To mix or not to mix?

Evaluating breeding performance in mixed species bird enclosures within European zoos.

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Abstract

Housing animals within mixed species aggregations is often believed to offer a more naturalistic captive environment by providing behavioural and social enrichment, and has become an integral design feature for many zoos across the world. There is however, a common perception among zoo professionals that for birds in particular, breeding performance may be reduced when housing them within mixed species environments. In order to investigate this perception, three objectives were outlined, which aimed to evaluate the impact that mixed species housing has on bird breeding performance within European zoo collections. Objective one compared the breeding performance of bird species housed within mixed species enclosures versus when those species were housed in single species enclosures. This was followed by objective two which identified the factors that may be influencing bird breeding performance when housed within mixed species enclosures only. Finally objective three discussed the use of historical zoo records for evaluating breeding performance within mixed species enclosures.

To test these objectives the breeding performance of birds housed in mixed (and where applicable single species) enclosures were collected via questionnaire (n=88 zoos) and via historical records (n=2 zoos). Analysis revealed that 55% of species tested were considered to breed better when housed as a single species. Furthermore a number of factors were found to impact on breeding performance within mixed species enclosures; including breeding sociality, fledge time and the presence of non-bird taxa, however these factors were found to be effected by bird phylogeny. Comparisons with results from historical records suggest that questionnaires were a suitable method for assessing breeding performance. In addition records data highlighted that birds housed in mixed enclosures were subject to many transfers' between enclosures, which may be impacting on the ability to breed successfully. As the first attempt at quantifying the influence that mixing bird species has on breeding performance, evidence supports the perceptions that for some species breeding may be reduced. This result is not consistent across all species and thus requires further investigation to assess how these breeding issues may be impacting upon future population sustainability of birds housed in European zoos.

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Chapter 1: Introduction

1.1 General introduction

As zoological collections continue to develop, they have evolved from displaying animals for entertainment to showcasing the *ex-situ* and *in-situ* conservation of wildlife (Curio, 1998; Conway, 2000, 2003, 2010; WAZA, 2005; Zimmerman, *et al*., 2007; Dick & Gusset, 2010; Hosey, *et al*., 2013). Pressure from legislative bodies, increased public awareness and an ever growing external conservation need has driven a rise in engagement with conservation issues within the zoo community (Conway, 2003, WAZA, 2005; Zimmerman, *et al.*, 2007). As a result, zoos have the unique ability to act for the conservation of wildlife through many avenues; most significantly through public education and the *ex-situ* conservation breeding of threatened species (Conway, 2000, 2003; Mallinson, 2003; WAZA, 2005; Dick & Gussett, 2010; Mascarelli, 2013).

Nevertheless, for many years zoos have been tackling the issue of improving their breeding management; with the aim of becoming substantial ‘producers’ rather than ‘consumers’ of the wildlife they house (Wilkinson, 1987a). Despite this effort, there is increasing evidence that numerous zoo animal populations are unsustainable (Rahbek, 1993; Reitkerk, *et al*., 1997; Sheppard, 1995; Beissinger, 2001; Leus & Bingaman Lackey, 2008a, 2008b; Dickie, 2009; Lees & Wilcken, 2009; Walter, *et al.,* 2009; Conway, 2011; Leus *et al*., 2011). More specifically, an evaluation by the European Association for Zoos and Aquariums (EAZA) has estimated that under the current management (European endangered species breeding programme [EEP] and European studbook [ESB]) a significant number of species, across all taxa, cannot maintain viable genetic and demographic populations within zoos (Anderson, *et al*., 2009; Dickie, 2009, Leus, *et al*., 2011). In addition Schulte-Hostedde and Mastromonaco (2015) suggest that for the progress of breeding programme management evolutionary history should be considered, in relation to the differences between the wild environment which a species has evolved in and the captive environment it is housed in. However at present the zoo and scientific community are now focusing their attention on genetic sustainability with regards to reproductive success within their conservation breeding programmes (AZA, 2006; Leus & Bingaman Lackey, 2008a; Dickie, 2009, Leus *et al*., 2011; Mascarelli, 2013).

In particular, many zoo-housed bird species have been highlighted as having a significant risk of poor future population sustainability (Leus & Bingaman Lackey, 2008a, 2008b; Leus, *et al*., 2011; Walter, *et al*., 2009). However, this evaluation only reflects the condition of managed and closed populations as information on the state of non-managed bird species is currently limited (Leus *et al*., 2011). Moreover, the 2007 European Union ban on the trade in wild birds, enacted due to the threats posed by avian influenza to commercial farm birds, may have added further pressure on conservation breeding programmes by reducing the ability to supplement captive populations from wild sources (Leus & Bingaman Lackey, 2008a, 2008b; Dickie, 2009; Walter *et al.,* 2009; Leus *et al*., 2011).

Globally, birds represent an important diverse taxa with approximately 30-40% of all extant bird species described being housed within zoological collections worldwide (Conde, *et al*., 2011; ISIS, 2014). In 2008, European zoos housed 2575 species and over 1160 sub-bird species (Leus & Bingaman-Lackey, 2008b). Nonetheless only 2.6% of extant avifauna forms part of global breeding programmes (Collar & Butchart, 2014). Of these, 103 species form part of managed breeding programmes in Europe (EAZA, 2013). Although less than 3% of the current extant bird species are involved in conservation breeding programmes this should not detract from the role that zoos can play in conservation (Collar & Butchart, 2014). For example zoos have pioneered the *ex-situ* breeding of many critically endangered bird species; such as the Visayan tarictic hornbill (*Penelopides panini*) (Oliver & Wilkinson, 2007). In addition zoos have made substantial contributions to the *in-situ* conservation of birds such as the Californian condor (*Gymnogyps californianus*), the blue-crowned laughingthrush (*Garrulax courtoisi)* (BIAZA, 2012), and the black-winged starling (*Acridotheres melanopterus*) (Wilkinson, *et al*., 2004; Collar, *et al*., 2012; Owen, *et al*., 2014). Thus highlighting the role that zoo's may play in the future prospects of the world's bird species and the importance of managing *ex-situ* populations.

With this in mind, as conservation breeding programmes can have significant value in the supplementation and/or reintroduction of species into the wild (Baker, 2007; Seddon, *et al.,* 2007) having productive sustainable *ex-situ* breeding programmes is of significant importance. At present, Birdlife International (2013) estimate that under current conditions one in eight wild bird species are threatened with extinction at a global level. These numbers continues to grow annually (Collar, *et al.,* 2012; Birdlife International, 2013). This highlights the increased need to consider captive population sustainability in relation to the long-term prospects of wild bird species, recognising those species that are currently threatened and also species which may be vulnerable to extinction in the future. Subsequently, emphasising the need for investigation into particular problem areas within the management of captive zoo housed birds. Within the zoo community the impacts of housing and enclosure design on breeding performance has been highlighted as a key focus for birds (Wilkinson, 1987a, 1987b; BIAZA BWG, 2006 unpub.), therefore this project will be centred around bird housing and husbandry within zoological collections.

1.2 Bird exhibitory and mixed species enclosures

From the first zoological collections in Egypt and China 3000 years ago (Lauer, 1976; Coe, 2001), to the modern collections of today, zoos have had a long illustrious history with the keeping of bird species for display and conservation purposes (Baratay & Hardouin-Fugier, 2002). In the Fourteenth Century, English aristocracy began with private collections of parrots and passerines housed in small and elaborately designed cages, often made from jewels and precious metals (Baratay & Hardouin-Fugier, 2002; Hosey, *et al*., 2013). This method of exhibitory was popular for many years, eventually opening to public visitors (King, 1998; Baratay & Hardouin-Fugier, 2002). Many of the first private zoological gardens are the lasting foundations of today's modern zoos (Baratay & Hardouin-Fugier, 2002).

In particular over the last 100 years, zoos have developed their methods of animal display, driven by changes in legislation (Baratay & Hardouin-Fugier, 2002;) scientific knowledge (Fiby, 2008; Zoo Design Symposium, 2004) and the visitor experience (Hosey, *et al*., 2013); with the increasing demand to observe animals in a more naturalistic environment (Conway, 2003; Fiby, 2008; Melfi, *et al*., 2007; Bracko & King, 2014) and changes in public perception of animal welfare standards (Reading & Miller, 2007; Hosey, *et al*., 2013). For example Carl Hagenbeck's naturalistic approach to enclosure design was viewed as innovative in the early 1900's (Baratay & Hardouin-Fugier, 2002) and saw a move from animals exhibited in rows of cages towards displays based on faunal regions and multi-species environments (Hosey, *et al*., 2013), a design template which is now common place in many zoos. Additionally, within a competitive economy the need to attract the public and address the needs of the visitor is seen as a high priority (Zoo Design Symposium, 2004; Melfi, *et al.,* 2007, Hosey, *et al*., 2013), with many zoos exhibiting popular charismatic mega-fauna to encourage visitors through the gates (Conway, 2003; AZA, 2006).

With this in mind, from a collection planning perspective, many bird species may be considered '*fillers*'; *i.e.* species which may not be viewed as a significant visitor attraction (BIAZA BWG, 2006 unpub.). Evidence suggests that birds do not hold the same level of visitor attraction as other taxa, such as mammals or amphibians (Moss & Esson, 2010). Furthermore, visitor dwell time spent at bird enclosures is significantly lower than other taxonomic groups (Moss & Esson, 2010). In addition, positive relationships have been found between body size and animal popularity (Ward, *et al*., 1998; Moss & Esson, 2010), with birds again losing out in the popularity stakes. Conversely, there are some bird species which could be considered as popular attractions within zoos; such as penguins (*Sphenisciformes*), owls (*Strigiformes)* and other birds of prey *(Falconiformes* and *Accipitriformes*). This could be attributed to various factors including larger body size (Ward, *et al*., 1998), levels of media exposure, and links to cultural heritage or the ability to anthropomorphise these species (Liskova & Frynta, 2013). Therefore as a taxonomic group, although birds may not be considered a big visitor attraction, this should not devalue their importance within zoological collections.

Despite the potential disparity in taxonomic popularity, birds remain popular with private collectors (King, 1998) and an important taxon for conservation action (Birdlife International, 2013). Birds have continued to be a significant part of zoo collection plans and are one of the most researched taxa within zoos, second to mammals (Pankhurst, *et al*., 2008). Nonetheless considerable areas of science and husbandry relating to birds are understudied within zoos; including the geographic origin of captive birds (Gautschi, *et al*., 2003), effects of inbreeding (Seddon, *et al*., 2007; Williams & Hofmann, 2009), selection for and adaptation to captivity (Synder, *et al*., 1996; Shepherdson, *et al*., 2004; Swaisgood, 2007; Frankham, 2008), and interactions of species within mixed species enclosures (Crotty, 1981; BIAZA BWG, 2006 unpub.; Foulds, 2007 unpub.).

Having said this, to help support the management of many bird species, the zoo community has produced a number of species-specific husbandry guidelines, utilising information collated from surveys, historical records and expert experiences (Miller, 2015; AZA, 2014; EAZA, 2014). However, when considering current available literature, captive bird research is often restricted to these guidelines and industry magazines (e.g. *Avicultural Magazine, International Zoo News, Ratel*), rather than publications in peer-reviewed journals. Most recently, research has begun to focus on bird aviary design within European Zoos (Bracko & King, 2014). Although this project is an observable progression for zoo aviculture and enclosure design, published empirical research focusing on bird breeding productivity in relation to zoo enclosure design is limited (e.g. orange-winged amazon *Amazona amazonica,* Millam*, et al*., 1995; Humboldt penguin *Spheniscus humboldti*, Blay & Cote, 2001; Hawaiian honeycreeper *Drepanididae spp.*, Shepherdson *et al*., 2004). Accordingly the impact of enclosure design on breeding remains a significant area for research focus (Hosey, *et al*., 2013).

Historically zoos have maintained their birds in relatively small enclosures with perhaps one or two species housed together; a method of exhibitory that has now become less common within many westernised zoos (Crotty, 1981; Baratay & Hardouin-Fugier, 2002). As previously mentioned zoos have seen a trend in the design of large naturalistic immersive mixed species enclosures; yet knowledge on the effectiveness of these types of enclosure is limited (Hammer, 2002; Hosey, *et al*., 2013), resulting in a need to assess the impact that this style of housing may be having on breeding potential and subsequent population sustainability of birds in particular.

Even though mixing species is not a new practice, it has become an integral design feature for many zoo enclosures across the world (Crotty, 1981; Thomas & Maruska, 1996; Coe, 2001, Hammer, 2002; Veasey & Hammer, 2010; Hosey, *et al.*, 2013). This area of species management remains an area of animal management which lacks rigorous scientific analyses; with mammalian mixes having receiving the most research attention (e.g. *general overview,* Hammer, 2002; *primates*, Wojeciechowski, 2004; Dalton & Buchanan-Smith, 2005; Buchanan-Smith, 2012; Leonardi, *et al*., 2010; *Carnivora*, Dorman & Borne, 2010). One reason why this topic remains understudied is due to the difficulties presented when carrying out multi-zoo research projects (Melfi & Hosey, 2012). No two enclosures are the same, with the ability to control the environment being limited and with many variables to consider. In addition, within mixed species environments the number of variables to consider increases immensely (Melfi & Hosey, 2012). Even with these difficulties it remains important to invest in assessment of areas such as housing condition, in order to increase the effectiveness of future zoo management practices, such as collection planning and enclosure design. In addition, due to these complexities and the volume of bird species that are housed in zoos no specific guidelines have been produced for the management of mixed species bird enclosures. Consequently mixed species enclosures are considered an important research priority for zoo biologists (Hosey, *et al*., 2013).

Managing mixed species enclosures is considered more challenging than single species settings (Crosta & Timossi, 2009); nevertheless this type of housing may offer a number of advantages. It is often believed that exhibiting mixed species aggregations allows for a more naturalistic captive environment by providing behavioural and social enrichment to the animals (Thomas & Maruska, 1996; Coe, 2001; Hammer, 2002; Dorman & Borne, 2010; Veasey & Hammer, 2010). In primates evidence suggests that mixed species enclosures act as a source of social enrichment via increasing the complexity of interactions (Leonardi, *et al*., 2010). Presenting animals within this naturalistic settling can also enhance the visitor experience (Crotty, 1981; Coe, 2001; Fiby, 2008, Hosey, *et al*., 2013) via the exhibition of species which may share similar habitats or zoogeographical distributions (Crotty, 1980; Thomas & Maruska, 1996; Hammer, 2002; Veasey & Hammer, 2010). In addition as zoos face pressure on their limited resources, mixing can enable the management of many species within one shared space (Crotty, 1981; Thomas & Maruska, 1996; Hammer, 2002; Dalton & Buchanan-Smith, 2005; Boritt, 2008; Dorman & Borne, 2010; Veasey & Hammer, 2010; Dick, 2012).

Despite these potential benefits a number of disadvantages have been suggested including the potential for resource competition and inter-species aggression (Thomas & Maruska, 1996; Hediger, 1950; Coe, 2001; Veasey & Hammer, 2010; Dick, 2012). This competition could be attributed to species incompatibility. Mixed enclosures may also experience problematic husbandry and increased exposure to disease or parasites (Hediger, 1950; Coe, 2001; Hammer, 2002; Veasey & Hammer, 2010; Papini, *et al*., 2012; Tritto & Barbon, 2012). For example if consumption of heterospecific offspring could increase transmission of parasites between species. In addition there is evidence that parasites may mutate overtime (Anderson & May, 1982), further impacting the potential parasite infestations that may occur within mixed species enclosures. Similarly an increased risk of physiological and psychological stressors may result in an impact on the long-term welfare of the species (Mason, 2010). For instance injuries received from aggressive encounters and/or symptoms caused by chronic stress response may increase susceptibility to disease (Thomas & Maruska, 1996; Davis, 2009; Mason, 2010). This may then lead to increased chance of disease transmission when housed in a multi-species environment. In contrast, evidence from mixed species primate enclosures suggests that common squirrel monkey (*Saimiri sciureus*) and brown capuchin (*Cebus apaella)* do not demonstrate chronic stress when mixed together (Leonardi, *et al*., 2010). This may be related to their propensity for sympatric associations in the wild (Leonardi, *et al*., 2010), resulting in a predisposed compatibility within captive environments. Having said this, the potential for increased exposure to chronic stressors for less compatible species may reduce the breeding productivity of the species housed within the enclosure (Thomas & Maruska, 1996; Mason, 2010; Veasey & Hammer, 2010), impacting both directly and indirectly on future population sustainability.

