because the gene of interest was originally engineered into an \textit{E. coli} cloning vector containing the antibiotic resistant genes. \textit{Agrobacterium} binary vector systems also sometimes contain bacterial antibiotic resistance genes and have been used to introduce transgenes into plants (Gasson, 2000).

Currently, many GM plants are cultivated for different reasons ranging from: carriage of genes resistant to a particular pesticide, herbicide or insect; the rendering of plants male-sterile; delaying the ripening of fruit; or simply to be a transformation marker (Ishimania et. al., 2006; Uzogara, 2000). These transgenes in GM plants often contain
prokaryotic sequences. There has been major concern into the potential for these transgenes to migrate from GM plants to human or animal intestinal microbes (Heritage, 2004; Heritage, 2005). One of the main concerns is that antibiotic resistance genes used in the construction of GM plants may end up in pathogenic bacteria that reside in the gastrointestinal (GI) tract (Wilcks et al., 2004).

Many species of bacteria may develop natural competence, or the ability to take up naked DNA, in the gastrointestinal (GI) tract, and this development, along with factors like the integrity and quality of the DNA from GM plants that reaches the GI tract, are major factors when considering the risk associated with consumption of GM foods. The GI tract is broken up into many parts, with the proximal portion being the part where the DNA is released from the food matrix and is exposed to breakdown via nuclease activity and low pH in the stomach (Wilcks et al., 2004). Many of the antibiotic resistance genes present in GM plants are under the control of plant promoters and would normally need the addition of a bacterial promoter in order to be functional in a recipient bacterial cell. However, it was also shown that the sequences of the plant promoter themselves were recognised by the bacterial transcription apparatus (Jacob et al., 2002, Lewin et al., 1998). Duggan et al. found that free DNA survives in a functional state for a considerable amount of time in ovine saliva but survives a much shorter amount of time in rumen fluid and effluent due to high concentrations of free endo and exo-nucleases (Duggan et al., 2000), indicating that the possibility for natural transformation in the oral cavity is a distinct possibility.

Recently, Kleter et al. (2005) evaluated the health considerations regarding the transfer of microbial transgenes present in genetically modified crops. 10 different
transgenes routinely used in market-approved crops were examined using a number of criteria e.g. microbial source, natural function of gene examined, prevalence of gene in other organisms. Two of the transgenes examined were DNA adenine methylase (\textit{dam}) and the \(\beta\)-glucuronidase (\textit{uid}A) genes from \textit{E. coli} and the \textit{cry} genes from \textit{Bacillus thuringiensis}. The microbial genes reviewed in the study did not give rise to any health concerns, but Kleter et al. advised that any transgenes not mentioned in this study should be subjected to examination using their outlined criteria.

A review by Thomson (2001) outlines the steps and the consequences of gene transfer from a GM crop to intestinal bacteria. The author examines the various worst-case scenarios (where gene transfer is affected) and the consequences of each step are discussed. It was found that horizontal gene transfer events between GM crops and intestinal bacteria have occurred, but they are quite rare. However, because these rare events may have an ecological impact, genes introduced into a GM plant should be subjected to risk assessment.

In a review by Goldstein et al. (2005), where they discussed human safety considerations of genetically modified plants with respect to antibiotic resistance genes, the authors came to the conclusion that at the moment there is no documentation of intact functional antibiotic resistance gene transfer from plants to bacteria, and because these genes are readily available in bacterial reservoirs already, the frequency of such plant to bacteria transfer events is trifling. The selective effect of antibiotic use in the environment contributes more to the evolution of resistant strains by spontaneous mutation and transfer of existent resistant plasmids.
A number of years ago, both the U. S. Food and Drug Administration (FDA) and the World Health Organisation (WHO) concluded that there is no risk in consuming DNA from biotech crops. (WHO, 1991; US-FDA, 1992). The reasoning behind their conclusion is that humans and other animals have always consumed DNA from a wide variety of sources including plants, animals, bacteria, parasites and viruses, so consuming DNA from another source, such as biotech crops, should cause no extra risk.

