Pigs vs people: the use of pigs as analogues for humans in forensic entomology and taphonomy research

Szymon Matuszewski1 • Martin J. R. Hall2 • Gaétan Moreau3 • Kenneth G. Schoenly4 • Aaron M. Tarone5 • Martin H. Villet6

Abstract
Most studies of decomposition in forensic entomology and taphonomy have used non-human cadavers. Following the recommendation of using domestic pig cadavers as analogues for humans in forensic entomology in the 1980s, pigs became the most frequently used model cadavers in forensic sciences. They have shaped our understanding of how large vertebrate cadavers decompose in, for example, various environments, seasons and after various ante- or postmortem cadaver modifications. They have also been used to demonstrate the feasibility of several new or well-established forensic techniques. The advent of outdoor human taphonomy facilities enabled experimental comparisons of decomposition between pig and human cadavers. Recent comparisons challenged the pig-as-analogue claim in entomology and taphonomy research. In this review, we discuss in a broad methodological context the advantages and disadvantages of pig and human cadavers for forensic research and rebut the critique of pigs as analogues for humans. We conclude that experiments using human cadaver analogues (i.e. pig carcasses) are easier to replicate and more practical for controlling confounding factors than studies based solely on humans and, therefore, are likely to remain our primary epistemic source of forensic knowledge for the immediate future. We supplement these considerations with new guidelines for model cadaver choice in forensic science research.

Keywords Forensic entomology • Forensic taphonomy • Pig carcasses • Human corpses • Animal models • Decomposition ecology

“...We are unlikely to ever know everything about every organism. Therefore, we should agree on some convenient organism(s) to study in great depth, so that we can use the experience of the past (in that organism) to build on in the future. This will lead to a body of knowledge in that ‘model system’ that allows us to design appropriate studies of nonmodel systems to answer important questions about their biology” [1].

“Model species are usually easy to rear, observe, or otherwise experimentally manipulate. They therefore allow knowledge to be built up rapidly and efficiently, because confounding factors are known and thus can be controlled in subsequent experiments” [2].

Introduction

While collaborating with medical examiners in the late 1800s, French entomologist Pierre Mégnin [3] advanced the first...
formal definition and testable mechanism of ecological succession and recognized the predictability of carrion-arthropod succession and resource partitioning in human corpses and their application in forensic analysis [4, 5]. These investigations gave birth to the twin disciplines of carrion ecology and forensic entomology. Subsequently, most studies of vertebrate decomposition used non-human carcasses ranging in size from amphibians to elephants (Table 1). Payne innovatively used pig cadavers in his ground-breaking ecological experiments on decomposition [6–8]. Wider interest in forensic entomology and taphonomy arose in the mid-1980s, and such studies initially focussed on pigs or rabbits (Table 1). By the late 1980s, the domestic pig was being recommended as an analogue for humans in forensic entomology research and training workshops [9–11]. Starting in the early 1990s, field studies and statistical models were proposed to test different aspects of the pig-as-analogue claim in forensic entomology [12–14].

Examples of taphonomic studies have been cited from as far back as Leonardo da Vinci in the fifteenth century, but the field began to achieve formality in the 1940s [15]. In the 1970s, palaeoanthropology used taphonomy to interpret the deposition of hominids remains in fossil-rich sites, particularly to provide information about how the hominids lived and died [16, 17]. Integration of fossil-focused taphonomy with physical anthropology led to the differentiation of forensic taphonomy, which relied on extensive comparisons of palaeontological, archaeological and modern case studies [18]. The development of pigs as model organisms in forensic taphonomy provided a more experimental approach for forensic taphonomy and established some major patterns regarding vertebrate decomposition (Table 1, Fig. 1).

The advent of outdoor human taphonomy facilities (often mistemned “body farms” [19]) facilitated experimental studies using human cadavers. First amongst these was the University of Tennessee Anthropological Research Facility, while the first outside the USA was the Australian Facility for Taphonomic Experimental Research (AFTER) [19, 20]. At least eight facilities now exist, six in the USA, one in Australia and one in the Netherlands [20–22]. The facilities have allowed experimental comparison of decomposition in human and non-human models under a variety of conditions [14, 23, 24]. Since then, debate has arisen over the relevance of taphonomic studies for forensics (e.g. [19, 25, 26]), and the proper associated experimental (and ethical) protocols [27, 28]. There is variation in the source populations contributing to taphonomy facilities; moreover, their source cadavers (usually elders dying of natural causes) systematically differ from cadavers involved in forensic scenarios (usually adults dying of unnatural causes). Therefore, for a variety of reasons, the findings from these facilities may be difficult to extrapolate to other human populations and to typical forensic cases.

Recent publications have raised the opportunity to consolidate what has been learned from animal models in decomposition studies, and to examine the implications of this knowledge for the design of field experiments in forensic entomology and taphonomy, specifically, whether animal carcasses can effectively substitute for human cadavers, which is the major aim of this review. Our major focus is research on principles concerning cadaver decomposition, including the associated arthropods and their succession. Therefore this paper does not extensively address topics related to the accuracy and precision of PMI estimation techniques developed in forensic entomology or taphonomy.

**Lessons from pig cadavers**

The use of animal models to advance knowledge dates back to the ancient Greek times with dogs and chicks used to study human anatomy, physiology and ontogeny [29]. Nowadays, animal models are used to study a large array of human related-issues, e.g. diseases [30], mental and neuropsychiatric disorders [31] or orthopaedic and dental implants [32]. In a similar way, our current understanding of animal decomposition is largely derived from experiments with non-human cadavers, with pig carcasses contributing overwhelmingly to this knowledge (Table 1). Payne’s [6] experimental work using piglets was a watershed event in carrion ecology for its impact and originality. After trying carrion from different vertebrate animals (amphibians, mammals, birds), Payne settled on domesticated pigs because he knew the time of their death, he could acquire them in large numbers of uniform age and mass, and their relatively hairless skin and lack of feathers made insect sampling easier than from alternative carcasses. In his experiments, Payne used cages with different mesh sizes to provide open and limited access to insects to document daily changes in carcass decay and dismemberment. He found that carcasses protected from insects mummified, remaining intact for months; whereas, carcasses exposed to insects lost 90% of their starting mass in just 6 days. This result showed that insect access is a key determinant of cadaver decay.

Inspired by Payne’s experimental protocol, forensic entomologists started using pig cadavers in studies focused on inventoritng carrion-arthropod faunas and successional patterns, which have been described for a long list of countries and habitats (Table 1). Although the species involved varied between biogeographical regions, ecological guilds were consistent and functioned in a very consistent way (Table 1). Pigs have illustrated patterns of decomposition over timescales of days, seasons and years (Table 1). Seasonal components of variation in the insect community are relatively well understood and several quantitative models have been proposed to describe the ecological succession that occurs in the arthropod community on a cadaver (Table 1). Much of the early work
### Table 1: Selected cadaver studies in carrion ecology, forensic entomology and taphonomy. References to this table are listed in Electronic Supplementary Material