For birds in particular there is a common perception amongst zoo professionals that many species may experience reduced breeding performance when housing them within a mixed species environment (Wilkinson, 1987b; BIAZA BWG, 2006 unpub.; Foulds, 2008). The issue was first highlighted in 1987 within a survey in which bird managers within European zoos expressed their concerns for the future of birds in their collections (Wilkinson, 1987a). This survey indicated that sustainability of breeding programmes for "difficult" species and husbandry issues in mixed species bird enclosures were their two highest concerns (Wilkinson, 1987b).

In order to investigate these continued perceptions, the British and Irish Association of Zoos and Aquariums Bird Working Group (BIAZA BWG) commissioned a preliminary assessment of breeding within mixed species aviaries as part of their Mixed Aviaries Focus Group initiative. The assessment, which began in 2007, represented the first attempt at evaluating mixed species bird enclosures within Europe. The results of the 2007 study have provided the basic foundations for this study. The preliminary study, which was carried out by Yvette Foulds-Davis (the principle investigator), involved the survey of BIAZA member zoological collections to gain an overview of perceived breeding problems within mixed species bird enclosures. Results from this study identified perceived problems in 39% of bird species (Foulds, 2008, Appendix A). The most prevalent problems were said to relate to behavioural interference (inter and intra-specific) and environmental factors; such as nest site availability.

In 2008, a second survey was developed focusing in more detail on these perceived reasons. Pilot results for the second survey revealed that 61% of species had never bred in their enclosure; with the most prevalent perceived reason for problematic breeding was due to interference from other bird species within the enclosure (Foulds, 2008). These initial results gave support to the perception that some bird species held within mixed species enclosures may have experienced reduced breeding performance. Following this initial research, the BIAZA BWG outlined three key themes within mixed aviary management which required further investigation; 1) enclosure design; 2) species compatibility; and 3) bird behaviour and nutrition, with the future aim of developing standardised management guidelines (BIAZA BWG, 2009). Limited progress was then made following the completion of the preliminary study. Subsequently the potential problems experienced within mixed species bird enclosures remained a significant research priority within the British and European zoo community.

In 2011, in an attempt to update the previous research priorities outlined by the BIAZA BWG, the principle investigator conducted an online opinion survey to gain feedback from bird keepers, curators and zoo managers on their thoughts for the direction of future research priorities for mixed species bird enclosures. Survey responses were received from zoo professionals across Europe (n=59), with species compatibility and parent-reared breeding success voted as the two most important elements for future investigation (Foulds, 2011 unpub.). As the previous investigation suggested that mixed enclosures some bird species do display reduced levels of breeding performance, it has become pertinent to evaluate how breeding performance compares when birds are housed under different conditions and to investigate specific factors which may be impacting upon breeding performance within mixed species environments.

Taking into consideration the aforementioned issues relating to future population sustainability this study represents the first general analysis of the how current trends in housing birds within European zoological collections may affect bird breeding performance.

1.3 Thesis outline

The overarching aims of this study were to produce an initial assessment of the impact that housing birds in mixed species zoo enclosures may have on bird species breeding performance and to identify key factors that may influence this success. This study also makes comparisons of how bird species perform with regards to enclosure design, species-specific ecology and phylogeny. The three main objectives were as follows:

1. To compare the breeding performance of bird species housed within mixed species bird enclosures versus when those species are housed in single species bird enclosures.

2. To identify significant factors that may be influencing the breeding performance of bird species when housed within mixed species bird enclosures.

3. To discuss the use of historical zoo records for evaluating breeding performance within mixed species bird enclosures.

Subsequently this project aims to aid in the future development of standardised best practice guidelines for mixed species aviary management and to act as a foundation for further investigation by the zoo community.

Chapter 2: Evaluating breeding performance of zoo housed birds in relation to enclosure design, husbandry practices and species typical ecology.

2.1 Introduction

Although multi-species enclosures are now a prevalent trend within modern zoo design, as previously mentioned this area of zoo management is highlighted as a priority for scientific investigation (Wilkinson, 1987b; Hosey, *et al.*, 2013). Most notably there has been limited empirical research into the husbandry practices and effectiveness of mixed species bird enclosures (BIAZA BWG, 2006 unpub.) even with evidence supporting the perception that mixing may have a negative impact on bird breeding productivity (Wilkinson, 1987b; BIAZA BWG, 2006 unpub.; Foulds, 2008). Furthermore the insufficient level of investigation is of particular concern when considering the aforementioned challenges relating to bird population sustainability. Consequently, the zoo industry considers the issues relating to mixed species bird enclosures to be an important area for future evaluation (Wilkinson, 1987b; BIAZA BWG, 2006 unpub.).

2.1.1 Mixed species associations

There are many known benefits of mixed species associations within the wild which can include increased predator vigilance and the provision of additional foraging opportunities (e.g. Estrildid finches *Estrildidae* Rubinstein, *et al*., 1977; *Passeriformes spp*. Hino, 1998). As a result of these benefits there may be potential reproductive enhancements for wild populations (Wolters & Zuberbuhler, 2003; Griffin, *et al*., 2005). These naturally occurring sympatric associations are impacted by a number of factors including habitat type and quality, resource availability and level of predation risk (Munn & Terborgh, 1979; Terborgh, 1990; Krebs & Davies, 1997; Heymann & Buchanan-Smith, 2000). One such example is the aggregation of tropical birds and tamarins *Saguinus spp.* which are affected by the abundance of micro-foraging habitats (Hankerson, *et al.*, 2006). Although related to wild associations these factors should also be considered when investigating the effectiveness of mixing species within zoos. With this in mind factors such as the number of nest sites, number of feeding stations and species-specific diet types are considered within this project.

In wild bird aggregations the compatibility of species within these mixed flocks could be associated with body size (*Laridae*, Ellis & Good, 2006; *Charadriidae* and *Scolopacidae*, Burger, *et al*., 1979). In tits (*Paridae)* body size correlates directly with foraging site i.e. different sized species exploit different sites within a shared food resource (Alatalo & Moreno, 1987). In other studies evidence suggests that body size may impact on dominance relationships between bird species (Brown & Maurer, 1986), which could also play a role in the compatibility of species. Evidence that body size can affect feeding and nesting behaviours between species also exists, for example in neotropical vultures (black vulture *Coragyps atratus* and Andean Condor *Vultur gryphus*, Carrete, *et al.,* 2010) and snowfinches *Montifringilla spp*.), Zeng & Lu, 2009). Hawkins (1970) suggests that stronger and more aggressive species are likely to have an advantage over smaller or weaker species resulting in displacement from food sources. In consequence, ecology and body size could be impacting on the success of species within mixed enclosures, and are factors considered within this project. In contrast, body size may not be such major factor when the species that are housed together operate within different ecological niches. Therefore when species do share the same ecological requirements it may be suitable for them to be of similar size to reduce the potential for dominant interactions from larger species. Although this may also have the opposite effect if no clear inter-specific rank order exists within the enclosure.

Conversely it may also be suitable to consider levels of inter-species aggression rather than just body size alone. Ripley (1961) detailed the issue of neglect of young due to inter-specific aggression. Consequently species which experience aggression within mixed enclosures may reduce their levels of parental care. There is a perception that *Gruiformes* may be aggressive when housed in mixed enclosures, resulting in reduced success for species that are housed with them (AZA, 2006). A study by Boritt (2008) suggests that smaller *gruiforme* species (e.g. Madagascar button quail (*Turnix nigricollis*) are more effective in mixed enclosures as they often exhibit lower levels of aggression. Conversely, species that demonstrate higher levels of aggression irrespective of their size (*e.g*. red-legged seriema *Cariama cristata*, Guam rail

Gallirallus owstoni and grey-winged trumpeter *Psophia crepitans*) are considered less suitable for mixing (Boritt, 2008). Therefore, body size, aggressive behaviour and ecological requirements may be interacting factors that could impact on the compatibility of different species and their potential for reproductive success within their captive environment. Aggressive behaviour has not been directly analysed within this project and remains an area requiring further investigation.

In addition, several studies have identified the presence of inter-specific resource competition between bird species that share similar ecological niches, within a controlled laboratory setting (e.g. doves, *Streptopelia spp.*, Poling & Hayslette, 2006) or a wild free-ranging environment (e.g. sparrows *Passer spp.*, Wagner & Gauthreaux, 1990; finches *Fringillidae spp.,* Brazill-Boast, *et al*., 2010). Moreover, in some cases an increase in inter-specific aggressive interactions has been observed (e.g. finches *Fringillidae spp.*, Pearce, *et al*., 2011). Additionally, one study found that common myna (*Acridotheres tristis*) were less likely to approach a food source if another species was already there, thus reducing numbers of food sites to choose from (Haythorpe, *et al*., 2012). Similar conflicts may be prevalent within mixed species zoo enclosures, which in turn may have a negative impact on breeding performance. Furthermore if limitations are placed on access to resources such as food or nest sites, this can have a direct impact on breeding performance (Martin, 1987, Hatchwell, *et al*., 1999).

2.1.2 Enclosure design for mixing species

Enclosure design requires a balance between the needs of the animal keeper, the visitors and the animals themselves (Zoo Design Symposium, 2004; Melfi, *et al.,* 2007; Hosey, *et al*., 2013). Crosta and Timossi (2009) believe that zoo enclosures should be designed with the aim of securing the future genetic viability of the captive bird populations. For this reason the focus of enclosure design should be to promote and enhance the breeding productivity of the species housed within them. Likewise the role a particular enclosure also needs to be considered. For example if the enclosure is considered to be of education value only, thus does not house breeding individuals. Having said this, Sheppard (1995) argues that with the limited space available to enable future sustainability of bird populations, each enclosure should have the facilities which enable breeding of any species if required. At present there has been no recorded study which has assessed bird breeding in relation to the role of different enclosures. This element is outside of the remit of this project, but does further highlight the importance of evaluating the impacts of housing condition on the breeding of birds within zoos.

Buchanan-Smith (2012) highlights the importance of enclosure design when considering the success of species mixes, with a variety of factors needing to be considered when investigating mixed species enclosures. These include aspects of inter-species compatibility (Hediger, 1950; Thomas & Maruska, 1996; Coe, 2001; Hammer, 2002; Veasey & Hammer, 2010) and the environmental parameters which may affect an animal's behaviour (Perkins, 1992). The housing provided needs to meet the requirements for each species and reduce the opportunity for negative competition or conflict (Thomas & Maruska, 1996; Veasey & Hammer, 2010). Although some level of conflict may be natural (e.g. acute stress), whereas continued conflict and competition may result is chronic stress and thus impact on the animal's long term welfare and in turn its breeding productivity (Clubb, *et al*., 2009; Mason, 2010).

Many zoos may use zoogeographical regions within their collection planning and enclosure design (Fiby, 2008). Therefore species chosen for mixed enclosures may come from a similar region or habitat type. In some cases these may be mixes that would occur naturally within the wild or species whose natural home ranges may not overlap, which could also affect their compatibility (Thomas & Maruska, 1996). The direct impact of these different mixes is uncertain and could be linked to individual species-specific requirements within each mix. It may be that some naturally co-existing species may not do well within captivity when housed together. For instance, several species of hummingbird (*Trochilidae spp.)* co-occur in the wild but are difficult to mix *ex-situ* due to their territoriality and levels of aggression (Krebs, *et al.*, 2002). This could be attributed to competition for resources.

Alternatively this incompatibility could be attributed to the need for specialised housing and/or husbandry practices that have not been provided; for instance the provision of separated areas which provide privacy or protection from other species (Thomas & Maruska, 1996; Jeggo, *et al*., 2001; Dalton & Buchanan-Smith, 2005; Dorman & Borne, 2010; Veasey & Hammer, 2010). Furthermore some allopatric species may also be suitable for mixing even though they are unlikely to encounter each other in the wild. For birds it has previously been common practice to mix a ground living pheasant species with a medium size passerine, even when these came from different zoogeographical and/or habitat ranges. For example, a mix of an Asian pheasant (for example Lady Amherst's pheasant (*Chrysolphus amherstiae*) with a neotropical passerine such as Mexican green jay (*Cyanocoax yncas*) or San Blas jay (*Cyanocorax sanblasianus*), which has proved very workable in terms of a compatible breeding mix (Wilkinson, *in litt.*). In studies of primates, red capped mangabeys (*Cercocebus torquatus*), black and white colobus monkeys (*Colobus guereza*), mandrills (*Mandrillus sphinx*) and sooty mangabeys (*Cercocebus atys*) are species that do not share a natural home range, but have been housed together successfully within zoos and are thought to gain social enrichment benefits from these associations (Wojeciechowski, 2004). However the types of interactions that occur in these forced associations within zoo environments remains unclear in many cases.

As previously mentioned in relation to wild birds, competition for resources is likely to impact on the compatibility of different species, which is directly linked to species-specific ecology. It is considered that species which operate within different ecological niches are more likely to be compatible within a zoo environment (Bratton & Dimeo-Ediger, 1993; Hediger, 1950; Thomas & Maruska, 1996). This increased compatibility could be linked to reduced competition for resources (Hediger, 1950). Thomas & Maruska (1996) suggest that enclosures which provide more resource opportunities are more successful overall; for example multiple feeding sites, water sources and shelter. In addition perching sites and areas for retreat for smaller or more passive bird species may be beneficial (Thomas & Maruska, 1996, Coe, 2001). In Goeldi's monkeys (*Callimico goeldii*) and pygmy marmosets (*Cebuella pygmaea*) their space utilisation can by related to their ecological niche which the species operate with that enclosure (Dalton & Buchanan-Smith, 2005), for example in the case of birds a ground dwelling versus perching species. This is supported by Thomas & Maruska (1996) who suggest that risk of competitive interactions is decreased when species with different ecological niches are housed together. This idea can be further supported by the Volterra-Gause model of animal associations, which states that two species should not inhabit identical niches within an ecosystem (Gause, 1934; Hardin, 1960).

There are exceptions to this rule due to other confounding factors such as predation risk, for example some species may share the same ecological niche, thus compete for resources, though may find alternative benefits to their mixed species associations (Ripley, 1961). Although this theory relates to wild populations, it may also be related to compatibility of species within a captive environment. With this in mind, it could be predicted that enclosures with species that share different ecological requirements may be considered to be more productive in terms of their reproductive fitness and inter-species compatibility (Bratton & Dimeo-Ediger, 1993). Conversely zoos often provide less diverse diets to their birds, thus if the same types of food are available to all species that may not have the same ecological niche, but do share a similar dietary requirement this may increase resource competition for species that would not normal compete in the wild (Klasing, 1998).

As well as aspects of species compatibility, the overall density and group composition within a particular enclosure could affect species productivity. For example population density of captive zebra finch (*Taeniopygia guttata*) was found to correlate with reproductive output, where birds housed in lower density aviaries producing more offspring (Poot, *et al*., 2011). This study also found that high densities of finches had significantly more aggressive interactions (Poot, *et al.*, 2011). A similar pattern may exist in mixed species environments in relation to the density of conspecifics and other species housed within each enclosure. However due to the methods used for data collection in this study density is not a factor that has been analysed and thus remains an area for future investigation. Although density was not tested for, it was considered that the number of different species that have are mixed together was a potential factor, for instance enclosures that have lower numbers of species mixed together, may have less competition for resources and thus be the most productive. This has not previously been tested, thus was a factor considered within this analysis.

