



Insects as vectors of foodborne pathogenic bacteria

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Summary

Food safety is an important consideration worldwide. To maintain and improve our current knowledge of foodborne disease outbreaks, we must understand some of the more imminent issues related to food safety. A variety of agents are responsible for transmitting the estimated 76 million cases of illnesses caused by foodborne pathogens every year. This review explores why insects pose a serious health concern, in terms of worldwide food safety initiatives, by looking at evidence in published literature. We highlight at least eleven different species of insects, including the lesser mealworm, Alphitobius diaperinus (Panzer); secondary screwworm, Cochliomyia macellaria (Fabricius); synanthropic flies [flesh fly, Sarcophaga carnaria (L.); house fly, Musca domestica (L.); fruit fly, Drosophila melanogaster (Meigen); and stable fly, Stomoxys calcitrans (L.)], American cockroach, Periplaneta americana (L.); German cockroach, Blatella germanica (L.); Oriental cockroach, Blatta orientalis (L.); Pacific beetle cockroach, Diploptera punctata (Eschscholtz); and Speckled feeder cockroach, Nauphoeta cinerea (Olivier), which act as vectors for Salmonella spp. or Escherichia coli and illustrate how these insects are successful vectors of foodborne disease outbreaks. We propose that insects be considered as one of the latest issues in food safety initiatives. Not only are some insects extremely important contributors to diseases, but now we suggest that more research into insects as potential carriers of E. coli and Salmonella spp., and therefore as contributing to foodborne disease outbreaks, is granted.

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Keywords

Foodborne pathogens; vehicles of transmission; lesser mealworm; synanthropic flies; secondary screwworm; etiological agents of foodborne disease; *Salmonella* spp.; cockroach; food safety; insects

Introduction

Most bacteria associated with insects belong to the Gammaproteobacteria, which includes foodborne pathogenic bacteria such as *E. coli*, *Salmonella* spp., *Shigella*, and others (Gil et al., 2004). The potential presence of foodborne, pathogenic bacteria, such as *E. coli* and *Salmonella* spp., in insects may be in part responsible for the public health issue that the United States currently faces.

The prevalence of outbreaks and the economic and societal costs associated with a variety of harmful and sometimes deadly bacterial strains has steadily risen. Each year in the U.S., foodborne pathogens cause an estimated 76 million cases, 325,000 hospitalizations and 5,200 deaths (Mead et al., 1999). An estimated total of \$1.426 trillion in economic and societal costs are based on the 76 million cases, and the medical care concerning physician visits, treatments, and hospitalizations of those infected account for great costs (Roberts, 2007). Such a profound figure for the economic costs of those not seeking medical care is due to other costs from the general public, food service industry, and regulatory and public health sector (Buzby and Roberts, 2009). Food recalls reflect a pressing need for heightened food safety, especially when confronting the complex or unknown transmissions of foodborne pathogens.

The role of insects in spreading foodborne disease

Insects naturally harbor bacteria but the presence of foodborne, pathogenic bacteria, such as *Salmonella* spp., in insects is observed less often (Priest and Goodfellow, 2000; Figure 1). When *Salmonella* spp. and *E. coli* are associated with insects, there may be confusion in defining the role of insects in such an association. Insects can serve as carriers, vehicles of transmission, hosts, reservoirs, and mechanical and biological vectors; in this review, we are most interested in highlighting the potential of insects acting as mechanical and biological vectors as well as acting as carriers of *Salmonella* spp. and *E. coli*, which are etiological agents of foodborne disease; we have preliminary evidence to suggest that insects may transmit etiological agents of foodborne disease.

Because foodborne pathogens survive for some time outside their environmental reservoir, insects can be physically infected upon contact with fecal matter or other poorly monitored biohazards teeming with foodborne pathogens and then physically carry these pathogens, an example of a mechanical vector. In contrast, a biological



Figure 1. The expression, "there is a fly on my food", could have added significance as sometimes insects transmit pathogenic bacteria.

vector contains a pathogen multiplying or developing inside the vector's body (Goddard, 2009). If, for any amount of time, foodborne pathogens are surviving internally in an insect, then we shall consider them to at least be biological vectors. The Centers for Disease Control and Prevention typically refers to vectors of foodborne disease outbreaks as vehicles of transmission, whereas a foodborne pathogen reservoir is identified as an environmental source of the pathogens. It is also important to consider that not every individual of a particular implicated species herein carries foodborne pathogens. In fact, most insects do not even harbor *Salmonella* spp. or *E. coli*. Rather, there are documented associations between *Salmonella* spp. and *E. coli* and many species of insects.