| Author(s) | Date of publication | Locality | Animal model | Major research focus |
|-----------|---------------------|----------|--------------|----------------------|
| Chapman and Sankey [1] | 1955 | England | Rabbits | Arthropod inventory; habitats |
| Bornemissa [2] | 1957 | Australia | Guinea pig | Arthropod inventory; succession |
| Reed [3] | 1958 | USA | Dogs | Arthropod inventory; succession |
| Payne [4] | 1965 | USA | Pigs | Surface decomposition; insect access |
| Payne et al. [5] | 1968 | USA | Pigs | Underground decomposition |
| Payne and King [6] | 1972 | USA | Pigs | Water decomposition |
| Nabaglo [7] | 1973 | Poland | Bank voles | Surface/underground decomposition; insect inventory; succession; seasons |
| Comby [8] | 1974 | Costa Rica | Lizards, toads | Arthropod inventory; succession; habitats |
| Johnson [9] | 1975 | USA | Small mammals | Arthropod inventory; succession; seasons |
| Smith [10] | 1975 | England | Fox | Arthropod inventory; succession |
| Coe [11] | 1978 | Kenya | Elephants | Surface decomposition; insect inventory |
| McKinnerney [12] | 1978 | USA | Rabbits | Arthropod inventory; succession; scavenging |
| Jiron and Cartin [13] | 1981 | Costa Rica | Dogs | Arthropod inventory; succession |
| Abell et al. [14] | 1982 | USA | Turtles | Arthropod inventory |
| Rodriguez and Bass [15] | 1983 | USA | Humans | Insect inventory; succession |
| Schoenely and Reid [16] | 1983 | USA | Various mammals | Cadaver mass; insect inventory |
| Lord and Burger [17] | 1984 | USA | Gulls | Arthropod inventory; succession; seasons; habitats; scavenging |
| Rodriguez and Bass [18] | 1985 | USA | Humans | Underground decomposition |
| Early and Goff [19] | 1986 | Hawaii | Cats | Surface decomposition; arthropod inventory; succession |
| Micozzi [20] | 1986 | USA | Rats | Freezing; wounds |
| Braack [21] | 1986 | South Africa | Impala | Insect inventory |
| Peschke et al. [22] | 1987 | Germany | Rabbits | Insect inventory; succession; habitats; seasons |
| Tullis and Goff [23] | 1987 | Hawaii | Pig | Surface decomposition; arthropod inventory; succession |
| Blacklith and Blacklith [24] | 1990 | Ireland | Birds, mice | Insect inventory; habitats |
| Kapikian and Streit [25] | 1990 | Germany | Rats | Insect inventory; succession; habitats |
| Hewadikaram and Goff [26] | 1991 | Hawaii | Pigs | Cadaver mass |
| Vass et al. [27] | 1992 | USA | Humans | Compounds released into soil during decomposition |
| Shean et al. [28] | 1993 | USA | Pigs | Sun exposure |
| Anderson and VanLaerhoven [29] | 1996 | Canada | Pigs | Insect inventory; succession |
| Keiper et al. [31] | 1997 | USA | Rats | Water decomposition; habitats; arthropod inventory |
| Richards and Goff [32] | 1997 | Hawaii | Pigs | Arthropod inventory; succession; habitats |
| Avila and Goff [33] | 1998 | Hawaii | Pigs | Burnt cadaver decomposition; habitats; succession |
| Komar and Beattie [34, 35] | 1998 | Canada | Pigs | Cadaver mass; habitats; clothing; post-mortem artefacts |
| Tomberlin and Adler [36] | 1998 | USA | Rats | Water decomposition; insect inventory; seasons; habitats |
| Boul et al. [37] | 1999 | France | Rabbits | Insect inventory; succession; habitats |
| Defong and Chadwick [38] | 1999 | USA | Rabbits | Insect inventory; succession; habitats |
| Turner and Wiltshire [39] | 1999 | England | Pigs | Under ground decomposition |
| VanLaerhoven and Anderson [40] | 1999 | Canada | Pigs | Underground decomposition; insect inventory; succession; habitats |
| Carvalho et al. [41] | 2000 | Brazil | Pigs, humans | Insect inventory |
| Davis and Goff [42] | 2000 | Hawaii | Pigs | Intertidal habitats; succession |
| Shalaby et al. [43] | 2000 | Hawaii | Pigs | Hanging cadaver decomposition; succession |
| Arnaldos et al. [44] | 2001 | Spain | Chickens | Insect inventory; succession |
| Carvalho and Linhares [45] | 2001 | Brazil | Pigs | Insect inventory; succession |
| Marchenko [46] | 2001 | Russia | Dogs, cats, rabbits, pigs | Decomposition in various scenarios; seasons; habitats; insect repellents; clothing, plant response to cadavers |
| Wolff et al. [47] | 2001 | Colombia | Pigs | Insect inventory; succession |
| Yan et al. [48] | 2001 | USA | Pigs | Adipocere formation |
| Centeno et al. [49] | 2002 | Argentina | Pigs | Insect inventory; seasons; habitats; succession |
| Hobischak and Anderson [50] | 2002 | Canada | Pigs | Water decomposition; habitat; arthropod inventory; succession |
| LeBlanc and Strongman [51] | 2002 | Canada | Pigs | Insect inventory; habitats |
| Archer and Elgar [52, 53] | 2003 | Australia | Pigs | Insect inventory; seasons; colonisation patterns |
| Bharti and Singh [54] | 2003 | India | Rabbits | Insect inventory; seasons; succession |
| Kočárek [55] | 2003 | Czech Republic | Pigs | Insect inventory; seasons; habitats; succession |
| Shahid et al. [56] | 2003 | USA | Pigs | Arthropod saturation in human taphonomy facilities |
| Author(s) | Date of publication | Locality | Animal model | Major research focus |
|-----------|---------------------|----------|--------------|----------------------|
| Watson and Carlton [57–59] | 2003, 2005 | USA | Bear, deer, alligators, pigs | Insect inventory; seasons; succession; animal models comparison |
| Anderson and Hobischak [60] | 2004 | Canada | Pigs | Marine decomposition |
| Archer [61, 62] | 2004 | Australia | Pigs | Succession; seasons; annual variation; abiotic determinants of decomposition rate |
| Arnaldos et al. [63] | 2004 | Spain | Chickens | Insect inventory; seasons; succession |
| Grassberger and Frank [64] | 2004 | Austria | Pigs | Urban decomposition; insect inventory; succession |
| Tabor et al. [65, 66] | 2004, 2005 | USA | Pigs | Insect inventory; succession; seasons |
| Vass et al. [67] | 2004 | USA | Humans | Volatiles of decomposition |
| Anderson [68] | 2005 | Canada | Pigs | Arson and insect evidence |
| Moura et al. [69] | 2005 | Brazil | Rats | Succession mechanisms; seasons; habitats |
| Perez et al. [70] | 2005 | Colombia | Pigs | Urban decomposition; insect inventory; succession |
| Schoenly et al. [71] | 2005 | USA | Pigs | Arthropod saturation in human taphonomy facilities |
| Weitzel [72] | 2005 | Canada | Pigs | Underground decomposition; seasons |
| DeJong and Hobaek [73]; DeJong et al. [74] | 2006; 2011 | USA | Rats | Investigator disturbance; insect inventory; succession |
| Hobischak et al. [75] | 2006 | Canada | Pigs | Sun exposure; insect inventory; succession |
| Joy et al. [76] | 2006 | USA | Pigs | Blow fly inventory; habitats; annual variation; maggot mass |
| Lang et al. [77] | 2006 | Australia | Possums | Insect inventory; colonisation patterns |
| Adlam and Simmons [78] | 2007 | UK | Rabbits | Repeated cadaver disturbance |
| Gruner et al. [79] | 2007 | USA | Pigs | Blow fly inventory; seasons; annual variation |
| Martinez et al. [80] | 2007 | Colombia | Pigs | Insect inventory; succession |
| O’Brien et al. [81] | 2007 | Australia | Pigs | Scavenging |
| Schoenly et al. [82] | 2007 | USA | Pigs, humans | Sampling techniques; human/pig comparison |
| Benninger et al. [83] | 2008 | Canada | Pigs | Compounds released into soil during decomposition |
| Eberhardt and Elliot [84] | 2008 | New Zealand | Pigs | Insect inventory; succession; habitats |
| Fiedler et al. [85] | 2008 | Germany | Pigs | Adult fly inventory; succession; habitats |
| Huntington et al. [86] | 2008 | USA | Pigs | Blow fly multigenerational colonisation |
| Matuszewski et al. [87] | 2008 | Poland | Pigs | Insect inventory; succession; habitats |
| Moretti et al. [88] | 2008 | Brazil | Mice, rats | Insect inventory; succession; seasons |
| Sharanski et al. [89] | 2008 | Canada | Pigs | Insect inventory; succession; seasons; sun exposure |
| Urrahy-Rodrigues et al. [90] | 2008 | Brazil | Pigs | Post-mortem artefacts |
| Voss et al. [91] | 2008 | Australia | Pigs | Inside-car decomposition; colonisation patterns |
| Wang et al. [92] | 2008 | China | Pigs | Insect inventory; succession; seasons |
| Charabidze et al. [93] | 2009 | France | Rats, Mice | Insect repellents; colonisation patterns |
| Dekeirsschieter et al. [94] | 2009 | Belgium | Pigs | Volatiles of decomposition |
| Kalinová et al. [95] | 2009 | Czech Republic | Mice | Carrion beetle attractants |
| Kelly et al. [96, 97] | 2009, 2011 | South Africa | Pigs | Wounds; wrapping; clothing |
| Kjorlien et al. [98] | 2009 | Canada | Pigs | Scavenging; habitats; clothing |
| Neder et al. [99] | 2009 | USA | Alligators | Succession |
| Özdemir and Sert [100] | 2009 | Turkey | Pigs | Insect inventory; succession; seasons |
| Pakosh and Rogers [101] | 2009 | Canada | Pigs (limbs) | Water decomposition; seasons; surface/underground decomposition; scavenging; nutrient cycling |
| Parmenter and MacMahon [102] | 2009 | USA | Various mammals and birds | Insect inventory; succession; seasons; habitats |
| Segura et al. [103] | 2009 | Colombia | Pigs | Insect inventory; succession |
| Van Belle et al. [104] | 2009 | Canada | Pigs | Compounds released into soil during decomposition; seasons; surface/underground decomposition |
| Voss et al. [105] | 2009 | Australia | Pigs | Insect inventory; succession; seasons; habitats |
| Bachmann and Simmons [106] | 2010 | UK | Rabbits | Underground decomposition; colonisation patterns |
| Battán Horenstein et al. [107–109] | 2010, 2011, 2012 | Argentina | Pigs | Insect inventory; succession; seasons; habitats |
| Bonacci et al. [110] | 2010 | Italy | Pigs | Insect inventory; seasons; succession |
| Carter et al. [111] | 2010 | Australia | Rats | Underground decomposition |
| Chin et al. [112] | 2010 | Malaysia | Pigs | Hanging cadaver decomposition |
| Cross and Simmons [113] | 2010 | UK | Pigs | Wounds |