Taking into consideration the aforementioned points regarding mixed species associations the project represents the first detailed analysis of breeding performance within mixed species bird enclosures across multiple zoos.

2.1.3 Aims

Firstly this chapter aimed to assess the current perception that mixed species bird enclosures experience a lower breeding performance than single species housing. Based on current perceptions it may be suitable to hypothesise that some bird species do experience reduced breeding performance when housed in mixed species enclosures than when those species are housed within single species enclosures. In order to investigate this claim, comparisons of the levels of breeding performance for different bird species has been made in relation to whether that species was housed in mixed or single species housing condition.

Secondly, with guidance from currently known patterns in bird behaviour and trends in zoo enclosure design an assessment of the variables that may affect breeding performance for birds housed within mixed species bird enclosures has also been made. These variables include species-specific behaviour, biology and ecology (such as dietary pattern, breeding sociality and body size) and specific elements of enclosure design and management (such as breeding management status, number of feeding and nest sites, presence of other taxa). Both of these analyses will measure how well each species performs as a whole within each enclosure rather than the performance of individual birds or pairings.

The results of this project will be used to advise on future management practices for mixed species aviaries within UK and European zoo collections.

2.2 Methods

2.2.1 Data collection

All data were collected between 31st January and 30th September 2012 via a questionnaire designed specifically for this project [*Table 1*; *Table 2*]. Following initial piloting with staff at Marwell Zoo the finalised questionnaire was sent via email to 243 zoological collections across Europe using the EAZA and BIAZA membership contact lists. In addition survey participation was promoted by the Chairs of the EAZA *Ciconiiformes* and *Psittaciformes* Taxon Advisory Groups (TAGs) and the British and Irish Association for Zoo and Aquariums Bird Working Group (BIAZA BWG) steering committee.

A questionnaire was chosen due to the ability to collect data from multiple zoos over a short period of time (Burgess, 2001; Plowman, *et al*., 2006). In addition it was determined that each zoo collection would be able to provide adequate information via the questionnaire without the presence of the principle investigator. This was deemed to maximise the number of participating collections and reducing financial cost of the project (Plowman, *et al*., 2006). Moreover, having piloted this method within the preliminary study (Foulds, 2008) this was considered to be suitable for meeting the needs of the project objectives. The questionnaire was split into two sections which requested information from each collection on 1) the design features of each mixed species bird enclosure [*Table 1*] and 2) on the bird species that were housed within each of the mixed species enclosures that had been specified within section one [*Table 2*]. For the purpose of this study three types of mixed species enclosures and one type of single species enclosure were defined [*Table 3*].

Table 1. *Screen shot of blank template of section one of the questionnaire focusing on the design of mixed species bird enclosures which was sent to each of the zoo collections (choice options for the drop down menus can be seen in Table 3 and 4).*

Section 1. Enclosure details								Comments Please use this to specify any significant management changes that are used within this enclosure. E.g. Birds moved in winter
Enclosure name or ID number	Estimated Enclosure size			Type of enclosure	Vegetation coverage	Are any non-bird species held in this enclosure?	Does the enclosure have a trap/catch up facility?	
	Indoor floor space m2	Outdoor floor space m2	Average height m (whole enclosure)					
Please provide the name or code (ARKs name if possible)	Please choose from the size range in the drop down menu	Please choose from the size range in the drop down menu	Please choose from the size range in the drop down menu	Please choose one of the categories from the dropdown menu	Please estimate the level of planting from the choices in the dropdown menu	If yes, please list the species	If yes, please specify what this is used for (choices in the dropdown menu)	
EXAMPLE	21-50	n/a	0-3	On-show -barrier	Moderate – multi-level	0	Catch up	X is moved during ...

Table 2. *Screen shot of blank template of section two of the questionnaire focusing on bird species housed within the mixed species enclosures which was sent to each of the zoo collections.*

Section 2. Bird species									Comments
Enclosure name or ID number	Bird species	How many males and females?	How many feeding stations are available for this species?	What type and how many nesting areas are available for this species?	Do you want to breed this species within this aviary?	When breeding what breeding management is most necessary to breeding this species?	How would you rank the breeding performance of this species within this enclosure in the past 5 years?	If you also house this as a single species, how would you rank breeding performance?	
Please provide the aviary name or code (ARKs name if possible)	Please list all bird species (scientific name) housed within this enclosure (one per line)	Please provide an estimate of the group composition	Please list the type of food site and the number	Please give the type of nests and the number	Please tick Yes or No	Please score 1 to 3: 1 = Hand rearing 2 = Combination -hand rearing and parent-rearing 3 = Parent-rearing 4 = Fostering	Please score 1 to 5: 1 = No breeding attempts 2 = Eggs laid – failed to hatch 3 = Eggs hatched but did not fledge 4 = has breed in the past 5 = Breeds each year	Please score 1 to 5: 1 = No breeding attempts 2 = Eggs laid – failed to hatch 3 = Eggs hatched but did not fledge 4 = has breed in the past 5 = Breeds each year	
EXAMPLE	Species X	1.1	2	2 Cavity	☑ Yes ☐ No	3	4	2	

Table 3. *Definitions of the four enclosure types specified within the questionnaire.*

Type of enclosure	Description
On-show mixed species enclosure (visitor barrier	An enclosure with no size limit that is on-show to the public (either fully or partly) that holds two or more bird species which share the same enclosed space and where visitors are separated from the animals via a physical barrier (other non-bird taxa may or may not be present).
On-show walkthrough mixed species enclosure	An enclosure with no size limit that is on-show to the public (either fully or partly) that holds two or more bird species which share the same enclosed space in which the public can walk within the same space as the birds and are not separated from them by a physical barrier (other non-bird taxa may or may not be present).
Off-show mixed species enclosure	An enclosure with no size limit that is not on show to the public that holds two or more bird species which share the same enclosed space (other non-bird taxa may or may not be present).
Single species bird enclosures	An enclosure with no size limit that holds only one species of bird – may be on-show or off-show (other taxa may or may not be present).

Section one of the questionnaire [*Table 1*] focused on enclosure design for each mixed species enclosure using predetermined variables [*Table 4*]. The variables chosen for this project were based on factors previously highlighted in current literature and discussion with members of the BIAZA BWG. Each collection was asked to provide the approximate size (indoor and outdoor where applicable), approximate percentage vegetation coverage, presence of non-bird taxa *[Table 4]* and the enclosure type for each of their mixed species bird enclosures [*Table 3*]. In addition the presence and use of any trap cage facilities was also requested, as this had been highlighted as an area of interest in discussions with members of the BIAZA BWG and curators from other European zoos. Furthermore, the choice of sub-options for each variable were based on discussions with members of the BIAZA BWG (Gordon Campbell, Laura Gardener and Adrian Walls), curatorial and research staff at Chester Zoo (Dr Sonya Hill, Dr Nick Davis and Andrew Owen) *[Table 4].* This was supported by reviewing information on enclosure sizes and design features listed on ZooLex (2011).

Table 4. *Predetermined independent categorical variables (n=10) specified within section one and section two of the questionnaire relating to enclosure design and bird management.*

Variable category	**Options**
Nest site provision (including number provided)	1. Box/Basket/Shed 2. Ledge/Cliff 3. Trunk/Cavity/Burrow 4. Platform 5. Vegetation/Ground/Build own
Trap cage facility	1. None 2. Yes
Other taxa present	0. No 1. Yes
Vegetation cover	1. Dense (70 %+) 2. Moderate 3. Sparse (up to 30%) 4. No planting
Enclosure type	1. Walkthrough 2. Barrier 3. Off-show 4. Mixture
Enclosure height	1. Up to 3m 2. 4-8m 3. 9-15m 4. 16m+ 5. Open
Outdoor enclosure size	1. Up to 50m2 2. 51-200m2 3. 201-500m2 4. 501-1000m2 5. 1001m2+ 6. None
Indoor enclosure size	1. Up to 20m2 2. 21-50m2 3. 51-200m2 4. 201-500m2 5. 501m2+ 6. None
Breeding husbandry	1. Hand-rearing 2. Combination 3. Parent-rearing 4. Fostering
Feeding station provision (number per species)	No category required

Within section two of the questionnaire [*Table 2*] each zoo collection was asked to provide information on the bird species that were housed within each of the enclosures that they had specified within section one. The overall group composition, the number and type of feeding stations and nest site per species and whether the collection wanted to breed the species within that enclosure were recorded. For all species that the collection wanted to breed further information was requested on the type of breeding husbandry most used for that species [*Table 4*].

In order to assess the breeding performance of each species within each enclosure all collections were asked to estimate how well each species had bred within that enclosure over a five year period using a predetermined and standardised scoring system. For the purposes of this study five breeding performance (BP) scores were defined [*Table 5*]. As well as to the information on breeding performance within each of the mixed species enclosures, every zoo was asked where applicable, to provide breeding performance scores for species that had also been housed within a single species enclosure [*Table 3*].

Table 5. *Definitions of the five breeding performance (BP) score categories utilised within the questionnaire.*

Score (BP)	Definition
BP1	No breeding attempts were made in the last five years.
BP2	At least one egg laid, but failed to hatch in the last five years.
BP3	At least one egg hatched but the chick(s) did not fledge in the last five years.
BP4	At least one chick has fledged in the last five years.
BP5	At least one chick has fledged every year for the last five years.

Following initial completion of the questionnaires the data returned from each collection did not yield a sufficient sample for bird species that had also been housed within single species enclosures. Therefore an additional online survey was sent out to all of the 243 zoo collections requesting further information on the breeding performance scores for bird species housed within single species enclosures only, using the same standardised format as the original questionnaire.

Overall survey data (questionnaires and online) were collected from 99 collections resulting in a 41% response rate from 21 countries across Europe. This was comprised of 70 collections which submitted the full questionnaire; 18 collections which provided single species breeding performance scores only (32 collections in UK and Ireland and 56 collections from the rest of Europe). In addition, 11 collections did not meet the survey criteria. A total of 428 mixed species enclosures were recorded which housed 585 different bird species (totalling 1924 data points). This represents approximately 20% of all species housed within European Zoos (ZIMS, 2014). Of the 428 mixed species enclosures 88% were recorded as on-show with a barrier, 21% walkthrough, 2% off-show and 1% considered a mixture of enclosure types.

A review of literature was also carried out in order to collect information on species typical ecology, biology and behaviour. This information was used to categorise each species based on different ecological and behavioural factors [*Table 6*]. The ecology and behaviour of 130 bird species were reviewed. Alongside the predetermined categories for enclosure design defined within the questionnaire [*Table 5*], the species-specific information was used to produce 21 categorical variables relating to aspects of ecology, behaviour and captive management *[Table 4 and 6].* These categories were used to assess the impact that these factors may have on breeding performance.

***Table 6**. Independent categorical variables (n=11) which were determined as components of species ecology, behaviour and management that may have an influence on the breeding performance of captive birds.*

Variable category	**Options**	**Source references**
Breeding management	1. European Endangered Species Breeding Programme (EEP) 2. European Studbook (ESB) 3. No official management	EAZA, 2013
Dietary Pattern (Categories adapted from Klasing, 1998)	1. Omnivore 2. Faunivore 3. Herbivore	IUCN Red List 2012, 2013*;* *Anseriformes*, Carboneras. 1992; *Psittaciformes*, Forshaw, 1981; *Gruiformes:* Taylor, 1996, Archibald & Meine, 1996; *Ciconiiformes*, Martinez-Vilalta & Motis, 1992; Elliot,1992; Matheu & del Hoyo, 1992; *Galliformes*, del Hoyo, 1994; Carroll, 1994; Mcgowan, 1994; *Falconiformes*, Thiollay, 1994; *Passeriformes*, Del Hoyo, *et al*., 2011*;* *Charadriiformes*, Gochfeld & Berger, 1996; *Sturnidae*, Bockheim & Congdon, 2001
Zoogeography (Categories adapted from WWF Ecoregions, 2012).	1. Palearctic 2. Afrotropical 3. Cosmopolitan 4. Indo-Malayan/Australasian 5. Neotropical	
Body size (Categories adapted from Handbook of Birds of the World, various dates)	1. Small (Under 100g) 2. Medium (101-750g) 3. Large (751-2000g) 4. Extra-large (2001g+)	
Nest categories	1. Cavity/Burrow 2. Saucer/Plate/Cup 3. Platform 4. Scrape 5. Mound	
Migratory pattern (Categories adapted from Birdlife International, 2013)	1. Resident 2. Migratory 3. Dispersive	
Habitat (Categories adapted from IUCN Habitats Classification Scheme Version 3.0, 2007)	1. Forest 2. Wetland/marine/estuarine 3. Scrubland/grassland 4. Savannah/desert/rocks	
Offspring type	1. Precocial (Open eyes, down, able to leave nest -follow adults or independent) 2. Semi-precocial (Able to leave nest, but fed by parents) 3. Semi-altricial (Down, not able to leave nest, parent fed) 4. Altricial (Closed eyes, no down, not able to leave nest, parent fed)	
Breeding sociality (Categories adapted from Handbook of Birds of the World, various dates)	1. Colonial (breed in social aggregations) 2. Solitary (nest alone or in small family groups) 3. Territorial (actively hold a territory via the use of display or aggression)	
Fledge time/Independence	1. Short (Up to 1 month) 2. Mid-length (1- 3 months) 3. Extended (3+ months)	
Mixed enclosure niche (Categories based on Sheppard, 1995)	1. Water (require a body of water within their enclosure) 2. Ground 3. Perch	Sheppard, 1995

2.2.2 Data analysis

Data analyses for this chapter were divided into two parts. The first relates to the comparison of breeding performance between mixed and single species enclosures (*Section 2.3.1*). The second relates to the evaluation of factors that may impact breeding performance within mixed species enclosures only (*Section 2.3.2*). Three filters were applied to the data for the purpose of analysis. The first filter was applied to the data from section two of the questionnaire. This filter removed any samples of species that the collection had not wanted to breed within that enclosure. A total of 76.4% of all data were specified as breeding priorities (1440 data points), *i.e.* the collection intended to breed that species within the specified enclosure (n= 509 species) from 87 zoo collections.

Of the remaining 509 species a low number of replicates for many of these species were collected. To allow for analysis of at least some of these species, a second filter was applied to the remaining species data. A minimum number of five replicates per species were chosen, thus individual species with a sample size less than five within any mixed species enclosure were discounted. This resulted in 90 bird species remaining [*Table 7*] from 80 different zoo collections. Although data for each species can from multiple collections the effect that being housed at a particular zoo was not tested in this study. These 90 species were then used to assess the second objective of evaluating the factors that may impact breeding performance within mixed species enclosures.