Epidemiology of insects as vehicles of transmission

We are often unsure of the vehicle of transmission of foodborne pathogens and disease. Between 1998 and 2002, 42 of the 88 reported deaths from foodborne disease, or 47.7%, were caused by unclassifiable or complex vehicles of transmission; 79.5% of the total deaths were listed as classifiable, meaning that 20.5% of the total deaths were caused by unknown vehicles of transmission (Lynch et al., 2006). Also between 1998 and 2002, unclassifiable or complex vehicles of transmission accounted for 50,387 cases (39.25% of cases) and 2,311 outbreaks (34.7% of outbreaks) of foodborne pathogens; 63.9% of the total cases and outbreaks were listed as classifiable, meaning that 36.1% of the total cases and outbreaks were caused by unknown vehicles of transmission (Lynch et al., 2006). None of the data implicates insects as vectors or reservoirs. There are distinct possibilities that insect vectors may have a role in the etiology of foodborne disease. Insects, particularly those that harbor foodborne pathogenic bacteria, provide a potential insight into how bacterial contamination occurs in our crops and livestock and may lead to outbreaks. This review explores published research on living insect vectors for Salmonella spp. and E. coli and discusses how the future of food protection may depend on insect vector transmission of foodborne bacteria to plants and other foods, or vice versa. Because Salmonella spp. cause an estimated 1.4 million cases of salmonellosis each year with Salmonella enterica subsp. enterica serovar Enteritidis as the most common serovar, we describe specific cases of confirmed vectors of Salmonella spp. (Voetsch et al., 2004; Lynch et al., 2006; Cianflone, 2008).

Like other organisms, bacteria and archaeans receive a binomen (e.g. *Salmonella enterica*) that can be followed by a subspecies rank (abbreviated, subsp., e.g. *enterica*) (Holt, 1989; Grimont and Weill, 2007). In addition, in bacteriology organisms may receive further names, such as serovar (e.g. Saintpaul), variant (e.g. Kauffman-White), etc. (Holt, 1989; Grimont and Weill, 2007). These infrasubspecific ranks are not regulated by the International Committee on Systematics of Prokaryotes (ICSP).

Insect species associated with Salmonella spp. and E. coli

Insects that have been implicated in associations with *Salmonella* spp. and/or *E. coli* include the histerid beetle, *Carcinops pumilio* (Erichson); hairy fungus beetle, *Typhaea stercorea* (L.); lesser mealworm, *Alphitobius diaperinus* (Panzer); dump fly, *Hydrotaea*

Table 1. Insect vectors associated with foodborne pathogens. Note, this list is not exhaustive.

Insect Vector	Associated foodborne pathogen
Histerid beetle, Carcinops pumilio ²	Salmonella spp.
Hairy fungus beetle, <i>Typhaea stercorea</i> ⁵	Salmonella spp.
Lesser mealworm, Alphitobius diaperinus ³	Salmonella spp.
Dump fly, Hydrotaea aenescens ⁶	Salmonella spp.
Rice weevil, Sitophilus oryzae ⁴	Salmonella spp.
Face fly, Musca autumnalis ⁷	Escherichia coli
Synanthropic flies [flesh flies Sarcophaga carnaria, houseflies Musca domestica, fruitflies Drosophila melanogaster, and stable flies Stomoxys calcitrans] ⁹	Salmonella spp. and E. coli
Secondary screwworm (blow fly), Cochliomyia macellaria ⁸	Salmonella spp. and E. coli
American cockroach, Periplaneta americana ¹	Salmonella spp. and E. coli
German cockroach, Blatella germanica ¹	Salmonella spp. and E. coli
Oriental cockroach, Blatta orientalis1	Salmonella spp. and E. coli
Pacific beetle cockroach, Diploptera punctata	Salmonella spp. and E. coli
Speckled feeder cockroach, Nauphoeta cinerea	Salmonella spp.