**Gene transfer in selected environments**

Gene transfer events occur in many diverse environments. The most significant environment for food borne pathogens is the gastrointestinal tract, with the possibility of commensal bacteria acting as a reservoir for the spread of virulence determinants from transient microbiota (Farthing, 2004). Horizontal gene transfer events have also been demonstrated in the rumen (McCuddin et al., 2006), in foodstuffs (Brautigam et al., 1997), in biofilms present on food processing equipment (Maeda et al., 2006) and in the oral cavity (Mercer et al., 1999) and are discussed below.

**Transfer of genes in the gastrointestinal tract**

The gastrointestinal tract (the alimentary canal or the gut), is the system of organs within multicellular animals which takes in food, digests it to extract energy and nutrients, and expels the remaining waste. More than 500 species of bacteria colonize the gastrointestinal (GI) tract (Gilmore and Ferretti, 2003). Differences in the type and total numbers of bacteria present depend, for example on the spatial location in the GI tract (Farthing, 2004). Microbial flora of the gut form part of a dense population
existing in close proximity, which often are part of biofilms. This environment is an ideal one for genetic transfer between different bacterial types (Scott, 2002).

There are numerous examples of conjugation as a means of gene transfer with regards food and the intestine (Eede et al., 2004), therefore it can be thought of as a common and very efficient way to transfer genes to these environments. The digestive tract of animals is thought to be conducive to gene transfer between lactococci and enterics, as supported by genome sequence analysis (Bolotin et al., 2004). Maisonneuve et al. (2000) investigated whether yoghurt had positive effects on plasmid transfer and transconjugant survival in the digestive tract of mice associated with human faecal flora, and found that the rates of transfer were at a lower efficiency and there was no stimulating effect. Salyers et al. (2004) have recently proposed that the human intestine, (i.e.) the GI tract, is rife with gene transfer events, with relatively harmless bacteria casually swapping genes between themselves. This becomes a problem if bacteria that normally are transitory in the human colon acquire virulence genes, particularly resistance genes, by conjugation, thus converting a non-pathogen into a potential pathogen via the transfer of virulence genes. Effectively, these microbial intestine dwellers act as vectors for antibiotic resistance genes (Salyers et al., 2004). Tetracycline and erythromycin resistance determinants encoded on transposons were shown to be transferable from Enterococcus faecalis to E. coli and L. monocytogenes in the digestive tract of mice (Doucet-Populaire et al., 1991, Doucet-Populaire, 1992).

Netherwood et al. (1999), performed in vitro and in vivo studies on the transfer of genes from a genetically modified probiotic in the avian GI tract, and came to the conclusion that the in vivo rate of transfer is higher than the rates obtained in vitro,
and that the true rate of transfer was underestimated due to the asynchronous nature of bacterial cells in the GI tract. Anaerobic bacteria make up 99% of the human gut flora (Vedantam and Hecht, 2003).

Commensal organisms, present in the gastrointestinal tract are thought to be reservoirs of determinants such as antibiotic resistance. There are a number of initiatives (e.g. reservoirs of antibiotic resistance (ROAR); dedicated to determine the dissemination levels of non-pathogenic antibiotic resistance) which try to elucidate the importance of non-pathogens as carriers of virulence determinants. Commensal bacteria can act as a reservoir for the dissemination of virulence genes from transient bacteria. Bacteria ingested with food are transient inhabitants of the GI tract; therefore they can contribute to the gene pool available to resident commensal microflora for genetic exchange. Studies by Blake et al. (2003) using simulated porcine ileal conditions provided clear evidence that antibiotic resistance determinants could be transmitted between commensal and pathogenic members of the Enterobacteriaceae.

The evidence for gene transfer in the colon has been observed in *Bacteroides* species by Shoemaker et al. (2001), where resistance determinants from other Gram-negative and also Gram-positive bacteria were found as part of the genome as conjugative transposons. Frequently, the environment of the gut is exposed to low levels of antibiotics (therapeutic agents, growth promoters, residues from food), which have been shown to stimulate the transfer of mobile genetic elements, such as conjugative transposons (Scott, 2002) and prophage elements (Úbeda et al., 2005). The murine GI tract has proven to be an environment where H-19B, a shiga toxin 1(Stx1)-encoding phage could be transmitted between two *E. coli* strains and the production of
infectious virions which are capable of infecting other \textit{E. coli} strains in the GI tract (Acheson et al., 1998).