Table 7. *Bird species which had a sample size of five or more within mixed species bird enclosures (n=90) [*Emboldened denotes each species which also had a sample size of five or more single species bird enclosures (n=34)].*

Anseriformes	
Aix galericulata	Mandarin duck
Aix sponsa	**Wood duck**
Anas acuta	Northern pintail
Anas bernieri	Madagascan teal
Anas clypeata	Northern common shoveler
Anas crecca	Eurasian common teal
Anas hottentota	Hottentot teal
Anas penelope	Eurasian wigeon
Anas querquedula	Garganey
Anas sibilatrix	Chiloe wigeon
Aythya nyroca	Ferruginous duck
Branta leucopsis	**Barnacle goose**
Branta ruficollis	**Red-breasted goose**
Callonetta leucophrys	Ringed teal
Dendrocygna bicolor	Fulvous whistling duck
Dendrocygna viduata	White-faced whistling duck
Marmaronetta angustirostris	Marbled teal
Mergellus albellus	Smew
Netta peposaca	Rosy-billed pochard
Netta rufina	Red-crested pochard
Somateria mollissima	Common eider
Tadorna tadorna	**Common shelduck**

Coliiformes	
Colius striatus	Speckled mousebird

Charadriiformes	
Himantopus himantopus	Black-winged stilt
Himantopus mexicanus	Black-necked stilt
Philomachus pugnax	Ruff
Recurvirostra avosetta	Pied avocet
Vanellus miles	Masked lapwing

Ciconiformes	
Bubulcus ibis	**Cattle egret**
Ciconia ciconia	**European white stork**
Ciconia nigra	**Black stork**
Egretta garzetta	Little egret
Eudocimus ruber	**Scarlet ibis**
Geronticus eremita	**Waldrapp ibis**
Nycticorax nycticorax	**Black-crowned night heron**
Platalea ajaja	Roseate spoonbill
Platalea alba	**African spoonbill**
Platalea leucorodia	Eurasian spoonbill
Plegadis falcinellus	Glossy ibis
Plegadis ridgwayi	Puna ibis
Threskiornis aethiopicus	**Sacred ibis**
Threskiornis spinicollis	Straw-necked ibis

Gruiformes	
Grus virgo	**Demoiselle crane**
Balearica regulorum	**Grey-crowned crane**
Eurypyga helias	Sunbittern

Columbiformes	
Caloenas nicobarica	Nicobar pigeon
Chalcophaps indica	Emerald dove
Ducula bicolor	Pied imperial pigeon
Gallicolumba criniger	Mindanao bleeding-heart dove
Gallicolumba luzonica	**Luzon bleeding-heart dove**
Geopelia cuneate	**Diamond dove**
Goura victoria	Victoria crowned pigeon
Otidiphaps nobilis	White-naped pheasant pigeon
Ptilinopus melanospilus	Black-naped fruit dove
Streptopelia turtur	European turtle dove

Coraciiformes	
Coracias cyanogaster	Blue-bellied roller
Tockus deckeni	**Von der Decken's hornbill**

Cuculiformes	
Musophaga violacea	**Violet turaco**
Tauraco erythrolophus	Red-crested turaco
Tauraco fischeri	Fischer's turaco
Tauraco leucotis	White-cheeked turaco

Falconiformes	
Gyps fulvus	Eurasian griffon vulture
Gyps rueppellii	Ruppell’s griffon vulture
Vultur gryphus	**Andean condor**

Pelecaniformes	
Pelecanus onocrotalus	**Great white pelican**
Scopus umbretta	**Hammerkop**

Galliformes	
Coturnix chinensis	King quail
Numida meleagris	**Hemeted guineafowl**
Polyplectron napoleonis	Palawan peacock pheasant
Rollulus rouloul	**Roulroul partridge**
Tragopan temminckii	**Temminck’s tragopan**

Passeriformes	
Copsychus malabaricus	**White-rumped shama**
Cossypha albicapilla	White-crowned robin
Cyanopica cyanus	Azure winged magpie
Euplectes orix	Southern red bishop
Garrulax courtoisi	Blue-crowned laughingthrush
Irena puella	Fairy bluebird
Lamprotornis superbus	**Superb starling**
Leiothrix lutea	**Peking robin**
Leucopsar rothschildi	**Bali starling**
Padda oryzivora	**Java sparrow**
Pycnonotus jocosus	**Red-whiskered bulbul**
Ramphocelus bresilius	Brazilian tanager
Scissirostrum dubium	Finch billed mynah
Taeniopygia guttata	Zebra finch
Zoothera citrina	Orange-headed ground thrush
Zoothera dohertyi	**Chestnut-backed thrush**

Phoenicopteriformes	
Phoenicopterus chilensis	**Chilean flamingo**
Phoenicopterus roseus	**Greater flamingo**
Phoenicopterus ruber	**Caribbean flamingo**

2.2.2.1 Mixed species versus single species enclosures

In order to investigate the first objective of comparing breeding performance between mixed and single species environments a third filter was applied to the remaining 90 species, whereby all species that had also been housed as a single species enclosure with a sample size lower than five were discounted. Following application of the final filter 34 different bird species were remaining [*Table 7*]. All statistical analyses were carried out using SPSS version 20.0.

Prior to any statistical analysis the proportion of enclosures where each of the 34 bird species had breed successfully was calculated, using the five BP scores as the measure of success *[Table 5].* This calculation was repeated for mixed and single species enclosures. These proportions were then tested for normality. As some of the data were not normally distributed an ARCSINE transformation was performed. To compare the proportions of breeding performance for each species within a mixed species enclosures with those in single species enclosures five Paired-Samples T-tests were then applied to each of the five BP scores for each of the 34 bird species.

Following this, in order to reduce the number of categories and increased the robustness of the data for statistical analysis the BP scores for each species were collated, resulting in two overall breeding performance categories. BP1, BP2 and BP3 were collated and redefined as those that had not bred successfully and BP4 and BP5 were collated as those that had bred successfully. Using the newly formed bred and not bred categorisation of breeding performance (previously listed as BP4 and BP5) the proportion of enclosures where each of the 34 bird species had breed successfully for mixed and single species enclosures were recalculated. A Paired Samples t-test was then applied using the simplified breeding performance, thus comparing those species that had bred successfully in mixed versus single species enclosures.

To enable analysis in relation to specific bird species the difference between the proportions of each individual species that had bred successfully in mixed and in single enclosures were calculated for each of the 34 species. This was calculated by subtracting the proportion or replicates of each species that had breed successfully within mixed enclosures from the proportion that had breed successfully in single enclosures for each of the 34 species. A one-way General Linear Model (MANOVA) was then applied to relate the difference between the five breeding performance proportions within the two housing conditions using 10 independent variables relating to specific-specific ecology and captive management (studbook management status, zoogeography, body size, wild nest type, wild diet type, migratory pattern, wild habitat type, mixed species enclosure niche, offspring type and breeding sociality) *[Table 4; Table 6].* Due to the low number of replicates available for each of the 34 species the ability to carry out detailed analysis at an individual species level was limited. However visual observations of the differences in the proportions that bred successfully for each individual species within the two housing conditions were made in an attempt to identify any patterns that may exist.

2.2.2.2 Mixed species enclosures: factors impacting breeding

For the second part of the analysis the full 90 species were used [*Table 7*]. The proportion of enclosures where each of the 90 bird species had breed successfully was calculated, using the five BP scores as the measure of success. These proportions were also recalculated using the simplified bred or not bred categories. A categorical binary logistic regression using a forward stepwise method was applied to the simplified bred and not bred proportions to compare breeding performance of the 90 species against 21 categories relating to species-typical ecology and the enclosure design features which those species had been housed within [*Table 4; Table 6*]. A backwards logistic regression was then applied using the five significant the variables identified within the forwards stepwise regression (fledge time, breeding sociality, presence of other taxa, number of species mixed and number of nest sites provided) and also studbook management, in order to investigate any further differences in these variables.

In addition in order to control for the potential impact of phylogeny upon breeding performance within mixed species enclosures a phylogenetic generalized least squares model (PGLS) was applied to the data using R. The tools *Caper* and *Phytools* were used to infer phylogeny of each of the 90 species based on phylogenetic tree data (Hackett All Species backbone - Hackett, *et al*., 2008) [*Fig. 1*] extracted from Birdtree.com (2014), which is based on the work of Jetz, *et al*., (2012; 2014). The proportion of replicates that had bred successfully for each species was then plotted against 11 ecological variables [*Table 6*] for which there were at least a minimum sample size of five in each of the categories. The other 10 variables *[Table 4*] relating to enclosure design could not be used as they did not have a sufficient sample size to allow for PGLS analysis. Finally, the PGLS was also used on the five breeding performance scores [*Table 3*] between mixed and single species enclosures to control for any effects of phylogeny [*Fig. 1*].

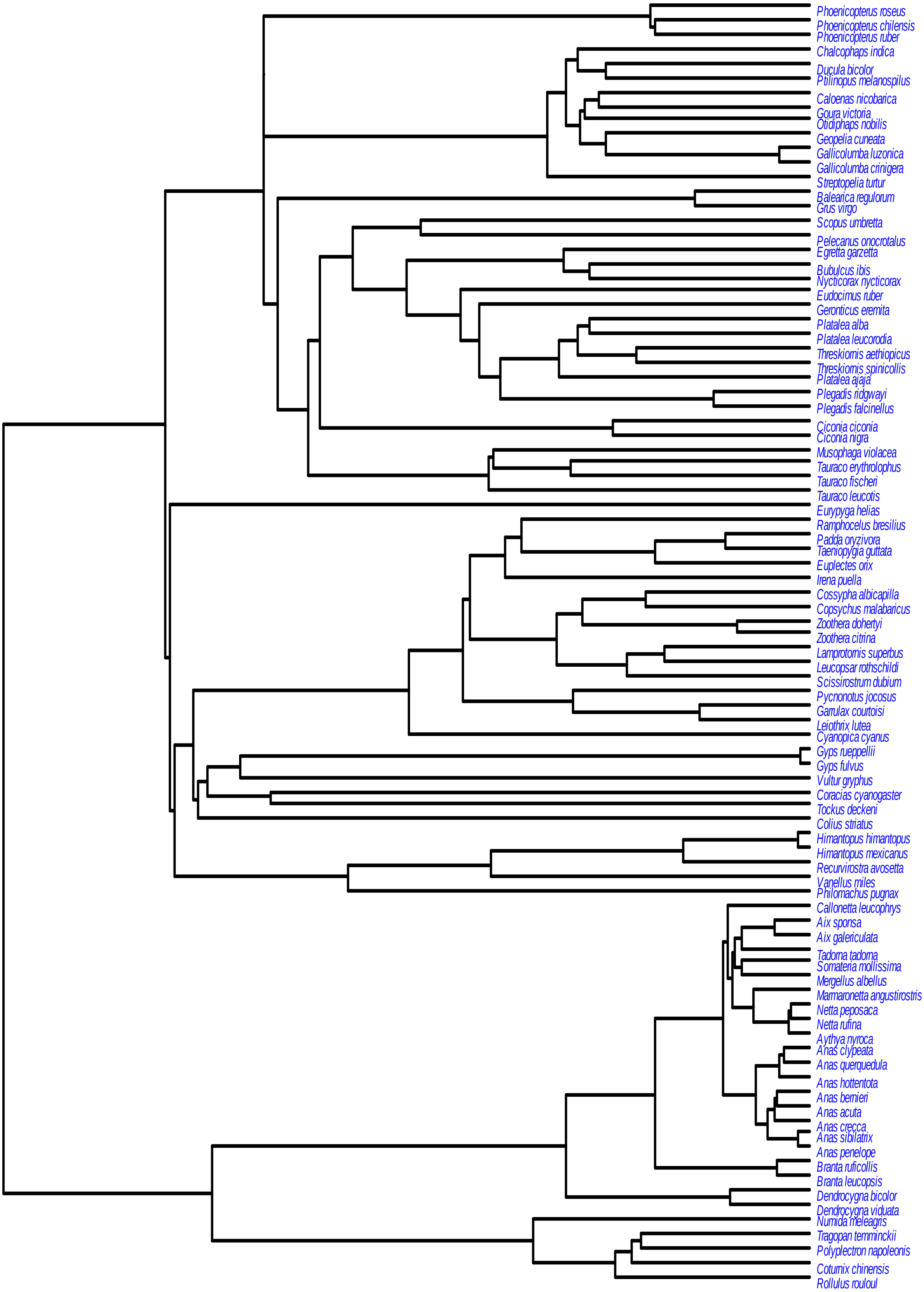

Figure 1. *Phylogram of the 90 bird species which had a sample size of five or more within mixed species bird enclosures.*

2.3. Results

2.3.1 Mixed species enclosures versus single species enclosures

When comparing breeding performance between mixed and single species environments 55% of species exhibited a higher proportion of successful breeding when housed within single species enclosures [*Fig.* 2]. Conversely, 35% of species demonstrated higher levels of breeding in mixed species enclosures [*Fig.* 2]. The remaining 10% (n=3 species) were estimated to breed to the same level in both housing types (*Phoenicopterus roseus*, *Vultur gryphus* and *Branta ruficollis*) [*Fig.* 2]. The first five Paired Samples T-test used to compare the five BP scores for species housed in mixed species enclosures against single species enclosures revealed that significantly more species in mixed enclosures were scored as BP1 ($t_{(33)} = 2.450, P = 0.020$); thus had not attempted to breed when housed in mixed species environments than when those same species were housed in single species environments. No further differences were found for the other four BP scores between the two housing conditions (BP2 [$t_{(33)} = 1.161, P = 0.254$]; BP3 [$t_{(33)} = -1.014$], $P = 0.318$]; BP4 [$t_{(33)} = -1.589, P = 0.122$]; BP5 [$t_{(33)} = -0.233, P = 0.817$]. A further Paired Samples T-test using the two simplified BP categories revealed that significantly more bird species bred successfully when housed in single species enclosures than they did in mixed species enclosures ($t_{(33)} = -2.218, P = 0.034$) [*Fig. 2*].

Ecological and social factors did not explain differences in breeding performance for any of the 34 species [*Table 7*] (one-way MANOVA using Wilks ʎ - Studbook management [$F_{(2,8)} = 0.257, P = 0.897$]; Zoogeography [$F_{(5,8)} = 0.591, P = 0.763$]; Body size [$F_{(2,8)} = 1.485, P = 0.295$]; Wild nest type [$F_{(6,8)} = 0.525, P = 0.832$]; Dietary pattern [$F_{(2,8)} = 1.406, P = 0.315$]; Migratory pattern $F_{(2,8)} = 0.325, P = 0.854$]; Wild habitat [$F_{(5,8)} = 0.791, P = 0.601$]; Mixed enclosure niche [$F_{(2,8)} = 0.931, P = 0.492$]; Offspring type [$F_{(3,8)} = 0.838, P = 0.574$]; Breeding sociality [$F_{(2,8)} = 1.410, P = 0.318$]). Finally when controlling for phylogeny in relation to breeding performance in mixed versus single species enclosures a strong significant result can still be observed ($F_{(1,32)} = 8.988, P = 0.00052$), thus highlighting the importance of phylogenetics in this case.