Data from ¹Mullen, 2009; ²Gray et al., 1999; ³Casas et al., 1972; ⁴Schuster et al., 1972; ⁵Hald et al., 1998; ⁶Olsen and Hammack, 2000; ⁷Hollis et al., 1985; ⁸Ahmad et al., 2006; ⁹Greenberg, 1973.

aenescens (Wiedemann); and rice weevil, Sitophilus oryzae (L.) (Casas et al., 1972; Schuster et al., 1972; Greenberg, 1973; Singh et al., 1980; Hald et al., 1998; Gray et al., 1999; Olsen and Hammack, 2000). Other carriers include: all synanthropic flies, a term used to describe over 350 fly species, including flesh flies, Sarcophaga carnaria (L.); houseflies, Musca domestica (L.); fruitflies, Drosophila melanogaster (Meigen); and stable flies, Stomoxys calcitrans (L.), among hundreds of others, that live around and coexist in human settlements; and the secondary screwworm (blow fly) Cochliomyia macellaria (Fabricius), which, along with synanthropic flies, harbor Salmonella spp. and E. coli (Greenberg, 1973; Olsen, 1998; Kobayashi et al., 1999; Ahmad et al., 2006; Forster et al., 2007; Forster et al., 2009) (Table 1). At least four species of cockroaches, including American cockroach, Periplaneta americana (L.), German cockroach, Blatella germanica (L.), Oriental cockroach, Blatta orientalis (L.), Pacific beetle cockroach, Diploptera punctata (Eschscholtz), and Speckled feeder cockroach, Nauphoeta cinerea (Olivier), are another major insectan group that have been implicated in the possible mechanical transmission of foodborne pathogens (Singh et al., 1980; Jones et al., 1991; Mullen et al., 2009) A potential vehicle of transmission of E. coli includes the face fly Musca autumnalis (De Geer) when inoculated for research projects; the bacteria's survival during the inoculation studies illustrates the potential transmission of foodborne pathogens (Hollis et al., 1985; Janisiewicz et al., 1999).

Many epidemiological studies have described the impact that insects have on *Salmonella* spp. transmission; we focus our discussion on insects regarding the vehicular transmission of *Salmonella* spp. (Oosterom, 1991). The secondary screwworm (blow fly) *C. maellaria* is a carrier for *Salmonella* spp., including *S. enterica* subsp. *enterica* serovar Typhimurium. It feeds on decaying organic matter and so only appears where decomposing animal carcasses are available (Byrd, 1998). Insects associated with

carrion are a cause for concern. Although there exists no direct connection to food safety, Urban and Broce (1998) found that *M. domestica* and *C. macellaria* are the most significant transmitting vectors of pathogens in Kansas dog kennels. This supports implicating the housefly and secondary screwworm as competent vectors for foodborne bacteria.

Alphitobius diaperinus, a type of beetle also known as the lesser mealworm, was shown to harbor *S. enterica* subsp. *enterica* serovar Saintpaul variant Kauffman-White in 3% of the mealworms collected from one locality of turkey-brooder houses (Casas et al., 1972). In addition, Harein et al. (1972) successfully isolated *Salmonella* spp. from *A. diaperinus*, and McAllister et al. (1994) found that more than 70% of surface-disinfected lesser mealworms were positive for *S.* Typhimurium, both internally and externally, for as long as 16 days after the first artificial exposure to *S.* Typhimurium. *A. diaperinus* is also able to serve as a vector for *S.* Typhimurium and *S. enterica* subsp. *enterica* serovar Paratyphi B variant Java, highlighting broiler houses and their chickens as a potential source of *Salmonella* spp. (McAllister et al., 1994; Hazeleger et al., 2008).

Another naturally occurring association between insects and Salmonella spp. occurs in synanthropic flies. Because flies serve as vectors of pathogens, extensive studies have been performed that illustrate its capacity as a vehicle for transmission of pathogens (De Jesús et al., 2004; Banjo et al., 2005; Forster et al., 2009). In one study, all 56 caught flies harbored multiple species of microorganisms and successfully transmitted these germs to plates of blood agar (Forster et al., 2009). Forster et al. (2007; 2009), for example, discovered various strains of pathogenic E. coli, including EAEC, EHEC, EPEC, and ETEC, both in the intestines and on the exoskeleton of the housefly, Musca domestica and stable fly, Stomoxys calcitrans. Houseflies in Mexico had a capacity to naturally carry Salmonella spp. from slaughterhouses to markets and other areas within close proximity (Greenberg et al., 1963). More recently, S. Enteritidis was isolated from M. domestica, S. enterica subsp. enterica serovar Infantis from M. domestica and the dump fly Hydrotaea aenescens, S. enterica subsp. enterica serovar Heidelberg from M. domestica, and S. enterica subsp. enterica serovar Mbandaka from A. diaperinus (Olsen and Hammack, 2000). Flesh flies, S. carnaria, can be found on decaying meat, vegetation, and flowers while M. domestica consumes both contaminated and noncontaminated food (Greenberg, 1971). Furthermore, an extensive list of insect vectorfoodborne pathogen associations exists in published literature, and we acknowledge that our review is not exhaustive of all insect vectors and all associated foodborne pathogens. Nonetheless, many serovars of Salmonella spp. have been associated with synanthropic flies (Table 2), especially M. domestica and C. macellaria, along with species of cockroaches (Table 3).