\textit{Transfer of genes in the rumen}

The rumen is the first compartment of cattle, sheep and goats. Without the rumen, these animals would not be able to digest high fibre plant materials as all of the digestion that takes place in the rumen is due to the presence of a mixture of microorganisms (Weimer, 1992). These microbes represent a diverse mixture of prokaryotic and eukaryotic organisms (McCuddin et al., 2006). With this mixture of microorganisms, the opportunity for gene exchange in the rumen environment is great. Transfer of antibiotic resistance determinants in the rumen was first documented in sheep in the 1970s, and since then indirect evidence has mounted for rumen transfer events. Rumen protozoa have been shown to play a part in gene transfer between bacteria inhabiting the rumen. McCuddin et al. (2006) investigated this role further between an antibiotic-resistant \textit{Klebsiella} donor and an antibiotic-resistant \textit{Salmonella} recipient, and found that inhabiting rumen flora did indeed enhance gene transfer of antibiotic resistance between these bacterial species.

\textit{Transfer of genes in food}

Food matrices such as ultra heat treated (UHT) milk, cacao drink and tomato juice have been reported to support transformation when external DNA was added along with the bacterial strains. Transfer of DNA to bacteria in foods by transformation necessitates unbroken DNA molecules of a certain length and a certain amount of homology between the bacterial DNA and the extraneous DNA present in the food (Kharazmi et al., 2003). It is also necessary that the recipient bacteria are
transformable in the food environment. Natural transformation in complex food matrices was examined in a naturally competent bacterium, *B. subtilis*, by Brautigam et al. (1997). A variety of milk products: UHT milk with different fat levels; pasteurised milk; and chocolate milk were evaluated as environments for transformation. Competence development occurred in all the milk products tested. Transformation of *E. coli* in a variety of foodstuffs was investigated and it was found that the highest transformation frequencies occurred in milk, soy drink, tomato and orange juice, and that DNA was released and taken up by *E. coli* under food processing conditions, meaning that gene transfer can occur in these environments, which is a food safety concern (Bauer et al., 1999). Gabin-Gauthier et al., (1991) found that conjugal transfer between lactococci occurred during cheese making, but at a lower frequency than under laboratory conditions.

Biofilms, biologically active matrices which consist of cells and extracellular substances, have become an important issue with regards to food hygiene. Biofilms are formed on any submerged surface in any environment where bacteria are present and can form on food products or food product contact surfaces, such as pipes and rubber seals, leading to undesirable potential contamination of the foodstuff. Attachment of bacterial biofilms to foodstuffs or contact surfaces leads to problems with hygiene and economic losses due to spoilage of food. Many pathogens have been shown to persist in biofilms, also making these biological matrices a food safety problem. Getting rid of bacteria which are present in biofilms raises many problems. Bacteria present in biofilms exhibit increased resistance to antimicrobial agents, probably due to many factors including: reduced diffusion of the agent; reduction of bacterial growth rate and the production of degradative enzymes. Bacteria in biofilms
have also been shown to have decreased susceptibility to a wide variety of antibiotics (Kumar and Anand, 1998). *E. coli*, which is not normally considered as naturally transformable requiring exposure to high Ca\(^{2+}\) concentrations to develop competence, has been shown to express modest competence within a colony biofilm (Maeda et al., 2004). Recently, horizontal transfer of nonconjugative plasmids in a colony biofilm of *E. coli* has also been shown (Maeda et al., 2006). The transfer of conjugative plasmids in biofilms has been discussed by Molin et al. (2003) and it seems that there is a difference between conjugative transfer of a R1 plasmid between suspended and sessile (biofilm-inhabiting) *E. coli* pairs. Transconjugants appeared very rapidly and their numbers increased at a high rate in the biofilm situation, whereas when the cells were suspended in a chemostat, transconjugants appeared more gradually. The incidence of antibiotic-resistant enterobacteria was investigated in a variety of agricultural foodstuffs by Boehme et al. (2004), who found that the amount of coliform bacteria present on “common vegetables” (which included carrots, cauliflower, mushrooms, lettuce) was a few orders in magnitude lower than the coliform bacteria present on sprouts, which were highly contaminated. Antibiotic resistance was rife on the sprout-contaminating microflora, whereas only a few resistant strains were found in relation to the common vegetable coliforms.