| Author(s) | Date of publication | Locality | Animal model | Major research focus |
|----------|----------------------|----------|--------------|----------------------|
| Matuszewski et al. [114–116] | 2010, 2011 | Poland | Pigs | Surface decomposition; insect inventory; seasons; habitats; succession |
| Michaud et al. [117] | 2010 | Canada | Pigs | Insect inventory; seasons; habitats |
| Reibe and Madea [118] | 2010 | Germany | Pigs | Colonisation patterns; habitats |
| Sahinoglu and Serf [119] | 2010 | Turkey | Pigs | Insect inventory; succession; seasons |
| Simmons et al. [120] | 2010 | UK | Rabbits | Insect access; surface/underground decomposition |
| Simmons et al. [121] | 2010 | Canada, Australia | Pigs | Insect access; cadaver mass |
| Swann et al. [122, 123] | 2010 | USA, Poland | Pigs | Compounds released during decomposition |
| Szpila et al. [124] | 2010 | USA, Poland | Pigs, rats | Colonisation of buried cadavers |
| Valdes-Perezgasga et al. [125] | 2010 | Mexico | Pigs | Insect inventory; succession |
| Ahmad et al. [126] | 2011 | Malaysia | Macaques | Wrapping |
| Anderson [127] | 2011 | Canada | Pigs | Indoor/outdoor decomposition |
| Anton et al. [128] | 2011 | Germany | Pigs | Insect inventory; succession; seasons |
| Barrios and Wolff [129] | 2011 | Colombia | Pigs | Water decomposition; arthropod inventory; succession; habitats |
| Bajerlein et al. [130] | 2011 | Poland | Pigs | Seasons; habitats; colonisation patterns |
| Bugajski et al. [131] | 2011 | USA | Pigs | Freezing |
| Cassar et al. [132] | 2011 | Australia | Pigs | Adipocere formation |
| DeVault et al. [133] | 2011 | USA | Mice | Scavenging |
| Dickson et al. [134] | 2011 | New Zealand | Pigs (heads) | Marine decomposition; bacterial succession |
| von Hoermann et al. [135] | 2011 | Germany | Pigs | Hide beetle attractants |
| Spicka et al. [136] | 2011 | USA | Pigs | Cadaver mass |
| Statheropoulos et al. [137] | 2011 | Greece | Pigs | Volatiles of decomposition |
| Voss et al. [138] | 2011 | Australia | Pigs | Clothing |
| Al-Mesbah et al. [139] | 2012 | Kuwait | Rabbits | Insect inventory; habitats; succession |
| Brasseur et al. [140] | 2012 | Belgium | Pigs | Volatiles of decomposition |
| Gnenthal et al. [141] | 2012 | UK | Pigs | Burnt cadaver decomposition |
| Martin-Vega and Bax [142, 143] | 2012, 2013 | Spain | Squids | Carrion and skin beetle inventory; seasons; habitats |
| Ortloff et al. [144] | 2012 | Chile | Pigs | Insect inventory; succession |
| Prado e Castro et al. [145, 146] | 2012, 2013 | Portugal | Pigs | Insect inventory; succession; seasons |
| Shelorni et al. [147] | 2012 | USA | Pigs | Insect repellents; blow fly colonisation patterns |
| Stadler et al. [148] | 2012 | Canada | Pigs | Volatiles of decomposition |
| Widya et al. [149] | 2012 | UK | Rabbits | Water decomposition; adipocere formation |
| Azwand et al. [150] | 2013 | Malaysia | Rats, rabbits, macaques | Insect inventory; succession; rat/rabbit/monkey comparison |
| Barton et al. [151] | 2013 | Australia | Kangaroos | Carrion and biodiversity |
| Benbow et al. [152] | 2013 | USA | Pigs | Insect inventory; succession; seasons |
| Bygarski and LeBlanc [153] | 2013 | Canada | Pigs | Insect inventory; succession |
| Dekeirsschieter et al. [154] | 2013 | Belgium | Pigs | Rove beetle inventory; seasons |
| von Hoermann et al. [155] | 2013 | Germany | Pigs | Carrion beetle attractants |
| Hyde et al. [156] | 2013 | USA | Humans | Cadaver microbiome |
| Johansen et al. [157] | 2013 | Norway | Mice | Blow fly attractants |
| Johnson et al. [158] | 2013 | Australia | Pigs | Thermogenesis in cadavers |
| Lowe et al. [159] | 2013 | Canada | Pigs | Textiles degradation on buried cadavers |
| Matuszewski et al. [160]; Mańdra et al. [161] | 2013, 2014 | Poland | Pigs | Insect inventory; habitats; seasons |
| Metcalf et al. [162] | 2013 | USA | Mice | Cadaver microbiome |
| Meyer et al. [163] | 2013 | USA | Pigs | Surface decomposition; seasons |
| Sutherland et al. [164] | 2013 | South Africa | Pigs | Cadaver mass |
| von der Luhe [165] | 2013 | Canada | Pigs | Compounds released into soil during decomposition |
| Abouzied [166] | 2014 | Saudi Arabia | Rabbits | Insect inventory; seasons; succession |
| Anderson and Bell [167] | 2014 | Canada | Pigs | Marine decomposition; arthropod inventory |
| Bhadra et al. [168] | 2014 | England | Pigs (heads) | Colonisation patterns |
| Caballero and Léon-Cortéz [169] | 2014 | Mexico | Pigs | Beetle inventory; succession; habitats |
| Author(s) | Date of publication | Locality | Animal model | Major research focus |
|-----------|---------------------|----------|--------------|----------------------|
| Corrêa et al. [170] | 2014 | Brazil | Rabbits | Beetle inventory; seasons |
| Farwig et al. [171] | 2014, 2016, 2015 | Poland | Pigs | Cadaver mass; clothing; insect inventory; long-term decomposition |
| Matuszewski et al. [172, 173]; Maďra et al. [174] | 2014, 2015 | USA | Pigs | Cadaver visitation by adult blow flies |
| Oliveira-Costa et al. [177] | 2014 | Brazil | Rabbits | Succession on burnt cadavers |
| Pechal et al. [178] | 2014 | USA | Pigs | Delayed insect access; colonisation patterns; succession |
| Pechal et al. [179] | 2014 | USA | Pigs | Cadaver microbiome |
| Pernault et al. [180–182] | 2014, 2015 | Australia | Pigs | Volatiles of decomposition |
| Whitaker [183] | 2014 | USA | Pigs, humans | Pig/human comparison of blow fly colonisation |
| Young et al. [184] | 2014 | England | Deer | Scavenging |
| Zurawski et al. [185] | 2014 | USA | Pigs | Nocturnal blow fly oviposition |
| Agapiou et al. [186] | 2015 | Greece | Pigs | Volatiles of decomposition |
| Alexander et al. [187] | 2015 | USA | Humans | Residual odour of decomposition in the soil |
| Auberon et al. [188] | 2015 | France | Rats | Blow fly development on contaminated cadaver |
| Baz et al. [189] | 2015 | Spain | Squids | Insect inventory; habitats |
| Card et al. [190] | 2015 | USA | Pigs | Clothing |
| Farrell et al. [191] | 2015 | Australia | Pigs | Insect inventory |
| Hyde et al. [192] | 2015 | USA | Humans | Cadaver microbiome |
| Iancu et al. [193] | 2015 | Romania | Pigs | Insect and microbe inventory; succession |
| Iancu et al. [194] | 2015 | Romania | Pigs | Insect and microbe inventory; succession |
| Lynch-Aird et al. [195] | 2015 | England | Pigs | Hanging cadaver decomposition |
| Martin-Vega et al. [196] | 2015 | Spain | Squids | Clown beetle inventory; habitats |
| Paczkowski et al. [197] | 2015 | Germany | Pigs | Volatiles of decomposition |
| Roberts and Dabbs [198] | 2015 | USA | Pigs | Freezing |
| Rysavy and Goff [199] | 2015 | Hawaii | Pigs | Underground decomposition; insect inventory |
| Silhuddin et al. [200] | 2015 | Malaysia | Rabbits | Insect inventory; succession; habitats |
| Stadler et al. [201] | 2015 | Canada | Pigs | Volatiles of decomposition |
| Sutkhit et al. [202] | 2015 | Thailand | Pigs | Insect inventory; habitats; succession; seasons; hanging; clothing |
| Spila et al. [203] | 2015 | Poland | Pigs | Insect inventory; succession |
| Ueland et al. [204] | 2015 | Australia | Pigs | Textiles degradation on surface cadavers |
| Zanetti et al. [205, 206] | 2015 | Argentina | Pigs | Underground decomposition; beetle inventory; seasons |
| Zearia et al. [207] | 2015 | Egypt | Rabbits, dogs | Insect inventory; succession; habitats |
| Anderson and Bell [208] | 2016 | Canada | Pigs | Marine decomposition; seasons |
| Cannamack et al. [209] | 2016 | USA | Pigs | Concealment; seasons |
| Lyu et al. [210] | 2016 | China | Pigs | Beetle inventory |
| Mashaly [211] | 2016 | Egypt | Rabbits | Burnt cadaver decomposition; insect inventory; succession; habitats |
| Metcalfe et al. [212] | 2016 | USA | Mice, Humans | Cadaver microbiome |
| Moffatt et al. [213] | 2016 | England | Pigs | Distribution of maggots length on carrion |
| Parry et al. [214] | 2016 | South Africa | Fishes | Fly inventory; habitats; seasons |
| Perez et al. [215] | 2016 | USA | Pigs | Distance between cadavers |
| Weidner et al. [216] | 2016 | USA | Pigs | Blow fly colonisation timing |
| Weiss et al. [217] | 2016 | USA | Pigs | Cadaver microbiome |
| Vasconcelos et al. [218] | 2016 | Brazil | Pigs | Fly inventory |
| Arnendt et al. [219] | 2017 | Germany | Pigs | Thermal imaging of cadavers |
| Connor et al. [220] | 2017 | USA | Pigs, humans | Human/pig comparison |
| Fancher et al. [221] | 2017 | USA | Humans | Compounds released into soil during decomposition |
| Marais-Wemer et al. [222] | 2017 | South Africa | Pigs | Underground decomposition |
| Martin-Vega et al. [223] | 2017 | Spain | Pigs | Colonisation patterns; seasons |
| Mashaly [224] | 2017 | Saudi Arabia | Rabbits | Beetle inventory; habitats; succession |
| Mcintosh et al. [225] | 2017 | Australia | Pigs | Burnt cadaver decomposition; succession |
| Michaud and Moreau [226] | 2017 | Canada | Pigs | Succession mechanisms |
| Niederegger et al. [227] | 2017 | Germany | Pigs | Wounds |
| Pacheco et al. [228] | 2017 | Canada | Pigs | Blow fly colonisation patterns |
followed the stage-based paradigm (e.g. [6]). Decay stages, named according to physiochemical changes seen in the cadaver, accompanied timetables of insect succession. Stage descriptions varied in both number and duration; moreover, the widely-held view was that the onset of each stage was marked by an abrupt change in the insect community, similar to Mégnin’s [3] notion of “squads”. Subsequent ecological and forensic studies found that succession in carrion largely follows a continuum of gradual changes [33–35]. Despite these findings, the use of stages of decomposition is still frequent in the forensic literature [35].