Cockroaches have been implicated in *Salmonella* spp. contamination as well (Singh et al., 1980; Jones et al., 1991). Long regarded as an organism with vector potential, cockroaches feed on both sanitary waste and human food, and this lifestyle certainly impacts food safety initiatives (Klowden and Greenberg, 1976). Cockroaches are also notorious pests in urban environments where population densities tend to be greater and more individuals can be exposed to mismanaged foodborne disease outbreaks.

Table 2. Serovars of *Salmonella enterica* subsp. *enterica* associated with species of synanthropic flies. Note, this list is not exhaustive.

Serovar of Salmonella enterica subsp. enterica	Associated synanthropic species of fly
	Cochliomyia macellaria
Amersfoort	Musca domestica, C. macellaria
Anatum	M. domestica, C. macellaria
Ballerup	M. domestica, C. macellaria
Blockley	M. domestica, Stomoxys calcitrans
Budapest	M. domestica
Cholerae-suis	M. domestica, C. macellaria
Derby	M. domestica, C. macellaria
Dublin	M. domestica, C. macellaria
*Enteritidis	M. domestica, C. macellaria
Florida	M. domestica, C. macellaria
Gallinarum	M. domestica
Give	M. domestica, C. macellaria
[†] Heidelberg	M. domestica
Hirschfeldii	M. domestica, Sarcophaga carnaria
[♦] Infantis	M. domestica
Kentucky	M. domestica, C. macellaria
Kottbus	M. domestica, C. macellaria
Meleagridis	M. domestica, C. macellaria
Minnesota	M. domestica
Narashino	M. domestica, C. macellaria
New Brunswick	M. domestica, C. macellaria
*Newport	M. domestica, C. macellaria
Onderstepoort	M. domestica, C. macellaria
*Oranienburg	M. domestica, C. macellaria
Oregon	M. domestica, C. macellaria
Panama	M. domestica, C. macellaria
Paratyphi A	M. domestica
Paratyphi B	M. domestica, C. macellaria, S. calcitrans
Pullorum	M. domestica
Reading	M. domestica, C. macellaria
*Saintpaul	M. domestica
Sandiego	M. domestica
Schottmuelleri	M. domestica
Typhi	M. domestica, C. macellaria, S. calcitrans,
1) Pin	S. carnaria, Drosophila melanogaster
*Typhimurium	M. domestica, C. macellaria
Worthington	M. domestica
Zanzibar	M. domestica, C. macellaria
Zanzidar	141. aomestica, C. maceuaria

Most citations come from Greenberg, 1971. *Top 10 observed serovar of *Salmonella enterica* subsp. *enterica* serovars in 2009 (Matyas et al., 2010). *(Olsen and Hammack, 2000).

Furthermore, cockroaches are likely vectors of *Salmonella* spp. when a source of the *Salmonella* spp. is made available to the cockroaches (Kopanic et al., 1994). This is of utmost concern given the significant quantity of cockroaches in poultry production and processing facilities, hospitals, homes, grocery stores, restaurants, among other

Serovar of Salmonella enterica subsp. enterica	Associated cockroach species	
Salmonella spp. (serovar undetermined)	Diploptera punctata	
Bareilly	Periplaneta americana	
Bovis-morbificans	P. americana	
Bredeny	P. americana	
Newport	P. americana	
Oranienburg	P. americana	
Panama	P. americana	
Paratyphi B	P. americana	
Pyogenes	Blatta orientalis	
Typhi	B. orientalis	
Typhimurium	B. orientalis, Nauphoeta cinere	

Table 3. Serovars of *Salmonella enterica* subsp. *enterica* associated with species of cockroaches.

Citations come from Mullen et al., 2009.

places of poor sanitation (Devi and Murray, 1991; Kopanic et al., 1994; Fathpour, et al., 2003).