Wang et al. (2006) examined retail food samples (ranging from milk, cheeses, yogurts, shrimp, deli beef, deli turkey, mushroom and spinach) for the presence of antibiotic resistance determinants. In the majority of retail food examined, antibiotic resistant micro-organisms were detected, indicating that the prevalence of antibiotic resistant commensal organisms in foodstuffs is quite high.
Natural genetic transformation in the oral cavity

The fate of free DNA in saliva was investigated by Mercer et al. (1999), and was found to be able to survive for a considerable amount of time in a semi-degraded state. This study also found that this DNA was able to transform naturally competent Streptococcus gordonii DL1, a natural member of the oral microflora.

The flux of virulence factors of *E. coli* O157:H7

Virulence genes of *E. coli* are present on several mobile genetic elements such as plasmids, phages, transposons and pathogenicity islands. New *E. coli* pathotypes, with new combinations of genetic information are constantly emerging. *E. coli* represents a potential pool of virulence genes which may play a key role in the origin of emerging diseases caused by *E. coli* and other bacteria, and which may occur in yet unexplored ecological niches (Kuhnert et al., 2000). In this section, the flux of Shiga toxin-producing *E. coli* (STEC) virulence factors in the bacterial population in the farm environment and potential adjacent areas will be examined.

STEC have been isolated from many animal species, including sheep, goat, deer, pig, cat, horse and gull, however cattle appear to be the major reservoir for *E. coli* O157:H7 and other STEC (Renter and Sargeant, 2002). The animals harbour this pathogen in their GI tracts and shed the bacteria in their faeces (Chapman et al., 1993). Enteric bacteria, like *E. coli* are able to survive in different environments, while the gut is their natural ecosystem (Witte, 2000). The ability of *E. coli* O157:H7 to survive under environmental conditions outside of the gastrointestinal tract is one of the factors enabling gene transfer from this pathogen in the environment. Faeces are an important vehicle for the distribution of *E. coli* O157, as this pathogen is able
to survive up to 18 weeks in this medium (Wang et al., 1996, Kudva et al., 1996).

Raw manure, untreated and treated slurry which all include faeces, is often utilized to
fertilize soil (Jones 1980; Mechie et al., 1997), which aids in the spread of this
pathogen. *E. coli* O157:H7 has been shown to survive in non-aerated ovine manure
pile for more than 1 year and in aerated ovine manure or bovine manure piles several
months (Kudva, 1998). The pathogen has survived in drinking water troughs
(Hancock et al. 1998; LeJeune et al., 2001) for at least 6 months and also in farm
water for long periods (McGee et al., 2002).

A great diversity of the *stx*- (shiga toxin gene) and *eae*- ( intimin gene) positive *E. coli*
isolates were detected in slaughterhouse wastewater that was ready to be released into
the environment (Loukiadis et al., 2002). River water collected upstream from the
slaughterhouses show a lesser contamination with this pathogen than river water
collected downstream from the slaughterhouses (Loukiadis et al., 2002). *E. coli*
O157:H7 has also been isolated, for example from animal feed and flies at dairy farms
(Shere et al., 1998). Barker et al. (1999) have shown that *E. coli* O157:H7 survives
and replicates in a common environmental protozoan, *Acanthamoeba polyphaga*,
which are widely distributed in soils and effluents. This ability to survival in protozoa
may have enabled the persistence of *E. coli* O157:H7 in the natural environment
(Brown et al., 2002). High levels of transfer of conjugative and mobilizable plasmids
from *E. coli* to a wide variety of strains of *Proteobacteria* were observed in the gut of
the soil microarthropod *Folsomia candida* (Hoffmann et al., 1998). In another study, a
conjugative plasmid was transferred between strains of *E. coli* in the gut of *Rhabditis
nematodes* (Adamo and Gealt, 1996).
E. coli O157:H7 possesses a potent combination of virulence factors. The main virulence factors in the disease progression of haemorrhagic colitis (HC) and haemolytic-uremic syndrome (HUS), caused by this organism, are Shiga toxins (Stx1 and Stx2) which are encoded by bacteriophages (O’Brien et al., 1984). It has been suggested by Urdahl et al. (2003) that animals kept in pens probably maintain a higher level of Stx in the intestine than tethered animals, because they would have more faecal-oral contact, thus more chance of cross-contamination. In Norwegian dairy cattle herds it is thought that loose housing presents the major risk factor for occurrence of Stx2 (Vold et al., 2000).