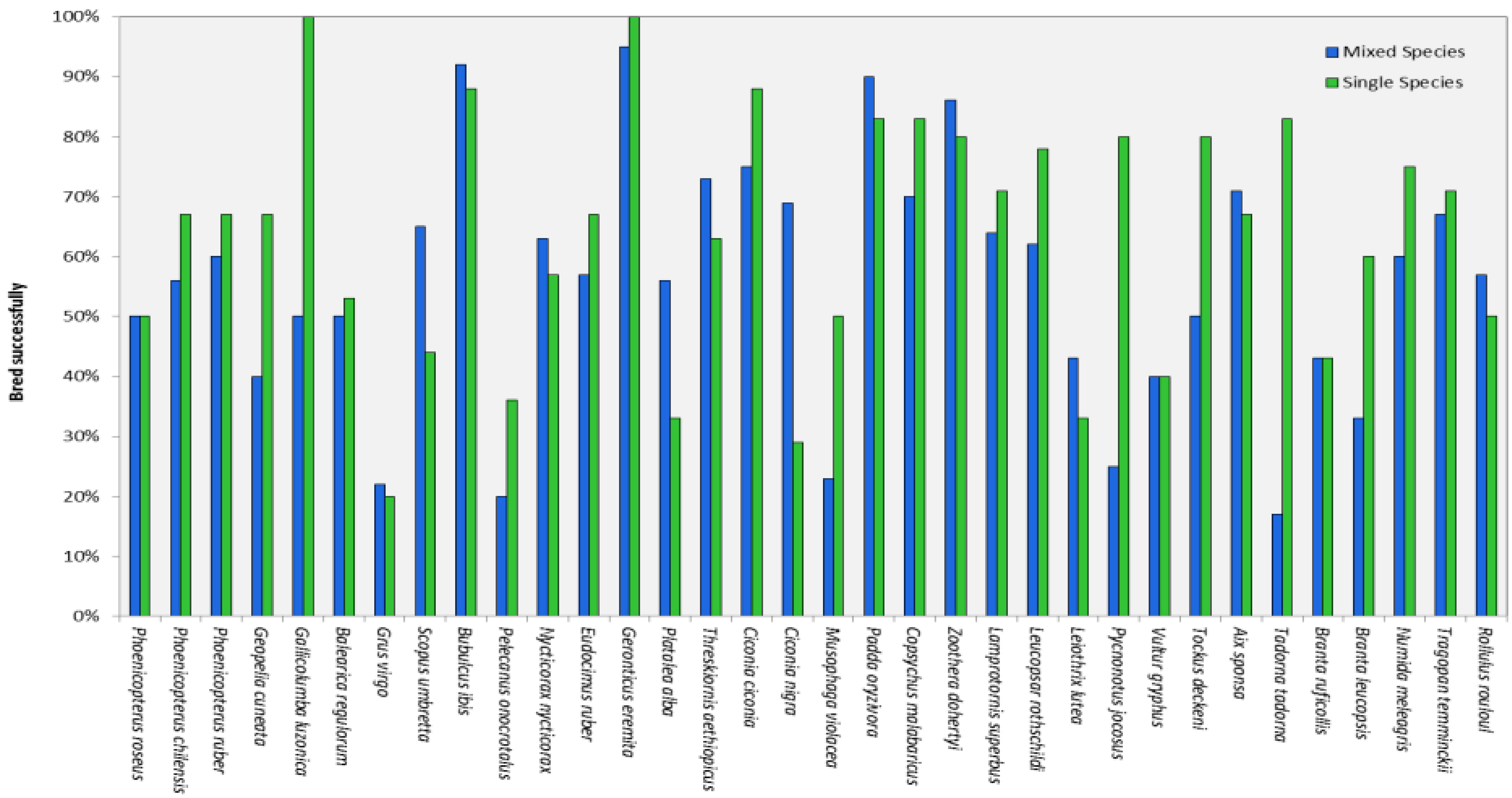

Figure 2. *Percentage of each bird species (n=34) which had bred successfully (reared at least one chick in five years) within mixed and single species housing, presented in phylogenetic order (Based on Hackett, et al., 2008).*

2.3.2 Mixed species enclosures – factors impacting breeding

In total 60.7% of all the samples of birds within mixed species enclosures had breed successfully. Overall 25.3 % of all the samples of birds had never attempted to breed in their enclosure (BP1), 9.7% had laid eggs which had not hatched (BP2), 4.3% had eggs that hatched but not fledged chicks (BP3), 24% had fledged at least 1 chick in the past five years (BP4) and 36.7% had consistently bred in their enclosure each year (BP5). The forward stepwise binary logistic regressions using the simplified breeding performance categories highlighted five variables that had a significant effect on the breeding performance of bird species housed within mixed species enclosures. Firstly breeding sociality was found to impact performance (*B = 0.294, P = 0.004*), where territorial species were proportionally less successful in fledging at least one chick per year than colonial *(B = -0.138, P = 0.007)* or solitary species (*B = -0.643, P=0.002*) when housed in mixed species environments [*Fig. 3*].

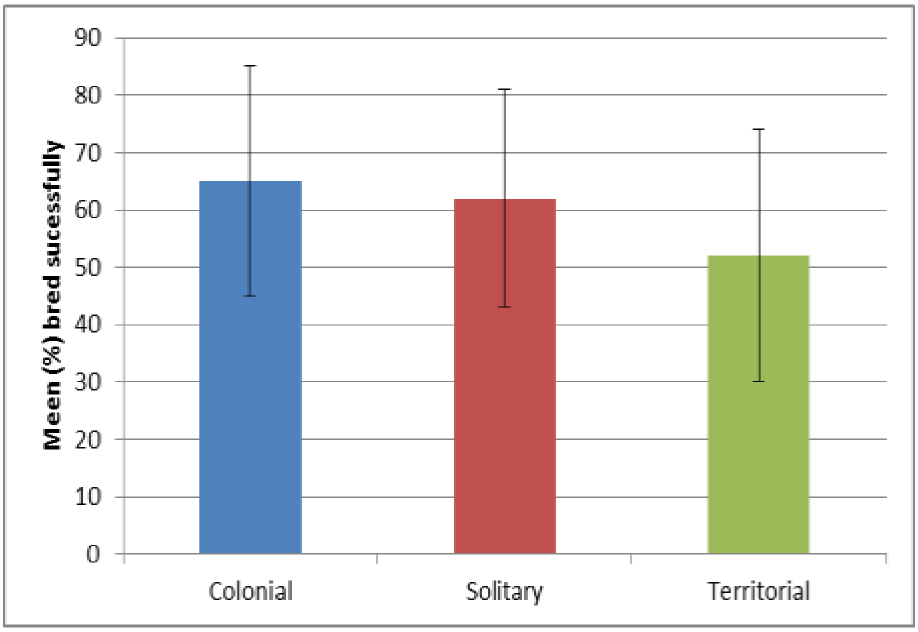

Figure 3. *Mean percentage (+/- S.D.) of successful breeding for bird species (n=90) in relation to their breeding sociality (Colonial species n=34, Solitary species n=32, Territorial species n=24) when housed in mixed species enclosures.*

The fledge time (*B = 0.030, P = 0.040*) of a species was found to have a significant impact on breeding performance, where species categorised as having a fledge time of 0-3 months (short and mid-length) had higher breeding success than species which have extended periods of development (*B = - 1.171, P = 0.006*) [*Fig. 4*].

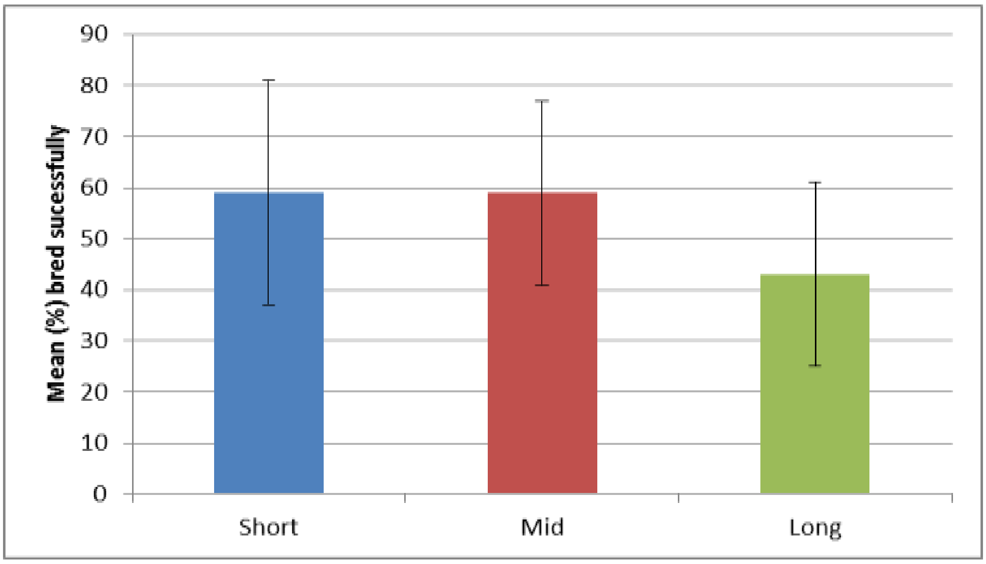

Figure 4. *Mean percentage (+/- S.D.) of successful breeding for bird species (n=90)in relation to the length of time to fledge (Short-fledge length species n=39, Mid-fledge length species n=47, Long-fledge length species n= 4) when housed in mixed species enclosures.*

Presence of non-bird taxa *(B = 0.557, P = 0.025*) within mixed species enclosures was found to impact breeding performance with higher levels of success being observed when no other taxa were present *(B = -0.564, P = 0.045).* Also the number of species mixed together *(B = 0.040, P = 0.003)* and number of nest sites was also found to significantly impact on breeding *(B = 0.091, P = 0.007),* though none of the individual sub-categories were found to be significant when tested with the backwards regression. None of the other variables were found to be significant (Dietary pattern *[B = 0.567, P = 0.451];* Zoogeographical region *[B = 0.052, P = 0.819];* Body size *[B = 0.394, P = 0.530];* Migratory pattern *[B = 0.489, P = 0.484];* Habitat type *[B = 2.366, P = 0.124];* Mixed enclosure niche *[B = 0.104, P = 0.747];* Offspring type *[B = 0.081, P = 0.776];* Nest type [B = 1.034, P = 0.309]; Indoor space *[B = 1.044, P = 0.307];* Outdoor space B = 0.104, P = 0.747]; Enclosure height *[B = 1.447, P = 0.229];* Enclosure type [B = 0.124, P = 0.725]; Vegetation cover *[B = 0.306, P = 0.580];* Number of feeding sites [B = 0.666, P = 0.415], Trap facilities *[B = 0.275, P = 0.094]*). Although studbook management was not significant *(B = 3.719, P = 0.054*), when comparing the three management options within this variable, those species that were EEP managed were more likely to breed successfully (*B = -0.420, P = 0.036*). Conversely species that did not have any studbook management were more likely to have lower breeding performance *(B = -0.584, P = 0.010).*

When controlling for phylogeny in relation to breeding performance against 11 of the species-specific ecological factors no significant results were observed for any of the variables considered [*Table 8*]. Although a trend can still be observed for breeding sociality ($F_{(2,\ 87)} = 2.481,\ P = 0.0897$).

Table 8. *Results of phylogenetic generalized least squares model (PGLS) of breeding performance in relation to eleven species-specific ecology and husbandry variables when controlling for phylogeny.*

Variable	Result
Studbook management	$F_{(2,87)} = 0.7548$, $P = 0.4732$
Dietary pattern	$F_{(2,87)} = 1.288$, $P = 0.2811$
Breeding sociality	$F_{(2,87)} = 2.481$, $P = 0.0897$
Zoogeographical region	$F_{(5,87)} = 1.606$, $P = 0.1672$
Offspring type	$F_{(3,87)} = 0.536$, $P = 0.6808$
Body size	$F_{(3,86)} = 0.9275$, $P = 0.4313$
Fledge time	$F_{(2,87)} = 1.069$, $P = 0.3476$
Nest type	$F_{(5,87)} = 0.6044$, $P = 0.6967$
Migratory pattern	$F_{(2,87)} = 1.628$, $P = 0.\ 2023$
Habitat type	$F_{(6,87)} = 1.119$, $P = 0.3587$
Enclosure niche	$F_{(2,87)} = 0.1023$, $P = 0.9029$

2.4 Discussion

As previously discussed, mixed species enclosures may be considered as beneficial to many aspects of captive management for a variety of taxa (Thomas & Maruska, 1996; Dorman & Borne, 2010; Veasey & Hammer, 2010). In contrast these types of enclosures may also offer their own suite of problems (Hediger, 1950). In particular the results of this study provide support for the hypothesis that some bird species are experiencing reduced breeding performance when housed within a mixed species environment. Proportionally more than half the bird species displayed higher levels of breeding performance when housed in single species enclosures *[Fig. 2*]. Having said this, approximately one-third of the bird species also did better in mixed species enclosures [*Fig. 2*], although this was still significantly lower than single species housing. This result highlights that breeding in mixed species enclosures may be problematic for some species, but is conversely a suitable environment for many others. Therefore it may be suggested that some species could be more predisposed to doing well in mixed species enclosures. This may be related to a number of variables, including behaviour, ecology and phylogeny.

Considering this, it could be expected that phylogenetics may have an effect on whether a species does well in a particular style of enclosure. However for the first objective of this study when controlling for phylogeny a significant result remained between mixed versus single species enclosures, indicating that any bird species across all taxonomic groups could have reduced performance in mixed species aviaries. This also demonstrates no obvious trend towards a certain type of bird being more suitable for either of the housing conditions. Additionally, as no clear pattern in ecology or behaviour was observed for any of the 34 species analysed, this may indicate that species-specific ecology is not a factor which impacts upon whether a bird species does well in a mixed or single species environment. However due to limitations on the number of species that could be analysed and small sample sizes for each species this aspect could not be considered in more depth and remains a subject for additional investigation.

That being said, as the results do illustrate a significant proportion of species which are experiencing reduced breeding success within mixed species environments, it is important to assess the potential cause of this reduction. Out of the 21 variables [*Table 4; Table 6*] that were analysed in this study, two ecological variables (breeding sociality and fledge time) and three variables relating to enclosure design or management were highlighted as significant. Breeding sociality and length of time to fledge were the only two ecological factors found to impact upon species breeding performance. As was predicted colonial species were most successful in mixed species enclosures [*Fig. 3*]. This links with the known behaviour of wild colonial species which are often gregarious and in many cases found in mixed associations in the wild (Ripley, 1961, Alatalo & Moreno, 1987; Terborgh, 1990; Kruger, 2002; Rubenstein, *et al*., 2008).

The results of this study also fit known patterns of behaviour for territorial species, for example species with a higher propensity for aggression (Boritt, 2008). This could be associated to levels of resource competition within each enclosure, both inter and intra-specific (Finch, 1990; Kruger, 2002; Boritt, 2008; Cornelius, *et al*., 2008). It may be that if a territorial species is housed in a situation where they are unable to hold a sufficient territory this may reduce the chances of breeding successfully (Hediger, 1950; Bratton & Dimeo-Ediger, 1993). This may depend how much territorial space a single breeding pair may require to be successful. In addition it may be important to consider whether mixed species enclosures provide enough space or complexity of space to allow territoriality to occur. However, to date there are no publications which have focused on this particular interaction within mixed birds enclosures, thus providing no evidence to support this suggestion directly. Examples of species classified as territorial which were considered less successful in mixed enclosures were from the order *Passerina* including; *Leucopsar rothschildi*, *Musophaga violacea* and *Copsychus malabaricus* [*Fig. 2*]. This pattern would fit with known breeding sustainability for many passerines (Ward, 2012; Leus *et al*., 2011), which suggests that this order may need additional consideration when attempting to breed within mixed species housing. In contrast, *Leiothrix lutea* and *Zoothera doheryti* did equally well in mixed enclosures, if not slightly better than when housed singularly [*Fig. 2*], further highlighting the complexity of this type of housing.

Although not expected, when compared to territorial species, solitary species also did better within mixed enclosures [*Fig. 3*]. These results may be due to the methods used for categorisation of species sociality or that the solitary species that did well were not aggressive species. However a combination of results can be observed when comparing how well solitary species did in mixed versus single enclosures. For example *Scopus umbretta* and *Rollulus rouloul* performed markedly better in mixed species environments [*Fig. 2*]. Whereas Luzon bleeding heart dove and Von der Decken's hornbill performed much better in single species enclosures [*Fig. 2*]. No clear pattern for why these particular results can currently be ascertained. In addition the length of time to fledging has a negative impact on breeding performance whereby species with extended fledge times (more than 3 months) do the worst in a mixed enclosures [*Fig. 4*]. An example of this would be the *Vultur gryphus*, although this species also displays lower levels of success in single species enclosures. In contrast this species is considered to have a population size within European zoos (Leus & Bingaman Lackey 2008a, 2008b), which may be linked to its long life span, thus it remains unclear why any of these patterns may exist. Additionally evidence suggests that condors can experience breeding issues, which have been related to nutritional problems (Pattee, *et al*., 2006) and social structure (Donázar & Feijóo, 2002). Therefore the results for this this particular species may be related to other confounding variables outside of the remit of this investigation.

From an enclosure design and husbandry perspective bird only enclosures did better than those which housed non-bird taxa. However there are not enough replicates for further analysis into which non-birds may have the most impact. This does highlight one of the potential problems within mixed enclosures which can be related to limiting interference between species (Dick, 2012). A previous study suggested that inter-species interference had been estimated as the biggest influence on the breeding success of birds within mixed enclosures (Foulds, 2008). This may relate to interference by bird and non-bird species, a potential effect that requires further investigation to identify if non-bird taxa interfere more than other bird species do. Moreover, Dick (2012) suggests that the size of the enclosure should be considered as the space available for all of the animals/species and its complexity is important. In this study, a numbers of factors that would normally be associated with enclosure complexity were not highlighted as significant. For example the planting level is thought to promote higher living standards for birds rather than barren enclosures (Rogers & Wylie, 1975; Rogers, 1984). In this case neither vegetation coverage nor enclosure size (height and floor space) was highlighted as a significant impacting factor.