Discussion

Insects that transport foodborne pathogens are important to the study of how the pathogens can survive and be transmitted to crops and then to other insects and the predators of insects, an example of biological magnification (Devi and Murray, 1991). This idea is a possible avenue for research since much research investigates the potential of certain insects to host E. coli or Salmonella spp. via experimental inoculation, and many studies have looked into the survival of pathogens in these model insects and the outside environment. E. coli has a half-life of about 1 day in water, while Salmonella spp. has an even greater ability to survive in soil, doing so for up to 1 year (Faust et al., 1975; Davies and Wray, 1996; Winfield and Groisman, 2003). Therefore, more field studies are needed to determine the extent that insects are natural vectors of emerging pathogenic bacteria, rather than testing these capacities in laboratory research since these very laboratory studies, involving experimental inoculation, do not conclude whether or not an insect is a natural vector (Olsen et al., 2001). A natural insect vector is documented in the literature as an organism found to be carrying emerging, foodborne pathogenic bacteria, such as E. coli and Salmonella spp., which are typically implicated in more disease outbreaks than that of other species of bacteria. Nonetheless, having knowledge of the list of possible insects capable of carrying living Salmonella spp. and/or E. coli can aid our understanding and prevention of foodborne disease outbreaks because we can target these organisms as potential contributors to outbreaks.

Whether the bacteria are solely present on the outside exoskeleton of insects, such as the lesser mealworm, is debatable. Crippen and Sheffield (2006) studied whether an external surface disinfection was enough to eliminate all bacteria from the exoskeleton.

Most of the disinfection procedures allowed a small percentage of bacteria to survive, but it was unclear if the bacteria survived in crevices of the exoskeleton and/or in the internal environment (Crippen and Sheffield, 2006). De Jesús et al. (2004) illustrated that *M. domestica* could transfer *E. coli* via contaminated legs, feet, body hair or mouthparts and through its excretions or regurgitated fluid after exposure to the pathogen. More research is needed to understand the role of the internal insect midgut in maintaining the survival of *Salmonella* spp. and to elucidate more specific locations of the residence of *Salmonella* spp. Furthermore, more metagenomic studies concerning foodborne pathogens in insects would be beneficial, particularly when relating this to next generation sequencing of these pathogens. Advances in next generation sequencing can elucidate feasibility of the insect gut as an environment for foodborne pathogens.

Potential routes of the spread and contamination of Salmonella spp. and other pathogenic bacteria via insects are quite vast in number although there is no consensus as to the most likely route (Oosterom, 1991; Omwandho and Kubota, 2010). Insects may be contaminated with *Salmonella* spp. or *E. coli* by contact or ingestion of unclean animal byproducts, animal feed, surface waters, sewage, fecal matter, refuse, soil, vegetation, sludge, or during any transportation or processing activities that incorporate or involve any of the aforementioned initial contaminated sources; and, directly or indirectly, may other environments, such as lakes and rivers, as well as farm animals, plants, compost, food, and humans, become infected with these pathogens from the insects (Oosterom, 1991; Omwandho and Kubota, 2010). We have assembled a preliminary flow chart of the modes of transmission of Salmonella spp. via insects, though further research efforts are needed to explain precisely if and/or how insects carry foodborne pathogenic bacteria to plants, used either directly as food or processed and later used in food, or vice versa (Figure 2). However, it is not only insects lower on the ecological food chain that can serve as vectors of foodborne pathogens. We have collected preliminary evidence, along with evidence in published literature, which suggests top predators in a community often end up with the pathogens from their meals (Devi and Murray, 1991). With an understanding of these interactions, we will be that much closer to better control of foodborne pathogen contamination due to insect vectors.

Because some insects, such as the lesser mealworm *Alphitobius diaperinus*, synanthropic flies [flesh fly *Sarcophaga carnaria* (L.), housefly *Musca domestica* (L.), fruit fly *Drosophila melanogaster* (Meigen), and stable fly *Stomoxys calcitrans* (L.)], American cockroach *Periplaneta americana* (L.), German cockroach *Blatella germanica* (L.), Oriental cockroach *Blatta orientalis* (L.), Pacific beetle cockroach *Diploptera punctata* (Eschscholtz), Speckled feeder cockroach *Nauphoeta cinerea* (Olivier), and secondary screwworm *Cochliomyia maellaria*, have been highlighted as vectors of, or having associations with, pathogenic bacteria, and due to the ability of many other insects to act as vectors when experimentally inoculated, we suggest insects be considered as serious contributors of foodborne disease. In addition, despite the complexity of the ecological patterns of insects, the relatively large number of complex or unclassifiable vehicles of transmission of foodborne diseases provides an even greater public health issue than