More recently, pigs became model animals in experimental research of forensic entomology and taphonomy (Table 1). Pigs have influenced recent theoretical developments in carrion and succession ecology and shaped our understanding of how vertebrate cadavers decompose in various environments, including indoor, suspended, buried, epigeic, intertidal, marine and freshwater settings. A wide spectrum of habitats has been investigated (Table 1) and found to show some idiosyncratic variations on otherwise very general patterns (Fig. 1). Results of these studies indicate that temperature and access or abundance of carrion insects are key environmental determinants of cadaver decomposition, whereas cadaver mass is a key cadaver-related determinant (Table 1, Fig. 1). At least five general decomposition patterns may be currently discerned: decay driven by either vertebrate scavengers, microbes, burying beetles, blow flies or blow flies with silphid beetles, with distinct key determinants of decomposition rate in each of the patterns (Table 1, Fig. 1).

Human cadavers vary in many characteristics that influence decomposition, most of which have been investigated using pigs (Table 1). Pre- or postmortem modifications such as wounds, burning, wrapping, dismemberment, contamination, concealment and clothing may affect the colonisation process and eventually decomposition to varying degrees, depending on their intensity and context of action (Table 1). Some modifications do not affect the whole cadaver, leaving parts of it to be colonized by insects in their usual manner, while other modifications such as clothing have effects on insect colonisation or succession that are too small or too variable to have practical consequences for estimates of post-mortem intervals (PMIs). Other modifications delay colonisation by insects but have little consequence once colonisation has occurred. The same modifications may however