Another important design feature to be considered is the provision of nest sites, as this was found to be an important factor influencing breeding performance across the 90 bird species analysed.

Nonetheless it is unclear exactly how nest site provision may be impacting on breeding performance in mixed aviaries. In this study 67% of the data represented birds which had not been provided with specific nesting areas or had been left to create their own nests. This may have resulted in the lack of comparative data available for analysis. Although it still remains clear that nest provision is important for mixed species enclosures, in particular when linked to individual choice and the complexity of the enclosure. Finding a place to live and reproduce is an important factor for the long-term fitness of any animal (Cody, 1985, Hatchwell, *et al*., 1999; Kerth, *et al*., 2001; Kruger, 2002). Choice of nest site can be influenced by a number of factors such as location, structure, predation risk and inter-species competition (Kruger, 2002). Additionally, nest building activity can promote readiness to breed and may increase success through hormonal changes (Cheng & Balthazart, 1982) and communication of readiness to breed (Krebs & Davies, 1997).

Therefore providing more than one feeding station and dividing nesting areas into multiple nest sites, thus allowing choice, is considered vital for effective mixed species enclosures (Dick, 2012). In addition it may be important to increase the amount of artificial nest sites to increase available resources and give more choice. For example Fargallo, *et al.* (2001) state that in wild kestrel (*Falco tinnunculus*) the provision of additional nests boxes of varied types increased reproductive success. A similar success may be observed if a similar practice was adopted in mixed species enclosures. This extra provision may also decrease the impacts of resource competition and potential for interference from other species. For instance, in cavity nesters the high levels of interference by other species has a negative impact on reproductive fitness (Finch, 1990; Cornelius, *et al*., 2008). Consequently cavity nesting species require access to appropriate nesting facilities which reduce the potential for intra and inter-specific interference (Newton, 1998, Cockle, *et al*., 2010). This may be one of the reasons why species such as the *Tockus deckeni* were found to breed better in single species enclosures [*Fig. 2*], which may have provided them with more appropriate nesting opportunities and less competition. It would be interesting to further investigate this by evaluating the needs of cavity nesters and levels of competition within mixed species environments.

Although five of the variables were found to impact on breeding, when controlling for the phylogeny of the 90 bird species in relation to the factors that may impact on breeding in mixed species enclosures, all previously significant results were no longer observed [*Table 8*]. This indicates that in this case the phylogenetics of each species does have an effect on its breeding performance when housed in a particular mixed enclosure design. Nevertheless, the overall results of this study do match with other published works which have shown that particular elements of an enclosure and/or husbandry practice can have a direct impact on the behaviour and reproductive performance of an animal within its captive environment. (*e.g. felidae*, Mellen, 1991; Asian elephants *Elephas maximus*, Taylor & Poole, 1998; black rhinoceros *Diceros bicornis*, Carlstead, *et al*., 1999; penguins *Spheniscidae*, Blay & Cote, 2001). For example *Spheniscus humboldti* were identified as more productive when housed in large groups; with a large pool area and where sand and gravel were provided as a nesting substrate (Blay & Cote, 2001), which supports the results of this study further highlighting the importance of appropriate nesting sites and materials for promoting good breeding performance.

As previously mentioned the success of wild mixed species aggregations is linked with the benefits this association provides and also the ecological niche in which each species operates (Hediger, 1950; Thomas & Maruska, 1996; Veasey & Hammer, 2010). Based on this it was predicted that species housed with others that shared similar ecological requirements could be less productive. The results of this study do go some way in supporting this with links to certain types of species doing better than others. However in this case the data did not allow for comparisons of success based on what other types of bird species were housed within each enclosure. Furthermore none of the enclosures surveyed had exactly the same mix of birds. With this in mind direct measures of species compatibility remain an area for further investigation. In addition, although not fully considered within this project, one of the confounding factors that will impact upon breeding performance is the husbandry implemented within particular enclosure. It is estimated that mixed species enclosures require a more complex husbandry regime and that staff should possess higher levels of training when in charge of such enclosures (Coe, 2001). In consequence one of the benefits to having single species enclosures may be the ability to tailor the enclosure to meet the specific needs of the one species and/or the individuals being housed.

Therefore more zoos may be able to better provide the necessary facilities and husbandry when housing birds on their own, hence why some species do better in these environments.

Moreover, despite not being indicated as significant within these analyses studbook management may be impacting on breeding performance. For example species which are considered a high priority for breeding are more likely to be managed more thoroughly, thus should demonstrate higher levels of breeding performance within their enclosures. For instance the conservation breeding of *Leucopsar rothchildi* and *Geronticus eremita* are considered integral to the survival of the species (Collar & Butchart, 2014; Collar, *et al*., 2012). These species are managed within European zoos at an EEP level and also demonstrate high levels of breeding within this project. In the case of the Waldrapp ibis this is very successful within a mixed species setting with 100% breeding successfully [*Fig. 2*]. Bali starlings are not as successful and may do better in single species enclosures [*Fig. 2*]. In consequence if a species is a significant priority for conservation breeding and is found to be more productive within single species housing then perhaps this particular species should not be housed within mixed enclosures if the purpose is to breed them. Collar & Butchart (2014) suggest that zoos need to integrate an *in-situ* conservation biology approach to the management of their birds, in hope of creating a more sustainable future for their bird populations. Therefore, zoos need to be making evidence-based decisions regarding the best ways in which they should house their priority bird species. This in turn, could then be used to better manage species that are not part of managed populations, perhaps by only housing non-breeding species within mixed species environments. Alternatively zoos could house only species that breed well within mixed species enclosures. However if the trend for this type of enclosure design continues, zoos may need to maintain variety in their enclosures in order satisfy visitor's needs. If some species do not do well and there are no single aviaries for them to be displayed in then they may not have a long term future in zoo collections. However this would depend on the level of success required to sustain that population.

This study supports current perceptions of breeding issues in zoo birds, but it only represents a small number of the birds species housed within zoos. For example none of the 428 enclosures that were reviewed had exactly the same mix of species, resulting in only 15% of the 585 different species collected within the survey could be analysed. This figure represents approximately 4% of the total number of species housed within European zoos (ZIMS, 2015); which may not be considered representative. Conversely this lack of replication of species may further highlight the bigger issue of population sizes and future sustainability for many species. When making comparisons of species within this study and those assessed for population sustainability *Eudocimus ruber*, *Geronticus eremita*, *Leucopsar rothschildi* and *Gyps fulvus* have the largest populations in European zoos and thus may be closer to having sustainable breeding populations (Leus & Bingaman-Lackey, 2008b). Of these species *Eudocimus ruber*, *Geronticus eremita*, *Leucopsar rothschildi* also demonstrate high levels of breeding performance within this study. In contrast a number of bird species have been listed as potentially unstainable by Leus & Bingaman-Lackey (2008a, 2008b) although none of the species listed were part of the 90 species that were investigated in this study. The study by Leus and Bingaman-Lackey (2008a, 2008b) was only related to managed populations (e.g. EEP and ESB level) resulting in many of the species within this study having not been evaluated for sustainability.

Overall the results of this project indicate that housing conditions can impact on breeding performance for some bird species. However this investigation only begins to scratch the surface of this complex issue. Due to limitations of experimental design and the final data collected there are a number of variables that have not been accounted for within this study, which could also be impacting on breeding performance, and therefore are recommended for future investigation. For instance, as data for each species came from multiple collections there may be an effect of zoo on an individual species ability to succeed, which could be linked to expertise of the zoo staff. However this study did not test for this, due to low levels of replication recorded for the vast majority of species. Furthermore no information on the level of expertise found in the bird keeping teams for each zoo was collected. Although it may be interesting to investigate if the level of training and or experience does impact directly on breeding performance, as this may aid in the development of training programmes and/or best practice for keeping staff.

Other variables that could also be considered include enclosure disturbance, such as changes to the physical structure of the enclosure, introduction of new birds or new species and also time spent within the enclosure or at each zoo. Most of these were not analysed in this study, time spent within an enclosure is a variable which is considered in part within Chapter three.

Additionally as was identified within review of literature, population density has been found to impact on aggression and also breeding productivity (Poot, *et al*., 2012). However this was not tested within this study and thus both population density of individual species per enclosure, as well as the overall density of the enclosure in relation to the all the species housed within it could be an additional confounding variable that requires future consideration. Moreover a more detailed analysis with larger sample sizes for each species would be required to develop a deeper understanding of species compatibility. Furthermore there would need to be more species housed under similar conditions, from the perspective of enclosure design and the species that are being mixed together. In addition considerations for mate choice and pair-bonding in birds were not considered within this study, thus should be factored into any future evaluations.

In captive situations, especially when only one specimen of each sex is present, as was evident in this study, mate choice will likely be reduced. Curio (1998) suggests that this could cause major conflicts and estimates that free choice is important for gaining the most productive captive propagation. Therefore if there are limited opportunities for mate choice within mixed enclosures then perhaps this could be impacting on productivity more than or equal to other confounding factors. Conversely, the same problems are likely to be prevalent within any housing environment, whether single or mixed species. Having said this, these problems may be reduced in single species enclosures with groups of the same species. Furthermore, Hawkins (1970) estimates that the promotion of breeding behaviours i.e. mating and nesting is linked to the provision of the right environmental parameters. With this in mind, this project will help to guide the creation of targets for future investigation into species which have been highlighted as doing better or worse under certain housing conditions. In particular future investigation is required at a detailed case study level to evaluate those species which demonstrated lower levels of breeding performance within mixed species environments.

This study has also provided the zoo industry with an overview of its bird enclosures and the types of species that are housed within them. In this study only 2% of the enclosures were listed as off-show mixed species facilities. This may suggests that many zoos have limited off-show facilities, a factor said to be linked with sustainability of captive bird populations (Sheppard 1995). Conversely it may be that off-show facilities were single species only and would not have been recorded in this study. This study does however highlight that fewer collections house their birds in both single and mixed species environments. If many species are not breeding effectively within mixed enclosures and there are limited alternative single species housing or off-show facilities this is likely to be impacting on the future of many bird species.

In 1997, the AZA made recommendations that at least 30% of a bird collection should be housed in dedicated off-show propagation facilities (Vince, 2008). This measure was put forward to tackle sustainability issues following evidence which demonstrated that breeding programmes which had highest success rates effectiveness were those that had dedicated off-show facilities (Vince, 2008). This recommendation was made over 15 years ago, yet it would seem that many zoos are still not meeting this level of off-show facility (Vince, 2008); the results of this study would support this. Besides this thus far no evidence has been collated to assess whether those zoos that are adhering to these recommendations have increased their breeding productivity. Off-show facilities and housing in single species enclosures are considered to be more expensive (AZA, 2005) and do not fit with visitor requirements. However Vince (2008) suggests that many zoos still need to invest in these types of facilities to secure their future reproductive sustainability. On the other hand this study challenges this statement suggesting that some species may not require the off-show facilities to breed, especially if these types of facilities are financially and/or space costly. Therefore careful consideration of the species being mixed and the design of the enclosure, plus refinement of management protocols for mixed species enclosures could enable a reduction in associated reproductive issues within these settings. The results of this study provide the foundation towards understanding some of the issues associated with mixed species enclosures and work towards a more sustainable future for many bird species, especially when resources and space may be limited.

2.5 Conclusion

This study reinforces the previously held perceptions that mixing bird species can result in a reduction to their breeding performance, with a significant number species which have either not attempted to breed or have not successfully reared offspring when housed within mixed species environments. However these results are not consistent across all types of bird as there are also species that can do well within mixed species environments. Additionally no affect can be observed in relation to phylogeny, suggesting that no particular taxonomic groupings have a predisposition towards doing better in one type of enclosure. Having said this when housed within mixed species enclosures various factors may be impacting upon this success. It is challenging to focus on specific elements of a species' ecological needs or elements of enclosure design that are responsible for this potential reproductive reduction. A number of factors may be highlighted as causing significant impact including breeding sociality of a species, the number of species mixed together, including the presence of non-birds and the provision of nest sites. In light of the lack of significance after controlling for phylogeny it would seem that these results are driven by particular taxonomic groups of birds. This may highlight that certain types of birds may be affected by elements of mixed species enclosure design more than others. However due to low sample sizes no clear identification of these particular groups can be made at this stage.

With this in mind, further investigation is likely to be required at an individual case study level to investigate these factors further. At the same time species compatibility within mixed species enclosures remains a significant priority for the BIAZA BWG Mixed Aviaries Focus Group (*pers. comm*.), though this was outside of the remit of this projects analysis. Additionally the potential effects of a number of other variables may need to be considered including species density and staff expertise. Moreover the role of each enclosure also needs to be considered, in particular for zoos which do not have additional propagation facilities. The suggested future directions and recommendations for improvements to the management of mixed species enclosures will be further discussed in Chapter 4.

Chapter 3. Historical records versus questionnaires for mixed species research: A comparative case study of historical records from two UK zoo collections.

3.1 Introduction

Record keeping within the zoo community is considered essential for the management of captive animal populations (Earnhardt, *et al*., 1995, Flesness, 2003; Hosey, *et al*., 2012; BIAZA, 2014; Miller, 2015). An animal record can be defined as "data, regardless of physical form or medium, providing information about individual animals, or samples or parts thereof, or groups of animals" (AZA, 2014). The keeping of historical records is policy for all zoos within the European Union falling under the remit of the European Council Directive 1999/22/EC (2002) which states that all licensed zoos should keep up-to-date and species appropriate records. In the UK this requirement is further enforced by the Zoo Licensing Act (1981) and supported by the Secretary of States Standards for Modern Zoo Practice (DEFRA, 2004). Zoos have however been keeping animal records for many years before this particular legislation came into force (ZSL, 2014). Over time these systems have become more sophisticated, in-line with technological developments, changes to legislation and with an increased understanding of the scientific relevance of keeping detailed animal records (Flesness, 2003).

At present a variety of record keeping systems are practiced within the zoo community. The two most significant being the locally managed Animal Records Keeping System (ARKS4) and the more recently developed web-based Zoological Information Management System (ZIMS) which was created to increase the efficiency of animal management recording (Hunt, 2008). These systems allow for the management of all species housed in zoos rather than just those that are part of formal breeding programmes (Hunt, 2008; ISIS, 2014: Miller, 2015). There are many differences in the functionality of the two applications, most significantly is the ZIMS global accession number, a unique identifier given to each individual animal which then follows it throughout its life (Hunt, 2008). Following its launch in 2010 the vast majority of collections have migrated to ZIMS, though some collections still use ARKS4 (Miller, 2015). The two systems link into a centralised repository; known as the International Species Information System (ISIS). Founded in 1973, ISIS aids zoos in their management of wildlife for conservation purposes (Seal, *et al*., 1976; Flesness, 2003) and was the main developer of ZIMS (Miller, 2015). Other notable record keeping programmes include SPARKS (Single Populations Animal Records Keeping System) for studbook management and MedARKs for veterinary medical notes (Flesness, 2003; AZA, 2014; ISIS, 2014; Miller, 2015). Most recently MedARKs has been integrated into the ZIMS application, thus further streamlining the recording process (ISIS, 2014). The next stage will be to incorporate the features of SPARKS to provide a full management tool kit within one application (ISIS, 2014).

As well as being an important aspect of daily animal management practices, historical records also provide the opportunity to carry out quantitative and qualitative research via the review of the information retained within them (Fidgett, *et al*., 2008; Crockett & Ha, 2010; Hosey, *et al*., 2012). Although not widely used (Hosey, *et al*., 2012) there have been several studies which have used records within their data collection methodology. In most cases these records have been used to determine measures of life history, such examples include *Cervidae* chronic wasting disease (Dube, *et al*., 2006); *Cervidae* life expectancy and feeding regime *(*Muller, *et al*., 2010); bird mortality (Ricklefs, 2000); bird age and fertility (Ricklefs, *et al*., 2003); birth sex ratios in various species (Faust & Thompson, 2000) and general behaviour (e.g. *primates*, Pullen, 2004; Davis, 2009; Hosey, *et al*., 2012).