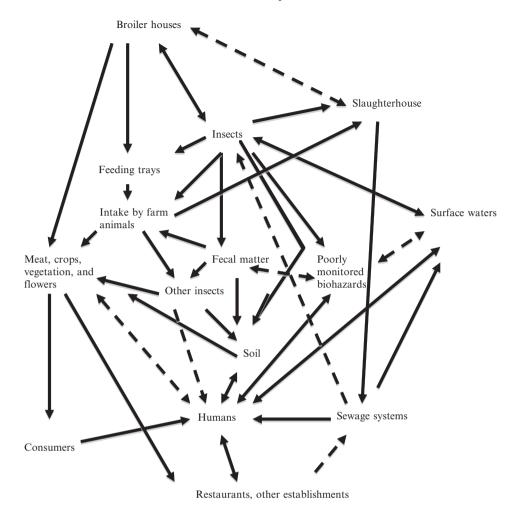


Figure 2. Potential routes of contamination of *Salmonella* spp. with an emphasis on insects. Dashed lines indicate more infrequently observed routes of contamination.

perhaps we have previously thought (Lynch et al., 2006). Therefore, we recommend additional research to uncover the potential variety of insect vectors of *Salmonella* spp. and *E. coli*, especially those involved in the interaction with crops and our food supply.

Acknowledgements

We further thank the anonymous reviewers for their valuable criticism. JMB is now supported by an internship from the Joint Institute for Food Safety and Applied Nutrition to the Food and Drug Administration of the United States of America. EKL is supported by a fellowship from the Oak Ridge Institute for Science Education to the Food and Drug Administration of the United States of America.

References

- Ahmad, A., A. Broce, and Z. Ludek. 2006. Evaluation of significance of bacteria in larval development of *Cochliomyia macellaria* (Diptera: Calliphoridae). Journal of Medical Entomology 43:1129-1133.
- Banjo, A. D., O. A. Lawal, and O. O. Adeduji. 2005. Bacteria and fungi isolated from housefly (*Musca domestica* L.) larvae. African Journal of Biotechnology 4:780-784.
- Buzby, J. C. and T. Roberts. 2009. The economics of enteric infections: Human foodborne disease costs. Gastroenterology 136:1851-1862.
- Byrd, J. H. 1998. Secondary Screwworm, *Cochliomyia macellaria* (Fabricius). University of Florida. IFAS Extension. EENY-022:1-3. http://edis.ifas.ufl.edu/pdffiles/IN/IN14900.pdf.
- Casas, E. L., P. K. Harein, and B. S. Pomeroy. 1972. Bacteria and fungi within the Lesser Mealworm collected from poultry brooder Houses. Environmental Entomology 1:27-30.
- Cianflone, N. F. C. 2008. Salmonellosis and the gastrointestinal tract: more than just peanut butter. Current Gastroenterology Reports 10: 424-431.
- Crippen, T. L. and C. Sheffield. 2006. External surface disinfection of the Lesser Mealworm (Coleoptera: Tenebrionidae). Journal of Medical Entomology 43:916-923.
- Davies, R. H. and C. Wray. 1996. Seasonal variations in the isolation of *Salmonella typhimurium*, *Salmonella enteritidis*, *Bacillus cereus* and *Clostridium perfringens* from environmental samples. Journal of Veterinary Medicine B 43:119-127.
- De Jesús, A. J., A. R. Olsen, J. R. Bryce, and R. C. Whiting. 2004. Quantitative contamination and transfer of *Escherichia coli* from foods by houseflies, *Musca domestica* L. (Diptera: Muscidae). International Journal of Food Microbiology 93:259-262.
- Devi, S. J. N. and C. J. Murray. 1991. Cockroaches (*Blatta* and *Periplaneta* species) as reservoirs of drugresistant *Salmonellas*. Epidemiology and Infection 107:357-361.
- Fathpour, H., G. Emtiazi, and E. Ghasemi. 2003. Cockroaches as reservoirs and vectors of drug resistant *Salmonella* spp. Iranian Biomedical Journal 7:35-38.
- Faust, M. A., A. E. Aotaky, and M. T. Hargadon. 1975. Effect of physical parameters on the In Situ survival of *Escherichia coli* MC-6 in an estuarine environment. Applied Microbiology 30: 800-806.
- Forster, M., S. Klimpel, H. MehLhorn, K. Sievert, S. Messler, and K. Pfeffer. 2007. Pilot study on synanthropic flies (e.g. *Musca, Sarcophaga, Calliphora, Fannia, Lucilia, Stomoxys*) as vectors of pathogenic microorganisms. Parasitology Research 101:243-246.
- Forster, M., K. Sievert, S. Messler, S. Klimpel, and K. Pfeffer. 2009. Comprehensive study on the occurrence and distribution of pathogenic microorganisms carried by synanthropic flies caught at different rural locations in Germany. Journal of Medical Entomology 46:1164-1166.
- Gil, R., A. Latorre, and A. Moya. 2004. Bacterial endosymbionts of insects: Insights from comparative genomics. Environmental Microbiology 6:1109-1122.
- Goddard, J. 2008. Infectious diseases and arthropods. Humana Press. A part of Springer Science + Business Media, LLC. Totowa, New Jersey, U.S.A. 251 pp.
- Gray, J. P., C. W. Maddox, P. C. Tobin, J. D. Gummo, and C. W. Pitts. 1999. Reservoir competence of Carcinops pumilio for Salmonella enteritidis (Eubacteriales: Enterobacteriaceae). Journal of Medical Entomology 36:888-891.
- Greenberg, B., G. Varela, A. Bornstein, and H. Hernandez. 1963. Salmonellae from flies in a Mexican slaughterhouse. American Journal of Hygiene 77:177-183.
- Greenberg, B. 1971. Flies and Disease. Volume 1: Ecology, classification, and biotic associations. Princeton University Press. Princeton, New Jersey, U.S.A. 856 pp.
- Greenberg, B. 1973. Flies and Disease. Volume 2: Biology and Disease Transmission. Princeton University Press. Princeton, New Jersey, U.S.A. 447 pp.
- Grimont, P.A. and F. Weill. 2007. Antigenic Formulae of the *Salmonella* Serovars. WHO Collaborating Center for Reference and Research on *Salmonella*. Ninth Edition. Paris, France. 166pp.
- Hald, B., A. Olsen, and M. Madsen. 1998. Typhaea stercorea (Coleoptera: Mycetophagidae), a carrier of Salmonella enterica serovar Infantis in a Danish broiler house. Journal of Economic Entomology 91:660-664.