Table 1 (continued)

| Author(s)                      | Date of publication | Locality     | Animal model | Major research focus                                                                 |
|--------------------------------|---------------------|--------------|--------------|---------------------------------------------------------------------------------------|
| Roberts et al. [229]           | 2017                | USA          | Humans       | Cadaver mass                                                                          |
| Scholl and Moffatt [230]        | 2017                | England      | Pigs         | Dismemberment; concealment in plastic sacks                                          |
| Wang et al. [231]              | 2017                | China        | Pigs, humans, rabbits | Human/pig/rabbit comparison; surface decomposition; succession; |
| Wang et al. [232]              | 2017                | China        | Pigs         | Exposure daytime; succession;                                                        |
| Weidner et al. [233]           | 2017                | USA          | Pigs         | Comparison of bait traps and cadaver inventories                                    |
| Cruise et al. [234, 235]       | 2018                | USA          | Pigs         | Insect inventory; succession; sampling techniques                                   |
| Daustartas et al. [236]        | 2018                | USA          | Pigs, humans, rabbits | Human/pig/rabbit comparison; surface decomposition; scavenging |
| Steadman et al. [237]          | 2018                | Spain        | Pigs         | Insect inventory; succession; seasons                                                |
| Díaz-Aranda et al. [238]       | 2018                | Poland       | Pigs         | Silphid beetles; succession; seasons; habitats                                       |
| Frątczak-Lagiewska and Matuszewski [239] | 2018 | Germany | Pigs         | Carrión beetle inventory; habitats                                                   |
| von Hoermann et al. [240]      | 2018                | Australia    | Pigs, humans | Decomposition rates; odour profiles; human/pig comparison                            |
| Knobel et al. [241]            | 2018                | Australia    | Pigs         | Thermal imaging of cadavers                                                          |
| Lutz et al. [243]              | 2018                | Canada       | Pigs         | Beetle colonisation and breeding on concealed carcasses                              |
| Mañas-Jordá et al. [244]       | 2018                | Mexico       | Pigs         | Fly inventory; succession; habitats                                                   |
| Marais-Wemer et al. [245]      | 2018                | South        | Pigs         | Surface/underground decomposition                                                    |
| Pérez-Marcos [246]             | 2018                | Spain        | Pigs, chickens | Fly inventory; pig/chicken comparison                                              |
| Salimi et al. [247]            | 2018                | Iran         | Rabbits      | Insect inventory; succession; seasons; habitats                                      |
| Shaya [248]                    | 2018                | Lebanon      | Pigs         | Clown beetle inventory; succession; seasons; habitats                                |
| Singh et al. [249]             | 2018                | USA          | Humans       | Arthropod and microbe inventory and succession in the soil below a cadaver          |
| Spies et al. [250, 251]        | 2018                | South        | Pigs         | Scavenging                                                                           |
| Szelecz et al. [252, 253]      | 2018                | Switzerland  | Pigs         | Compounds released into soil during decomposition; clown beetle colonisation of hanging and surface cadavers |
differently affect non-entomological processes, for example, clothing influences rate of cadaver cooling and therefore is considered important for some pathology-based methods for estimation of PMI, e.g. Henssge’s nomogram method [36]. Regarding insects, the implications of modification appear to be larger than the effect of the cadaver’s species.

In parallel, pig cadavers were used to test new forensic techniques or validate well-established ones (Table 2). They have provided proof-of-concept for techniques as simple as entomological sampling and as sophisticated as ground penetrating radar or thermal imaging to locate cadavers (Table 2). Many of these techniques have gone on to be applied to forensic investigations involving humans, demonstrating in this way the practicality of pigs as model cadavers.

**Are pigs an appropriate model for forensic entomology and taphonomy?**

A comparison of the advantages and disadvantages of pig and human cadavers for experimental forensic entomology and taphonomy research (Table 3) indicates that pigs are usually superior to humans in such experiments. Most importantly, pig cadavers may easily be replicated in large numbers and at low cost, whereas access to human corpses is restricted to taphonomic facilities or medical examiner’s offices with all of their associated inherent difficulties. At taphonomic facilities, waiting times for receiving replicate bodies on multiple-donation days are unpredictable and uncontrollable [37], even if minimum criteria are met for accepting cadavers as “replicates” (i.e. death within 48 h of acquisition, intact, unautopsied, unembalmed and refrigerated). The difficulty in amassing replicate human cadavers allows little experimental control over key decomposition determinants such as cadaver mass. The unpredictable and uncontrollable variation inherent in cadaver availability may limit the value of observations in humans and invalidate the experiment, by producing statistically underpowered comparisons that are insufficient to detect significant differences and by enlarging the risk of confounding effects. In addition, the practical realities of working with human remains can limit the types of information that can be gleaned from and about them. Moreover, the continual association of the taphonomy facilities with human cadavers can itself present a challenge. Although a 1998 field study at the Tennessee facility found little evidence of cadaver enrichment effects on the surface-active entomofauna or decay rates using pig carcasses [38, 39], a recent study of soil parameters [40] demonstrated that the Tennessee site is contaminated with high levels of decomposition products, which may limit the

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**Fig. 1** Determinants and general patterns of cadaver decomposition—synthesis based on findings of cadaver decomposition studies (Table 1). Numbers I–V denote general patterns of decomposition (differing according to dominant decomposers, key determinants of decomposition rate and the effect they have on decomposition). Numbers “0” and “1” denote absence and presence of scavengers or insects. Arrows next to rate determinants indicate whether a determinant, considered in isolation, is positively (↑) or negatively (↓) related to decomposition rate. Some determinants in this figure should be considered as sets of simple determinants, e.g. cadaver quality including body mass index, antemortem cadaver modifications (e.g. pharmaceuticals use), postmortem modifications (e.g. freezing during the winter) and others.
interpretation of certain nutrient-based taphonomic results as no reliable baseline sample can be obtained within the facility.

While, in many cases, researchers may be interested in how the decomposition process works in humans, the available human remains are either derived from inappropriate populations, cannot be linked to control samples or are too variable for robust experiments. Due to these practicalities, pig cadavers are usually the best choice available for most experimental purposes in forensic sciences. Moreover, pig cadavers may be used to compare treatments of relevance with forensic scenarios and to make inferences about human decomposition. If treatment A results in a slower decomposition than treatment B in pigs, in the absence of other information, we can reasonably assume a similar effect in humans, especially if it can be supported with other knowledge and logic. The possibility that a model animal and the humans that it models decompose differently does not make that model useless; it depends on the specific question being addressed. This conclusion has much wider applicability. For example, mouse cadavers were useful in demonstrating forensic applications of microbiology [41, 42]. Postmortem microbiome comparisons between different animals revealed the common appearance of some informative bacterial taxa across rodent, pig

Table 2  Forensic methods and techniques developed, refined or tested using pig cadavers. References to this table are listed in Electronic Supplementary Material