As a tool for direct investigation of breeding productivity the use of animal records is limited, though some examples can be found within current literature (e.g. *Felidae,* Mellen, 1991; Mitchell & Nevison, 2006; Californian condor *Gymnogyps californianus* Hartt, *et al*., 1994; *Ciconiidae,* Brouwer, *et al*., 1992; *Psittaciformes* Brouwer, *et al*., 2000; elephants *Elephus maximus* and *Loxondonta africanus*, Clubb, *et al*., 2009; *Spheniscus humboldti*, Blay and Cote, 2001). Many of these studies represent multi-zoo data sets, yet there is currently no published example of any project attempting to use this method within a mixed species setting. Therefore the aim of this chapter is to discuss the use of historical zoo records for evaluating breeding performance within mixed species bird enclosures. Additionally this chapter will act as a comparative case study of the breeding performance scores provided within the questionnaire (Chapter two) and the breeding performance extracted from the historical records for the same enclosures; with the aim of assessing the use of questionnaires as a reliable measure of the breeding performance.

In the case of a complex multi-zoo study such as this one, records data could be considered as more accurate due to broad level of details that can be extracted in comparison to what can be collected from a questionnaire (Melfi & Hosey, 2012). Nonetheless there are many advantages of using questionnaires within research (Plowman, *et al*., 2006). For instance advantages include practicality; cost and time efficiency (Burgess, 2001) and the ability create quantitative data sets (Plowman, *et al*., 2006). In contrast disadvantages can be linked questions relating to expression of opinion, difficulties in measuring truthfulness or level of effort from the respondent, misinterpretation of questions and question design e.g. designer bias, closed or open style questions (Benson & Holmberg, 1985; Burgess, 2001; Plowman, *et al*., 2006). Therefore questionnaires may often be considered an unreliable scientific method (Lablaw, 1981; Gendall, 1998). Despite this zoo records are still unlikely to be 100% accurate (Plowman, *et al*., 2006), but are considered a credible source of data (Flesness, 2003). All things considered and with the assumption information provided in the questionnaire was truthful and that records were used to guide completion of questionnaires with this study it is expected that no significant difference will be observed between the estimated breeding performances and the recorded historical breeding performance for bird species within a particular enclosure. Furthermore due to the potential limitations in the number of questions that can be reasonably posed within a questionnaire (Plowman, *et al*., 2006), the level of detail that can be extracted from historical records may then be considered more comprehensive.

3.1.1 Aims

Initially this chapter aimed to validate the results of the questionnaire study by asking the question ‘is a questionnaire sufficient in estimating the breeding performance of birds within mixed species enclosures?’ However following initial data extraction it was noticed that birds housed in mixed species bird enclosures were subject to many transfers, within the collection and between collections. There has currently been no study into how this may impact on bird breeding, thus the aims of this chapter were expanded to include a basic evaluation of how length of time spent within an enclosure might impact upon breeding productivity.

Therefore the two objectives were outlined for this chapter:

1. To compare the use of questionnaires against historical records in relation to the validity of the data gained from for breeding performance within mixed species bird enclosures.

2. To assess if the length of time a species spends within an enclosure has an effect on its breeding performance over a five year period.

3.2 Methods

3.2.1 Data collection

Historical records were collected from two zoos in the UK, which for purpose of this study will be referred to anonymously as Zoo 1 and Zoo 2. Firstly historical records for six enclosures were collected from Zoo 1 using ARKS4 via the production of enclosure report and egg information for six mixed species enclosures, for the period 1st September 2007 to 30th September 2012. This matched the five year period that had been requested within the questionnaire. Records from eight mixed species enclosures were also provided from Zoo 2 using ZIMS for the same date period. In total 136 species were recorded across both collections. Extraction of the following information was then carried out for each species per year within each of the 14 enclosures; the number of months the species was housed within the enclosure for that year, the group composition per year, the total number of eggs that did not hatch per year, the number of parent-reared chicks that fledged per year and the number of chicks that died before fledging per year. Additional notes were also taken on the age of the breeding pairs and how many chicks were hand-reared per year.

3.2.2 Data analysis

Prior to analysis two filters were applied to the full five year data set. Firstly, any samples where birds were not paired were excluded *i.e.* single sex groupings and any single specimens. Secondly, any pairs that had not been housed within the enclosure for at least one breeding season were also discounted. In this case a breeding season was considered to be a minimum of six months within that enclosure. The decision was guided by information collected on the natural breeding season lengths for those species. Thus only birds that were housed in pairs and had been within that enclosure for at least one breeding season were used for analysis. Following application of these filters 74 species were available for analysis across all 14 enclosures (representing 16% of total data that were extracted from the records). Only six species had more than one sample.

Following this in order to establish whether the questionnaire and the records data were matched for a given species and its enclosure, each species from the records data were scored based on the same system utilised within chapter two (bred or not bred within that enclosure) [Table 2]. Out of the remaining 74 species a total of 45 species had been given a breeding performance score for the questionnaire. The other 29 species had not been included within the questionnaire data received from the two zoos and thus were unable to be analysed. The difference in species recorded between the two methods may relate to fluctuations in group composition over the five year period that were not captured within the questionnaire data, potentially highlighting a limitation of questionnaires. The breeding performances for the remaining 45 species from the records data were then compared to the same species from the questionnaire data using a Spearman correlation.

Unlike the breeding performance data gained from the questionnaire, the historical records contained annual births and deaths for the five year period and also the length of time each bird had spent within the enclosure. Therefore it was possible to investigate the effect of length of time housed within an enclosure on species breeding productivity. Firstly, the annual breeding productivity of the remaining 74 species within each enclosure was calculated using the following equation (C/P)/X, adapted from Blay and Cote (2001). Where C represented the number of parent-reared chicks that fledged, P represented the number of pairs per species that could have produced young in a given breeding season and X represented the number of years each species was housed within that enclosure. The mean number of chicks fledged per year for that species per enclosure were then calculated. The mean number of chicks fledged for the 74 species were then tested for normality followed by the application of a Spearman correlation used to assess the relationship between the mean number of chicks that had fledged per species per enclosure and the number of years they had been housed within that enclosure. A one-way ANOVA with tukey was also applied to assess the difference in performance between the years.

3.3 Results

3.3.1 Questionnaires versus historical records

The first Spearman correlation revealed that the estimated breeding performances taken from the questionnaire for each of the 45 bird species were correlated with the matched values from the historical records data ($rs_{(45)} = 0.457, 0.002$). Breeding performance for 33 (61%) of species within the questionnaire were matched with the historical records for that same enclosure [*Table 9*]. In contrast, 11 species were estimated as having bred successfully within the questionnaire, though had not bred according to the records [Table 9]. Only one species, *Cygnus melanocoryphus,* was indicated as having not bred within the questionnaire, but had bred according to the records [*Table 9*].

Table 9. *A comparison of breeding performance scores for 45 species using records and questionnaires; detailing matched and unmatched scoring.*

Matched data (not bred in both)	Matched data (bred in both)
Caloenas nicobarica	*Aythya nyroca*
Callonetta leucophrys	*Branta rufficollis*
Ciconia ciconia	*Dendrocygna arborea*
Coracias caudate	*Dendrocygna viduata*
Cossypha niveicapilla	*Egretta garzetta*
Guttera pucherani	*Eurypyga helias*
Gyps fulvus	*Foudia madagascarensis*
Irena puella	*Gallicolumba criniger*
Onyochognathus morio	*Garrulax courtoisi*
Ploceus nigricollis	*Geronticus eremita*
Thalassonrnis leuconotus	*Goura victoria*
Tockus deckeni	*Musophaga violacea*
Unmatched data (Not bred in records, but bred in questionnaire)	*Netta rufina*
Aegypius monachus	*Oxyura leucocephala*
Anas querquedula	*Ploceus cucullatus*
Chalcophaps indica	*Pycnotus jocosus*
Ciconia nigra	*Rollulus rouloul*
Columba guinea	*Scopus umbretta*
Ducula bicolor	*Tauraco schalowi*
Marmaronetta angustirotris	*Zoothera citrina*
Pelecanus crispus	**Unmatched data (Bred in records, but not bred in questionnaire)**
Platalea leucordia	*Cygnus melanocoryphus*
Pyrrhocorax pyrrhocorax	
Vanellus vanellus	
Vultur gryphus	

3.3.2 Length of time in enclosure versus breeding success

In total, 41% of species (*n*=30) bred at least one chick successfully over the five year period [*Fig. 5*]. The Spearman correlation indicated no association between the number of years that a species was housed within an enclosure and the number of chicks that fledged successfully ($rs_{(80)} = 0.164$, $P = 0.146$). Also there was no difference in breeding success and number of years the species had been housed within the enclosure ($F_{(4,40)} = 0.612$, $P = 0.657$). However, none of the 74 species analysed were found to have bred when housed within an enclosure for only one year [*Fig. 6*].

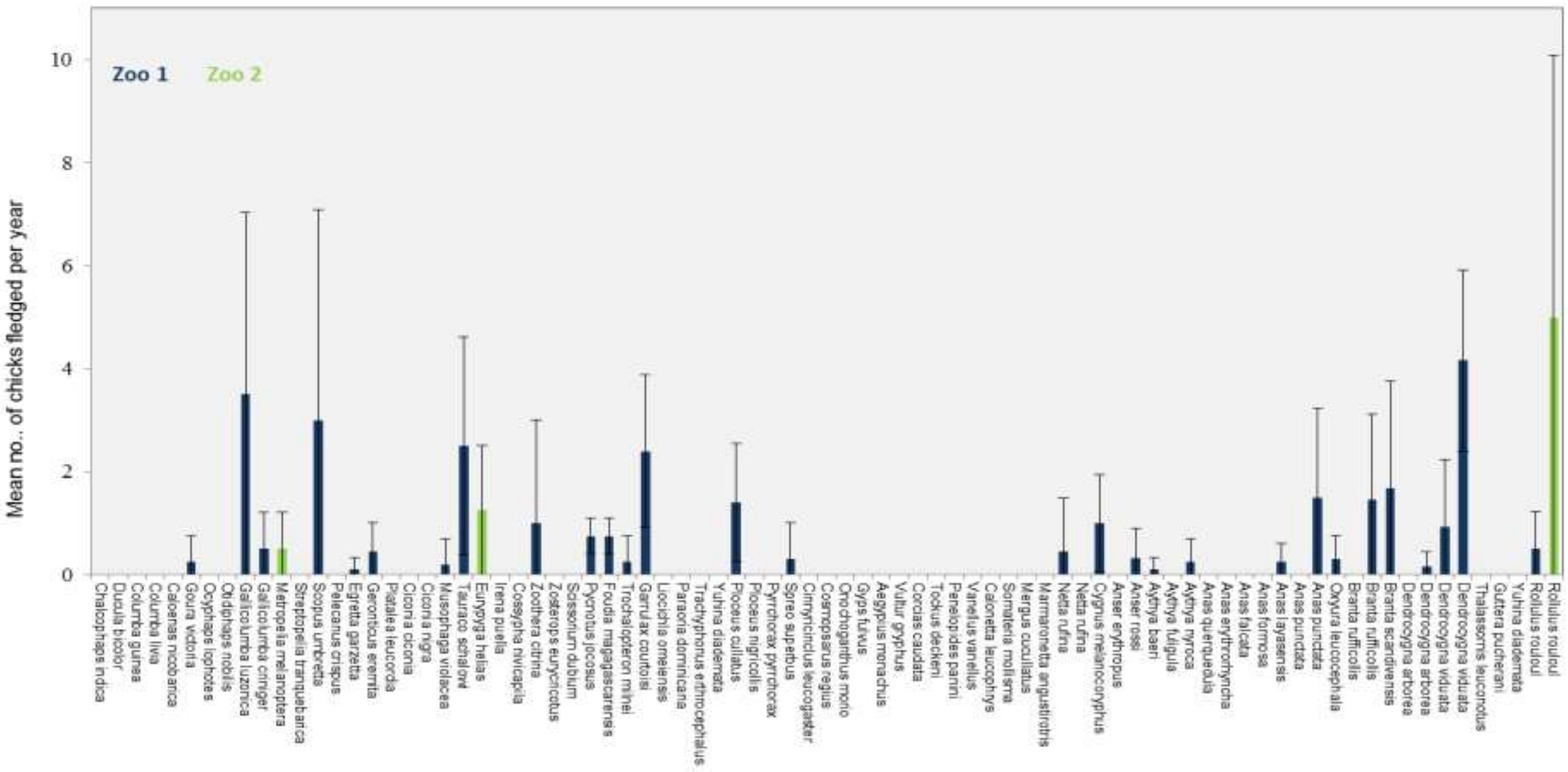

Figure 5. *Mean (+/-S.D.) number of parent-reared chicks that successfully fledged per pair, per breeding season for each species (n=74) per enclosure, within 14 mixed species enclosures at two zoos (phylogenetic order based on Hackett, et al., 2008) [unless otherwise highlighted replicates of the same species represent breeding productivity of that species in different enclosures within the same zoo].*

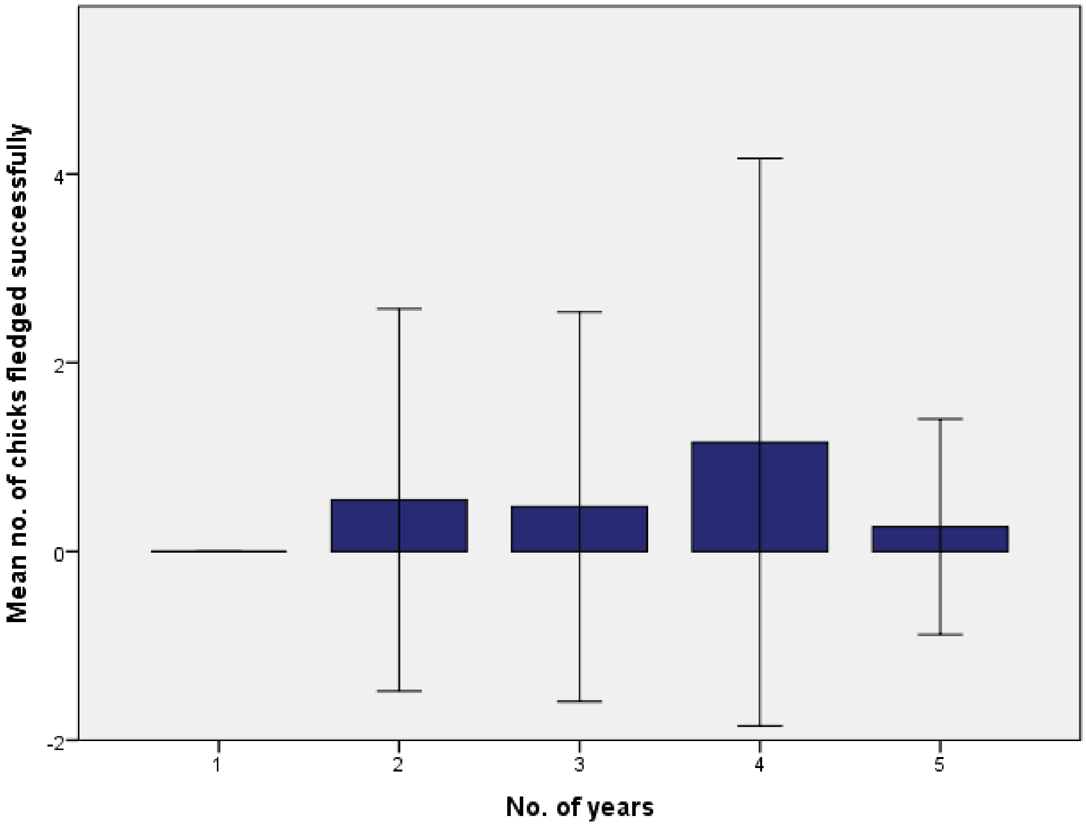

Figure 6. *Mean (+/- S.D.) number of chicks fledged across 74 bird species per enclosure (n=14) in relation to the number of years the species had been housed within that enclosure (n= 81) [1 year n=12, 2 years n=16, 3 years n= 18, 4 years n=12 , 5 years n=23].*

Of the 74 species analysed only one species was housed in both zoo collections, *Rollulous rouloul.* It should be noted that the lower levels of breeding productivity in zoo 1 are related to breeding management within this enclosure, where the majority of eggs laid in the five year period were recorded as having been taken from the enclosure.