- Harein, P. K., D. C. Ernesto, C. T. Larsen, and B. S. Pomeroy. 1972. Microbial relationship between the Lesser Mealworm and its associated environment in a turkey brooder house. Environmental Entomology 1:189-194.
- Harwood, R.F. Entomology in Human and Animal Health. 1979. Macmillan Publishing Co., Inc. New York, N.Y. U.S.A. 548 pp.
- Hazeleger, W.C., N. M. Bolder, R. R. Beumer, and W.F. Jacobs-Reitsma. 2008. Darkling Beetles (*Alphitobius diaperinus*) and their larvae as potential vectors for the transfer of *Campylobacter jejuni* and *Salmonella enterica* Serovar Paratyphi B Variant Java between successive broiler flocks. Applied and Environmental Microbiology 74:6887-6891.
- Hollis, J. H., F. W. Knapp, and K. A. Dawson. 1985. Influence of bacteria within bovine feces on the development of the Face Fly (Diptera: Muscidae). Environmental Entomology 14:568-571.
- Holt, J.G., editor. 1989. Bergey's Manual of Systematic Bacteriology. Volumes 1-4. Williams and Wilkins. Baltimore, Maryland.
- Janisiewicz, W. J., W. S. Conway, M. W. Brown, G. M. Sapers, P. Fratamico, and R. L. Buchanan. 1999. Fate of *Escherichia coli* O157:H7 on fresh cut apple tissue and its potential for transmission by fruit flies. Applied and Environmental Microbiology 65:1-5.
- Jones, F. T., R. C. Axtell, D. V. Rives, S. E. Scheideler, F. R. Tarver, R. L. Walker, and M. J. Wineland. 1991. A survey of *Salmonella* contamination in modern broiler production. Journal of Food Protection 54:502-507.
- Klowden, M. J. and B. Greenberg. 1976. *Salmonella* in the American Cockroach: Evaluation of vector potential through dosed feeding experiments. Journal of Hygiene, Cambridge 77:105-111.
- Kobayashi, M., T. Sasaki, N. Saito, K. Tamura, K. Suzuki, H. Watanabe, and N. Agui. 1999. Houseflies are not simple mechanical vectors of enterohemorrhagic *Escherichia coli* O157:H7. American Journal of Tropical Medicine and Hygiene 61:625-629.
- Kopanic, R. J., B. W. Sheldon, and C. G. Wright. 1994. Cockroaches as vectors of *Salmonella*: Laboratory and field trials. Journal of Food Protection 57: 125-132.
- Lynch, M., J. Painter, R. Woodruff, C. Braden, and Centers for Disease Control and Prevention. 2006. Surveillance for foodborne-disease outbreaks-United States, 1998-2002. Morbidity and Mortality Weekly Report 55:1-42.
- Matyas, B., A. Cronquist, M. Cartter, M. Tobin-D'Angelo, D. Blythe, K. Smith, S. Lathrop, D. Morse, P. Cieslak, J. Dunn, K. G. Holt, O. L. Henao, K. E. Fullerton, B. E. Mahon, R. M. Hoekstra, P. M. Griffin, R. V. Tauxe, and A. Bhattarai. 2010. Preliminary FoodNet data on the incidence of infection with pathogens transmitted commonly through food -10 States, 2008. Morbidity and Mortality Weekly Report 59:418-422.
- McAllister, J. C., C. D. Steelman, and J. K. Skeeles. 1994. Reservoir competence of the Lesser Mealworm (Coleoptera: Tenebrionidae) for *Salmonella typhimurium* (Eubacteriales: Enterobacteriaceae). Journal of Medical Entomology 31:369-372.
- Mead, P. S., L. Slutsker, V. Dietz, L. F. McCaig, J. S. Bresee, C. Shapiro, P. M. Griffin, and R. V. Tauxe. 1999. Food-related illness and death in the United States. Emerging Infectious Diseases 5:607-625.
- Mullen, G. R., G. Mullen, and L. Durden. 2009. Medical and Veterinary Entomology. Academic Press. Second Edition. London, England, U.K. 637 pp.
- Olsen, A. R. 1998. Regulatory action criteria for filth and other extraneous materials. III. Review of flies and foodborne enteric disease. Regulatory Toxicology and Pharmacology 28:199-211.
- Olsen, A. R. and T. S. Hammack. 2000. Isolation of *Salmonella* spp. from the Housefly, *Musca domestica* L., and the Dump fly, *Hydrotaea aenescens* (Wiedemann) (Diptera: Muscidae), at caged-layer houses. Journal of Food Protection 63:958-960.
- Olsen, A. R., J. S. Gecan, G. C. Ziobro, and J. R. Bryce. 2001. Regulatory action criteria for filth and other extraneous materials V. Strategy for evaluating hazardous and nonhazardous filth. Regulatory Toxicology and Pharmacology 33:363-392.
- Omwandho, C. O. A. and T. Kubota. 2010. *Salmonella enterica* serovar Enteritidis: A mini-review of contamination routes and limitations to effective control. Japan Agricultural Research Quarterly 44:7-16.