| Method/technique                              | References                                                                 | Pig cadaver use                                                                 |
|-----------------------------------------------|----------------------------------------------------------------------------|---------------------------------------------------------------------------------|
| Field protocol for experimental studies on PMI| Schoenly et al. [1, 2]                                                      | Tests of the protocol                                                            |
| Model organisms                               | Watson and Carlton [3, 4]; Schoenly et al. [2]; Wang et al. [5]; Connor et al. [6]; Daunartas et al. [7] | Comparisons of different animals; Comparisons of pigs and humans                |
| Human-size insect trap for studying succession| Schoenly et al. [1]                                                        | Recorded trap microclimate and carrion-arthropod families caught by trap          |
| Device for sampling cadaver-related aquatic insects | Vance et al. [8]                                              | Tests of trap efficiency in catching aquatic insects                             |
| Degree-day index for decomposition related processes | Michaud and Moreau [9]                                      | Development of the index and tests for its reliability                           |
| Reconstruction of temperature conditions      | Hofer et al. [10]                                                         | Reliability of temperature recordings on a death scene                            |
| Temperature methods for insect pre-appearance interval (PAI) | Matuszewski [1, 11, 12]; Matuszewski and Szafrulowicz [13]; Archer [14]; Matuszewski et al. [15]; Matuszewski and Madra 2015 [16]; Matuszewski and Madra-Bielewicz [17] | Development of PAI models; Tests of the method; Development of PAI models         |
| Total body score                              | Myburgh et al. [18]; Lynch-Aird et al. [19]; Nawrocka et al. [20]; Keough et al. [21]; Ribéreau-Gayon et al. [22] | Tests of the protocols for PAI field studies; Validation of PAI methods           |
| PMI estimation based on insect succession     | Michaud and Moreau [23]                                                   | Tests of predictability of insect occurrence based on degree-day accumulation     |
| PMI estimation based on insect development    | Michaud and Moreau [24]; Perez et al. [25]                                | Tests of sampling protocols for field studies; Evaluation of utility of insect taxa for derivation of confidence intervals about PMI estimate |
| PMI estimation based on insects               | Mohr and Tomberlin [26]                                                   | Tests of oocyte development of adult blow flies visiting cadaver as a PMI indicator |
| PMI estimation based on microbes              | Perez et al. [27]                                                         | Tests of minimum inter-cadaver distances for forensic field studies              |
| Exposed cadavers searching                    | Matuszewski [28]                                                         | Tests of presence/absence of insect taxa as an approach for PMI estimation        |
| Clandestine burial searching                  | Mądra-Bielewicz et al. [29]; Cruise et al. [30]                           | Tests of insect sex and size as PMI indicators; Tests of the protocols for cadaver field studies |
| Submerged cadavers searching                  | VanLaerhoven [31]                                                        | Validation of methods                                                            |
| Detection of gasoline in cadaver tissues      | Reibe-Pal and Madea [32]; Weatherbee et al. [33]                          | Comparison of methods                                                            |
| PMI estimation based on microbes              | Pechal et al. [34]                                                        | Tests of usefulness of microbe succession for PMI estimation                      |
| Exposed cadavers searching                    | Amendt et al. [35]; Lee et al. [36]                                       | Tests of thermal imaging techniques used from the air                            |
| Clandestine burial searching                  | Schultz et al. [37]; Schultz [38]; Salsarola et al. [39]                  | Tests of ground-penetrating radar                                                |
| Submerged cadavers searching                  | Healy et al. [40]                                                         | Tests of side-scan sonar                                                         |
| Detection of gasoline in cadaver tissues      | Pahor et al. [41]                                                         | Proof-of-concept sonar                                                           |
and human models [41–43]. Another example is the use of rabbit cadavers to provide local carrion insect inventories (Table 1). When early cadaver colonizers (e.g. blow flies) are the focus, rabbits are as informative as pigs or humans, but when middle or late colonizers (e.g. beetles of Silphinae or Cleridae) are studied, rabbit cadavers are inappropriate, because such insects rarely colonize carcases as small as rabbits [44, 45].

Comparative studies of pig and human cadavers revealed largely overlapping insect faunas [14, 44], with as much difference between individual pigs or humans as between pigs and humans [46]. Similarly, insect faunas compiled from human case studies (e.g. [47, 48]) largely resembled those from pig cadaver experiments (Table 1). Although alligator carrion revealed important faunal differences compared with large mammals (i.e. pigs, bears and deer), the latter group yielded highly similar insect community composition [49, 50]. These results indicate that, when compared across related cadaver taxa of similar size, carrion insects (i.e. necrophagous insects) show negligible preference for one cadaver taxon over another. Therefore, when pig cadavers are used to inventory local carrion-arthropod faunas, they appear to be as good as humans and are more practical (Table 3).

However, we suggest that pig cadavers larger than the recommended 20–30 kg domestic pigs [9, 10] should be used to compile full inventories of carrion entomofauna because smaller pigs yield an incomplete insect inventory (i.e. under-representation of middle or late colonizers [44, 45]). We therefore recommend cadavers a starting mass of at least 40 kg (and preferably 50–80 kg) as a standard to investigate local carrion-insect inventories. Smaller cadavers (piglets or rabbits) may be used in cases when early colonizers (e.g. blow flies) are the focus.

Most methods developed in forensic entomology or taphonomy are intended to be used with human cadavers. Therefore, at least their final validation should be performed with humans and preferably in real case scenarios. We are not aware, however, of any validation experiment in which performance of the forensic method developed using non-human cadavers has been evaluated using human cadavers. This is definitely an area for future experiments. Such research could enable forensic scientists to evaluate whether techniques based on data from human analogues (e.g. pig cadavers) are satisfactorily accurate when used in casework for human cadavers. As a result, we could distinguish techniques for which reference data could be amassed using human cadaver analogues and techniques for which human cadavers are necessary to get reference data. Nevertheless, analogues for humans, particularly large-bodied species, serve well in “proof-of-concept” studies (Table 2). Similarly, initial validation of forensic methods may be efficiently performed with pig cadavers (Table 2), particularly when different cadaver traits (e.g. mass) or environmental conditions (e.g. below/above ground) are to be compared.

All animals used in forensic entomology or taphonomy research are highly variable within species. This may lead to misinterpretation of experimental results, particularly when the experimental design of a study has weaknesses (see section 4 of this paper). However, the variation may also be advantageous, as it enables the researcher to choose the model best suited to the research. For example, if the scientific question obliges large replication, the experiment simply cannot be made with large pigs within standard research budgets, whereas piglets may be appropriate. If the researcher is interested in the thermal profile of decomposing remains, it may be more important to focus on the sunlight absorbance and mass of the model species than on its other traits. This argument may be extended to different animal models: experiments on initial colonisation patterns of blow flies may be more tractable using piglets or rabbits rather than adult pig or human cadavers. On the other hand, validation of the total body score (TBS) method for PMI estimation [51] needs humans or at least large pigs. Therefore, there is no universal model cadaver for research in forensic taphonomy or entomology, and the one that should be chosen depends on the scientific question and its experimental demands. This is an important point for the forensic science community to consider when designing experiments, analysing results or extrapolating conclusions.

**Critique of the pig model as an analogue for human cadavers**

**Background**

Use of domestic pigs in experimental forensic sciences has been challenged by recent comparisons of pig and human cadaver decomposition [23, 24]. One study [23] concluded that “pigs are not an adequate proxy for human decomposition studies”, and another [24] indicated that neither rabbits nor pigs “captured the pattern, rate, and variability of human decomposition”. Pigs may indeed decompose differently to humans, and therefore their experimental comparison is clearly worthwhile to forensic sciences. However, the intrinsic logistical difficulties associated with experiments involving human cadavers may impair such comparisons (Table 3), and therefore, questions arise about the validity of recent findings and conclusions. In the following sections, we discuss these questions and try to identify their consequences for the findings of the referenced experiments [23, 24] and the implications they have for the validity of the conclusion that pigs are inadequate analogues for humans in forensic research.
As we have discussed in section 3, all model organisms are highly variable intra-specifically. Biased sampling of this variation may lead to the misinterpretation of results of any model comparison. Both pigs and humans clearly exhibit variable sizes, pigmentation, hairiness, body mass index and other characteristics. Such factors may be confounded with treatments, and when they affect decomposition, they may make it impossible to assign results of a comparison between human and pig cadavers (or any other model) to a species effect (Fig. 2). As an example, if a study was conducted with male piglets and adult female humans only, it would not be possible to disentangle sex and age (or mass) effects from species effects. Therefore, sample selection within and between species is critical for such comparisons.