Transfer of shiga toxin between STEC and non STEC serotypes and STEC and other members of the Enterobacteriaceae occurs via the transduction of \textit{stx} phages (Beutin et al., 1999; Schmidt et al., 1999). In several studies the intraintestinal transmission of \textit{stx}-bearing bacteriophages to new bacterial hosts has been demonstrated, for example \textit{in vivo} (Acheson et al., 1998) and \textit{in vitro} (Schmidt et al., 1999). Phages were also shown to be transmitted extraintestinally (Muniesa and Jofre; 2004). Infectious Shiga toxin phages have been observed in the sewage of various countries and in faecal contaminated rivers (Muniesa et al., 1999; Muniesa et al., 2000; Muniesa and Jofre, 2004; Tanji et al., 2003), and also in surface water (Dumke et al., 2006). These phages have been shown to exhibit higher persistence to natural inactivation and disinfection treatments in aquatic environments (Muniesa et al., 1999; Tanji et al., 2003).

Naturally occurring phages that carry the Stx2 gene and infect \textit{E. coli} O157:H7 are able to persist in the water environment more successfully than their host bacteria and show a higher resistance than their host bacteria to chlorination and heat treatment. Furthermore, Stx2 genes which are incorporated in free phages persist outside the gut
much more successfully than the genes incorporated in the bacterial genome (Muniesa et al., 1999). In several studies of cattle, seasonal fluctuations of faecal shedding of *E. coli* 0157:H7 was observed. No significant seasonal differences in the levels of shedding of Stx2 gene-carrying bacteria in monitored human wastewater treatment plant and contaminated river waters was observed in a Japanese study (Kurokawa et al., 1999). Bacteriophages may be an important pool of toxigenic strains based on the numbers and persistence of bacteriophages in natural environments (Muniesa et al., 1999). García-Aljaro et al. (2004) indicated the potential contribution of bacteriophages to the mobility of the Stx2 gene should not be underestimated. Additionally the occurrence of the Stx2 gene in populations detected in sewage (phages or bacteria) demonstrates an exchange of this gene between these populations (García-Aljaro et al., 2004). The aminoglycoside apramycin has been used extensively in livestock in the UK since 1978 (Yates et al., 2004), studies have shown that apramycin-resistant commensal *E. coli* are absent in cattle that have never been treated with aminoglycosides.

**Conclusion**

Horizontal gene transfer occurs in many different locations under many diverse conditions. We have seen in this review that gene transfer events have occurred from plants to bacteria; bacteria to plants; in the gastrointestinal tract; in the oral cavity; and on food surfaces, to name a few instances. There is no doubt that there are still numerous places and circumstances to be discovered where gene transfer events can occur. Genetic exchange is widespread in the environment relevant to food borne microflora. The three mechanisms of gene transfer, conjugation, transformation and
transduction, are represented in this environment, and conjugation seems to be the most ubiquitous mechanism present from the studies examined.

We have seen from this review that natural transfer of genetic material between bacteria and the environment is ubiquitous, and this transfer is necessary for the generation of diverse species. Mobile genetic elements, by various methods, move in and out of bacterial genomes adding extra abilities and allowing proliferation of bacterial species in new niches. One of the main requirements for transfer of virulence determinants between strains is the proximity of the donor and recipient organisms. This information should be taken into consideration in future risk assessment of foodborne bacterial pathogens.
References


Running title: Conditions facilitating transfer of virulence factors


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