- Oosterom, J. 1991. Epidemiological studies and proposed preventive measures in the fight against human Salmonellosis. International Journal of Food Microbiology 12:41-51.
- Priest, F. G., and M. Goodfellow. 2000. Applied microbial systematics. Kluwer Academic Publishers. Dordrecht, The Netherlands. 479 pp.
- Roberts, T. 2007. WTP estimates of the societal cost of US food-borne illness. American Journal of Agricultural Economics 89:1183-1188.
- Schuster, D. J., R. B. Mills, and M. H. Crumrine. 1972. Dissemination of *Salmonella montevideo* through wheat by the Rice Weevil. Environmental Entomology. 1:111-115.
- Singh, S.P., M. S. Sethi, and V. D. Sharma. 1980. The occurrence of Salmonellae in rodent, shrew, cockroach and Ant. International Journal of Zoonoses 7:58-61.
- Urban, J. E., and A. Broce. 1998. Flies and their bacterial loads in greyhound dog kennels in Kansas. Current Microbiology 36:164-170.
- Voetsch, A. C., T. J. Van Gilder, F. J. Angulo, M. M. Farley, S. Shallow, R. Marcus, P. R. Cieslak, V. C. Deneen, R. V. Tauxe, and Emerging Infections Program FoodNet Working Group. 2004. FoodNet estimate of the burden of illness caused by nontyphoidal *Salmonella* infections in the United States. Clinical Infectious Diseases. 38 Supplement 3:S127-134.
- Winfield, M. D. and E. A. Groisman. 2003. Role of nonhost environments in the lifestyles of *Salmonella* and *Escherichia coli*. Applied and Environmental Microbiology 69:3687-3694.