| Table 3: Advantages and disadvantages of domestic pig and human cadavers in forensic entomology and taphonomy research related to human decomposition [6, 9–11, 14, 23, 24, 44, 65] |
|---|---|
| **Pig cadavers** | **Human cadavers** |
| **Cons** | 1. Dissimilar to human cadavers in some important aspects: |
| | a. Body proportions |
| | b. Gastrointestinal anatomy |
| | c. Diet (more uniform, larger proportion of plant products) |
| | 2. More uniform than humans |
| | 3. Unacceptable in some cultures |
| | 1. Difficult to replicate: |
| | a. Available in low numbers |
| | b. Time and cause of death beyond researcher control (self-donation, age, disease incidence etc.) |
| | c. Dissimilar to each other in: |
| | • Mass |
| | • Age, sex, ethnicity |
| | • Antemortem pharmaceuticals use |
| | • Body conditions (frozen/fresh, autopsied/non-autopsied, etc.) |
| | 2. Limitations of taphonomy facilities (body farms): |
| | a. Small area, potential for insufficient inter-cadaver distances |
| | b. Uniform abiotic conditions |
| | c. Frequently non-natural conditions |
| | d. Area saturated with cadavers |
| | 3. Limitations of casework (i.e. medical examiner samples): |
| | a. Restricted to observation |
| | b. Cannot control effects of routine processing of remains |
| | c. Sometimes no information about death circumstances and the cadaver itself |
| | 4. Risk of sensationalized research |
| | a. Complex ethical considerations/generally unacceptable |
| | b. Potentially negative publicity |
| | c. Potential for findings to be “oversold” |
| **Pros** | 1. Similar to human cadavers in some important aspects: |
| | a. Body mass range |
| | b. Anatomy |
| | c. Body composition |
| | d. Skin coverage with hair |
| | e. Gut microbiota |
| | f. Gross processes of decay |
| | 2. Easy to replicate: |
| | a. Cheap and available in large numbers |
| | b. Time and cause of death controllable |
| | c. Cadaver traits controllable |
| | d. Possible to work with unfrozen cadavers |
| | 3. Less sensationalized research and relatively straightforward ethical considerations |

1. No species-related differences
Experimental design

Confounded variables

Confounded variables make the outcome of an experiment ambiguous. Confounding effects arise when differences recorded in a response (dependent) variable as a putative result of experimental manipulation of explanatory (independent) variable(s) cannot be separated from other variables that may affect the response [52]. To confidently show that differences resulted from experimental manipulations, the groups under comparison should differ only in the manipulated variable(s), or more realistically, the groups should not differ systematically in any important variable other than the one under manipulation. Confounding variables should be controlled in the experimental design (and thus eliminated) or in its statistical analysis (and thus quantified). An important confounding variable likely to arise in pig and human comparisons is body mass.

Identifying differences in decomposition between species needs an experiment in which cadaver samples differ systematically only in the cadavers' species. In the experiments of Dautartas et al. [24] and Connor et al. [23], samples of pig and human cadavers differed systematically in cadaver mass: the humans were systematically much larger than the pigs (Table 4). Although there are anecdotal observations suggesting low importance of adult human cadaver mass [53] and

### Table 4 Cadaver mass of pigs and humans used by Dautartas et al. [24] and Connor et al. [23]

|             | Pigs                     | Difference between humans and pigs in mean cadaver mass | Humans                 | Dissimilarity score (h−p)/(h+p) |
|-------------|--------------------------|--------------------------------------------------------|------------------------|---------------------------------|
|             | Mean | Range | V  |                                | Mean | Range | V  |                                |                                 |
| Dautartas et al. [24] |      |       |    |                                |      |       |    |                                |                                 |
| Trial 1     | 64.6 | 60–68 | 4.8 | 13.2                           | 77.8 | 72–84 | 6.1 | 0.093                           |
| Trial 2     | 49   | 40–59 | 14.1| 25                             | 74   | 53–107| 30.8| 0.203                           |
| Trial 3     | 50.6 | 47–57 | 8.5 | 24.8                           | 75.4 | 57–85 | 15.1| 0.197                           |
| Connor et al. [23] | 35 (median) | 25–64 | n/a | ≥45* (median) | n/a (≥80)* | n/a | 0.391* |

n/a not available

*Authors did not report mass of their human cadavers. They used adult humans and mention that “...over half the human sample was overweight or obese.”. According to “Anthropometric Reference Data for Children and Adults: United States, 2011-2014” [Fryar et al., 2016, Vital Health Stat 3] average body weight of adult females in USA was 76.4 kg and adult males 88.8 kg. Based on these data, we assume that the median mass of the human sample from Connor et al. [23] was no less than 80 kg, so the difference in median between pig and human sample was no less than 45 kg.
experimental findings supporting the claim that in a mass range of 73–159 kg ($N=12$), nine cadavers over 100 kg, i.e. obese, adipose bodies) decomposition rate is not significantly related to human body mass [54], all rigorous studies revealed that in a forensically relevant mass range (10–90 kg) small pig cadavers decompose significantly faster than large ones [55–59]. This difference appeared only in the case of insect-colonized carcasses [56] and has been suggested to result from less efficient active decay in larger cadavers, as a consequence of competition over carrion between different insect taxa [45, 59]. It is also related to surface-to-volume ratios, which reflect the surface area of the tissue where insects can feed, and to the size of the individual insect relative to that of the resource. Based on these patterns, it may be assumed that, when insects are present, smaller pig cadavers’ progress through the TBS scale at a faster rate than larger human cadavers. This seems to be the case (Figs. 3 and 4) with the studies of Dautartas et al. [24] and Connor et al. [23], making some of their results ambiguous and uninterpretable with respect to human–pig differences.

**Independence of replicates. Distance between cadavers**

When cadavers are close to one another, they may cross-contaminate one another or “compete” for insect colonizers, or both, making them statistically non-independent [60, 61]. The cadaver that is more attractive to insects may mask the other, resulting in underrepresentation of insects and slower decomposition of the less attractive cadaver. In addition,
dispersal of larvae becomes a potential mechanism to affect larval competition if the carcasses are located close to one another. If such effects are not taken into account (i.e., watching for larval dispersal, deploying drift fencing), small inter-cadaver distances are likely to alter species composition or decomposition rate, and lead to a lack of independence of experimental units, a basic assumption or requirement of most statistical tests.

In forensic entomology experiments, cadavers have usually been placed at least 50 m apart (Table 1) because there is empirical support that such a distance is sufficient to minimize cross-contamination by dispersing fly larvae [62, 63] and to ensure independence of cadavers [60]. In forensic taphonomy experiments, particularly with human cadavers, the distance has usually been much smaller, probably as a result of the smaller areas of human taphonomy research facilities where such experiments are located. Dautartas et al. [24] report that their cadavers were placed at least 3 m apart, and although Connor et al. [23] provide no information on the distance between their cadavers, the outdoor facility where the study was located has an area of about one acre [22], so we can assume their between-cadaver distances were less than 50 m. Such distances indicate that the cadavers used in both studies were not demonstrably independent in terms of the insect communities attending them. Little is known about the effect of small distance between cadavers on the pattern and rate of insect-mediated decomposition [60, 61]; therefore, relevant consequences of small between-cadaver distance on the results of the above studies are currently difficult to identify.

**Inter-annual effects**

Different years generally have different weather profiles leading to different insect richness and abundances and/or different insect pre-appearance intervals (PAI) (Table 1). These may result in substantial annual differences in decomposition rate.

In the experiments of Connor et al. [23], pig cadavers were exposed in September 2012 through August 2013 (12 pigs, one each month), while an extra five pigs were exposed on the same day as their 2nd through 6th human cadaver. The authors gave no specific dates of the human cadaver exposure (between September 2012 and December 2015). However, according to Wikipedia [22], they started to use human cadavers at their outdoor facility in November 2013. Therefore, most pigs were exposed in 2012 and 2013 and most humans probably in 2014 and 2015. If that was the case, there was a high level of treatment segregation and the species effect was confounded with an inter-annual effect. Consequently, the findings reported by Connor et al. [23] may be the result, at least in part, of differences in the biotic and abiotic determinants of decomposition in the different years of exposure rather than differences between cadaver species.

**Subject variables**

Subject variables are characteristics of individuals that are idiosyncratic and may affect the research variables, primarily by increasing their measured variances, sometimes referred to as “statistical noise”. Wherever possible, such variables should be controlled by selecting experimental subjects to minimize their effects, usually through matching the individuals as closely as possible. This is generally possible with pigs or rabbits but can be impractical with humans. For instance, the study of Connor et al. [23] exposed some human cadavers effectively fresh at the day of death but others after 53 days of postmortem refrigeration. Refrigeration affects bacterial
communities that initiate decomposition, with consequences for the rate of decomposition and the attraction of insects [64], which must have resulted in amplifying variation in decomposition rates of humans in that study. This sort of consequence of working with human cadavers may predispose a study to generate misleading results.

**Quantifying decomposition**

The total body score (TBS) was originally developed as a point-based, semi-quantitative scale for scoring the decomposition of human cadavers [51]. It represents the total amount of accumulated decomposition identified from three body regions (head and neck, trunk, and limbs). The scale was modified for rabbit [25] and pig cadavers [65]. Keough et al. [65] observed significant differences between pig and human cadavers during early decomposition and proposed the amendment of the TBS scale for pig cadavers. The use of the same TBS scale to compare human and pig decomposition rate (e.g. [23, 24]) is incorrect. Given the differences observed between human and pig cadavers in gross morphological changes during decomposition [23, 24, 65], cross-species use of the same TBS scale is risky and should, ideally, be complemented with other measures of decomposition, such as daily or periodic weight loss (in %).

**Statistical analysis and the presentation of results**

Criticism is essential to the advancement of science but for a critique to be acceptable, its analysis must be robust. However, the analyses presented in Connor et al. [23] and Dautartas et al. [24] are inadequate to support their conclusions. In Connor et al. [23], the conclusion of a difference between human and pig cadavers is derived from a comparison of the slopes developed using linear mixed modelling. However, a simple look at the regression lines used to compare decomposition rates (see Fig. 4 in Connor et al. [23]) shows that the selected models are inadequate in terms of adjustment, leverage values and residuals. The figure also demonstrates that a statistical difference is found by the authors only because pigs were allowed to decompose for a longer period, as no human cadaver was scored at TBS values >31. TBS values >31 had a powerful leverage effect on the regression line because these scores were squared in the analysis. The analyses of Dautartas et al. [24] are also problematic because none of them accounts for repeated measurements on cadavers, resulting in temporal pseudoreplication, which is known to artificially decrease P values.

In addition, statistically detectable effects may be too small or too variable to have practical significance for estimates of PMIs [66]. Because cadavers are highly variable, not surprisingly, decomposition rates can be highly variable too. For this reason, when trends are reported, they should be accompanied by quantitative indications of variation (i.e. uncertainty). For instance, human and pig cadavers appeared to decompose differently in the study of Connor et al. [23], but when 95% confidence intervals are added to the trend lines (Fig. 4), the apparent differences disappear. The inclusion of those intervals would indicate that pigs of small size are adequate models for human decomposition unless the TBS is greater than 28, which is a different interpretation from the one originally drawn from that research.

**Alternative model organisms**

In some countries, pigs are not a realistic option for religious reasons, and other animal models are needed.

| Table 5 Guidelines for cadaver choice in forensic science research |
|---------------------------------------------------------------|
| Research type/subtype               | Guidelines                                                                 |
|-------------------------------------|---------------------------------------------------------------------------|
| Cadaver species                     | Cadaver mass                                                              |
| Experimental studies               | Domestic pig, rabbit or rodents, depending on the objective of the study, human for model comparison experiments | Depending on study objective |
| Early colonizers                    | Domestic pig, rabbit                                                     | No cadaver mass limitations |
| Early and middle colonizers         | Domestic pig                                                             | ≥ 20 kg starting mass, preferably 20–40 kg |
| All colonizers                      | Domestic pig                                                             | ≥ 40 kg starting mass, preferably 50–80 kg |
| Local insect inventory or succession studies, insect PAI studies | Domestic pig, rabbit or rodents, depending on method tested              | Depending on method tested |
| Proof-of-concept studies            | Domestic pig                                                             | 10–40 kg as juvenile analogues, 50–80 kg as adult analogues |
| Initial validation studies          | Domestic pig                                                             | Preferably whole mass range |
| Final validation studies            | Human                                                                    | |
Rabbits have been frequently used by forensic entomologists (Table 1), but obviously, they are too small to serve well for most forensic research. Carrion insect assemblies are distinctly less complex and persist for less time on small-sized cadavers compared with larger cadavers [44, 45]. Owing to their small size, the decomposition rate of rabbit cadavers is much faster than that of pig or human cadavers [24, 44]. Accordingly, the well-established importance of body size needs to be remembered when selecting alternatives, like sheep or goats, usually shorn to make insect sampling feasible and to reduce the potential impact of the fleece on decomposition, which is different from pig and human situations.

**Recommendations**

Previous papers suggested that a universal model cadaver for experimental field studies and training programs in forensic entomology would be a domestic pig weighing 20–30 kg of starting mass [9, 10]. No recommendation is currently available for taphonomy studies. However, a single and universal “model cadaver” for the forensic sciences is not useful. Different studies have different purposes, conditions and limitations. Therefore, more flexible guidelines on cadaver species and mass are needed (Table 5). A review of the guidelines proposed in this paper (Table 5) indicates that human cadavers appear necessary only in comparative studies involving other cadaver taxa and for final validation of forensic methods. In most cases, pig cadavers are an ideal choice, whereas other animal cadavers may be useful in supplemental or unavoidable (substitutional) cases. Moreover, researchers should usually use cadavers that are larger than the currently recommended size of 20–30 kg. Depending on the specific question of interest, other non-mass-related considerations may also be necessary.

**Conclusions**

Pig cadavers have provided a comprehensive experimental foundation for empirical studies of decomposition in forensic entomology, taphonomy and ecology, and are likely to remain the analogue of choice in most such studies for the immediate future. A pivotal limitation to the value of human cadavers is an adequate supply of donated bodies, especially when a well-replicated experiment is required. Some of these limitations can be avoided by conducting observational studies with samples derived from death investigations (i.e. through collaboration with medical examiners), which will be limited by the samples available, and may not be appropriate for all types of scientific questions. Analogue models such as pigs are likely to remain logistically more tractable, being more readily available, more uniform in size and age and less ethically complex to deploy. Pigs are a sensible compromise between availability, cost, ethics and similarity to humans, and there is no better candidate at this time. At present, experiments using analogues are easier to replicate and make control of confounding factors more practicable than studies based solely on humans, and they can be validated by including human remains alongside the analogues (e.g. [14, 44]). Therefore, an adequate query is not whether we should abandon pig carcasses, but rather how pig carcasses and other animal models differ from human cadavers in certain aspects of their decomposition, for example, decomposition rate and patterns of colonisation by insects. Such research would put into perspective all the developments made possible over the past four decades by the use of human analogues (Table 1). Moreover, human cadavers are definitely limited resources for forensic sciences. Therefore, they should be invested to test hypotheses which were found to be forensically interesting for analogues, e.g. pig carcasses.

The need for robust replication and control are a direct consequence of both the inherent complexity of animal decomposition and the need for reliable forensic evidence in court. Our recommendations provide a quality assurance baseline for cadaver experiments. Indeed, simulated and reconstructed casework using pigs is an ideal test and cross-validation of conditions at a death scene (i.e. litigation research). Pig carcasses should be placed, if possible and acceptable, at or near the same site and time of year as the death scene and should serve as a reference for case analyses [67, 68].

A certain level of imprecision is inevitable even in superbly designed decomposition experiments, and court testimony will always need to draw cross-validation of decomposition-based estimates from other fields of science. Future decomposition studies will need to underpin their own importance with rigorous quality control measures [27, 28]. A means to this end have been outlined here, and many of the recommendations apply as much to research with human corpses as to any other animal species.

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