3.4 Discussion

Although questionnaires may be considered problematic for complex data in large volumes (Plowman, *et al*., 2006), evidence from this analysis provides support for the validation of questionnaires as an useful method for assessing breeding performance in mixed species exhibits at a very basic level. Although the coefficient is low, a significant correlation can be observed when matching the responses of the questionnaires to that of the records data, which gives support for the reliability of the results gained from the questionnaire analysis detailed in Chapter 2 [*Table. 9*]. In the majority of cases the scores matched up between the two data collection methods. However there were data provided for 13 species (26%) that did not match up across the two methods [*Table. 9*]. For instance 12 species were specified as having bred within their enclosure when in fact according to the records they had not. In contrast there was only one case where a species had been indicated in the questionnaire as having not bred, when it actually had according to the records. A variety of reasons could be provided for this result, for example it may suggest that estimates of breeding performance provided within the questionnaire could have been given with an optimistic view of their breeding success, which may mean that breeding issues could be worse than the questionnaire data would suggest. This could mean that the estimates are not a true representative of the breeding issues for species and may give additional support to the evidence that some species are not doing as well within mixed species housing.

Alternatively there are many issues with the keeping of animal records and the reliability of information included within them (Hunt, 2008; Miller, 2015). Therefore some of these mismatches could have been related to human error within the record keeping system or that the birds had breed but it had not been recorded within the system, although it would be extremely difficult to assess this. With these factors in mind, the results of this assessment should be taken with caution. Although, overall the do still support the perceptions some mixing of species can result in breeding productivity issues. Furthermore there is a likelihood that the problem is worse than curators and keepers perceive it to be. In addition, the fact that population sustainability remains a major issues for so many captive species provides further support for these findings

Even with some potential errors within the data for both methods of data collection, the level of validation this analysis provides may prove useful for future multi-zoo research due to the significant investment it takes to extract breeding information from large records datasets. In the case of ARKS4, this programme proved very difficult to traverse when extracting information due to the layout of enclosure logs. The development of ZIMS has made this extraction process much more efficient. Also the global accession number is likely to make future analysis of breeding across an animal's lifetime much easier (Hunt, 2008). Having said this, if a project includes investigation of enclosure design features, then historical records would still need to be accompanied by questionnaires in order to collect the necessary information, as limited design information is currently housed within the ZIMS system. From an anecdotal perspective, as a recording system which can be used for empirical research ZIMS is a much more efficient system for data extraction than ARKS. Therefore this project would endorse its use and further development. The collection process from ARKS was lengthy and resulted in a time exhaustive extraction process which was very inefficient in relation to the volume of data that was actually usable. ZIMs was faster in terms of collecting the data from the system and resulted in a functioning spreadsheet which had already implemented some of the extraction processes which had to be completed manually from the ARKs print outs. This meant that the extraction time for data collected from ZIMs took less than half the time to extract the relevant information as it did from the ZIMs data.

Although the use of questionnaires has been given some validation in this study the use of historical records still remains desirable for providing a higher level of detail, thus allowing for additional assessments to be made. Although not a direct aim of this study, during the data extraction process it was identified that many species were subject to multiple internal transfers between enclosures during their lifetime or the period they were housed at that zoo. This raised the question of whether these transfers might have a negative impact on a species ability to breed. Due to the way in which information was extracted it was not possible to calculate exactly how many times an individual was moved, but the differences in the amount of years spent in one enclosure can be observed [*Fig. 6*]. This potential issue is further confounded by the fact that 84% of the data collected from the records was not viable for analysis due to the birds not being housed within the enclosure for at least one season. Moreover mixed species composition *i.e.* the types or number of species housed in each mixed enclosure varied from year to year, with only a few species that were actually housed together for the full five years. Therefore these movements coupled with changes to species mixes do suggest that the information provided within the questionnaire for this study does not take into consideration the changes in composition over the five years, which renders analysis of species compatibility difficult when only using the questionnaire data.

There are a variety reasons why the fluctuations in time spent within each enclosure and changes to the species mixed together may be a significant factor in the breeding potential of the birds, such as the impact on group and/or pair-bond stability. These changes may cause disturbance to the pairing or the individual, for example changes to the social status of the birds or having to establish new rank orders after the movement to another enclosure or change to the species mix. In captive siskins (*Carduelis spinus*) it was observed that group stability enhanced levels of tolerance and reduced aggressive interactions (Senar, *et al*., 1990). Moreover the duration of pair-bonds has also been found to positively correlate with bird fitness due to an increase in fledging success in longer and more stable pairings (Sánchez-Macouzet, *et al*., 2014). Social stability has also been studied in other taxa, for instance unstable environments have a negative impact on pregnancy and lactation in female guinea pigs (Sachser & Kaiser, 1996; Kaiser & Sachser, 2005). With these points in mind the volume of movements that occur within mixed species bird enclosures may highlight the need for zoos to assess the role of their bird enclosures. Although, this particular element was outside the remit of this study and thus is recommended as an area for future investigation. Moreover it may of interest to look at both the positive and negative impacts of moving birds including breeding productivity and also adult mortality rates.

Additionally these constant fluctuations in mixes of species observed within the records data it would be difficult to assess compatibility at a wider scale at present. This means that one of the objectives set out by of the BIAZA Bird Working Group remains untested at present. That being said, further investigation into this area could be supported by the ongoing development of the ZIMS application and functionality. ZIMS currently allows for the maintenance of global records for each individual animal and/or group, thus enabling records to follow an individual throughout its life (Hunt, 2008, Miller, 2015) and reducing potential errors which may have occurred within ARKS. This could be beneficial in the future due to the ability to observe the movements and breeding across an animal's lifetime rather than just the enclosure snapshot that ARKS was able to offer.

Based on the volume of transfers between enclosures it was expected that analysis of breeding versus time spent in an enclosure would highlight an issue, yet according to the results there was no relationship between the number of breeding seasons spent in the enclosure and the mean number of chicks that fledge for that species. Though, no species breed when they were only housed for one year suggesting that transfers within the first year could be detrimental to breeding success [Fig.6]. Furthermore, this result gives the estimates of breeding performance collected within the questionnaire more credibility as there would seem to be no effect on number of years in an enclosure. Therefore if a study is only able to gain data for one or two years then this does not mean that the results will be unreliable.

That being said, the calculations for the number of chicks fledge successfully per enclosure was based on a small sample size (in some cases only one pairing), thus it would be interesting to be able to test the effect of transfer and time in enclosures on a much wider scale. For instance only 16% of the data extracted remained after filters, which reduced the ability to carry out robust analysis for this chapter. It does however; highlight that in the case of the 14 enclosures only five had birds which were housed for at least one breeding season and also in the appropriate group composition for breeding. Of the 136 species included within this case study 46% were in a situation that would not allow for breeding within their enclosure i.e. single specimens or single sex groups. It could be suggested that this is a large proportion. However it is difficult to make a judgement on this as the role of these birds may not have been to breed them. These results are comparable to that found in a survey of *Passerines* (housed in both mixed and single species environments) which found that only 55% of pairs had bred within a five year period, although in most cases this was only one chick per season (Ward, 2012), which as with the results of this case study may not be considered sustainable. Furthermore collections that had multiple pairs of the same species of passerine were more likely to have a higher number of breeding occurrences than when only one pair was kept in the collection (Ward, 2012). Although not tested in this study, it would be interesting to investigate if a similar pattern could be observed within mixed species environments.

As previously highlighted a low sample size was recorded for many of the 74 species, with the numbers of pairs for each species ranging from one pair to seventeen pairs within a one year period. Even with the low sample sizes the annual breeding productivity could still be calculated for the 74 species [*Fig. 5*]. Of these species only 30 actually fledged at least one chick within the five year period that was assessed [*Fig. 5*]. It is difficult to ascertain how the results of this case study may compare to the success of these species in a wild setting due to gaps in the knowledge on average breeding success for many species. That being said, for some species zoos are doing much better than would be expected based on wild data, for instance *Scopus umbretta* in the wild are estimated to successfully fledge less than one chick per pair in the wild (Elliot, 1992), which is in contrast to the results of this study that suggests in captivity success is much higher at almost 4 chicks per pair [*Fig. 5*]. Conversely in the wild, *Geronticus eremita* are estimated to fledge 2.5 chicks per pair (Matheu and del Hoyo, 1992), though results of this study highlight a much lower success in zoos with 0.5 chicks surviving each year [*Fig.5*]. A similar pattern can be seen in *Gyps fulvus* with an average of 0.76 chicks fledging per pair in the wild (Thiollay, 1994), however zero success was recorded for this species within this case study, although due to low sample sizes these results should be taken with caution. Even with lower breeding rates than their wild counterparts *Geronticus eremita* and *Gyps fulvus* species are still considered to have large populations in European zoos (Leus & Bingaman-Lackey, 2008a; 2008b). These results may further highlight the inconsistency in breeding success for certain species when housed within a mixed species environment. This also begs the question that if certain species are not as successful as they might be in the wild then are they meeting the requirements for creating a sustainable population, though perhaps some breeding is enough? This reduced success may also be counterproductive to the potential role that zoos can play in the conservation of threatened bird species.

3.5 Conclusion

Questionnaires can provide a reliable estimate of breeding performance within mixed species exhibits in relation to general breeding patterns for the majority of species. These estimates may however underestimate the true picture of breeding for some species. There is suggestion that zoo curators and keeping staff may have a more optimistic view of breeding performance for some of their birds than their historical records would suggest. Furthermore human error may also result in breeding information being missed out within some historical records. However, historical records can be used to evaluate breeding productivity in mixed species bird enclosures.

There is an indication that the number of years that a species spends within an enclosure is not related to the number of chicks that fledge successfully, although no species have been shown to breed when housed within a mixed species enclosure for only one year. In addition there is currently no evidence to evaluate the impact of the number of enclosure transfers that individuals of a species experience on not only their breeding productivity, but also their behaviour and welfare. This constant fluctuation in the composition of mixed species exhibits renders the ability to assess species compatibility and long term breeding productivity very difficult. Therefore this area of zoo aviculture remains a priority for investigation. Additionally the role of each enclosure needs to be carefully considered in relation to the needs of a given species, the individual zoo collection and the long-term sustainability of all bird species, not just those that are part of managed breeding programmes.

Chapter 4: Summary and recommendations

4.1 Summary

This project represents the first attempt at quantifying the impact that mixing bird species could be having on the breeding performance of many bird species within European zoo collections. The need for investigation was driven by the lack of research previously completed on this style of enclosure design (Hammer, 2002; Hosey, *et al*., 2013), the perceptions that bird breeding performance was reduced in these environments (BIAZA BWG, 2006 unpub; Foulds, 2008) and the ongoing issues with population sustainability within zoos (Beissinger, 2001; Leus & Bingaman-Lackey, 2008a, 2008b; Lees & Wilcken, 2009; Walter, *et al*., 2009; Leus, *et al*., 2011). Although the analysis for this project proved difficult due to low sample sizes for many bird species, this study does reinforce the findings of other research which suggest that the environment that a captive animal is housed in impacts upon its behaviour (Bratton & Dimeo-Ediger, 1993; Hosey *et al*., 2013), welfare (Broom, 1991; Shepherdson, *et al*., 2004; Mason, 2010) and breeding success (Carlstead, *et al*., 1999; Blay & Cote, 2001; Clubb, *et al*., 2009).

Evidence from this study supports the perception that a number of bird species do suffer reduced breeding performance when housed within a mixed species environment. However this is not a consistent pattern across all species with some displaying no affect and with others showing an opposite trend with more breeding being observed when housed within mixed species aggregations. In addition this result was not found to be affected by phylogeny, suggesting that no specific taxonomic groups are predisposed to doing better or worse in either of the two housing conditions. More specifically when considering the factors that could be influencing breeding when species are housed within mixed species environments a number of factors relating to the design of the enclosure and species specific-ecology were highlighted as significant. In contrast to the mixed versus single species analysis, phylogeny was found to act upon the results of the second objective. Therefore this suggests that some types of species or taxonomic groups of birds are more susceptible to breeding issues when placed under particular conditions within mixed species exhibits.

The comparisons of the breeding performance estimates from the questionnaire against the breeding productivity extracted from the historical records provide backing for the use of questionnaires as basic and quick method of estimating breeding performance. However the levels of information that can be extracted from historical records remain superior to that of questionnaires, with the ability to collect real-time data, which has become easier to extract with the better functionality of ZIMS. Moreover, the results of this comparison may suggest that current perceptions of breeding within mixed species enclosures may actually take a more positive view than what can actually be observed from the breeding records in reality. This provides further support for the perceptions that mixed species exhibits are experiencing reduced breeding for many bird species.

Through closer inspection of the historical records additional issues not previously expected have come light including the length of time individual birds and/or pairings spend within one enclosure and the number of transfer that occur for many bird species. Although no association was found between the number of years that a species was housed within an enclosure and the number of chicks that fledged, no species bred when only housed within an enclosure for only one year. Furthermore over 80% of the samples were not usable, in part due to the limited length of time that birds had spent within the enclosure. It is already known that group and/or pair-bond stability is important for successful breeding, which highlights that time spent within an enclosure could have a negative impact of breeding if the species is not kept in the enclosure for more than one year. Additionally it begs the question of why birds seem to be moved around so much. As evidence of bird movements is only based on a case study of two collections in is unclear how common this practice may be across zoos in general. In addition it is currently unclear how the level of movements may compare to that of other taxa housed in mixed enclosures. Therefore this represents an area of mixed species enclosure management that requires significantly more investigation.

Overall this study has broadly achieved its aims by providing the first analysis of this complex and wide subject area. It has also given rise to many more questions and emphasised key elements of mixed species enclosure management that require further investigation. In short there seem to be issues with keeping some bird species in mixed species enclosures that are not yet fully understood. With this in mind, mixing species could be having a significant impact on the population sustainability of many bird species and should be priority focus for zoo collections in the future.

4.2 Recommendations and further research priorities

As a novel analysis within this particular area of zoo management a considerable amount of additional questions have now presented themselves. This section will discuss key recommendations and consider priorities for the development of management for mixed species bird enclosures. In addition, a number of recommendations for future investigation have been highlighted throughout this study and will be further discussed. The following factors are recommended as areas that should be included in any guidelines or standards produced for the management of mixed species bird enclosures.

1. Role of the mixed species enclosure: The number of transfers of birds and length of time spent within an enclosure could be an impacting factor on the breeding performance of many species and supports the need for the role of an enclosure to be considered. The AZA's recommendation of having one-third of aviaries off-show to promote breeding does not seem to have been successful due to limitations to resources in many zoos (AZA, 2005, 2006). Investigation into the effectiveness of off-show facilities has found that species/breeding programmes which had highest success rates were those that had dedicated off-show facilities (AZA, 2005). Having said that continuing issues in sustainability remain a major issue and suggest that the AZA's recommendations did not make a big enough impact with many zoos not investing significantly in their future reproductive sustainability (Vince, 2008).

2. Socio-ecology of the species being mixed together: Compatibility of species is a key factor for the success of a mixed enclosure (Coe, 2001; Hammer, 2002; Dorman & Borne, 2010). In particular as highlighted in this study breeding sociality can impact upon breeding performance in mixed enclosures. Therefore it may be suitable for collection

plans to focus on mixing species that have a tendency to live in mixed species associations or those that are colonial in nature. Conversely, territorial species may not do as well in mixed environments and additional provisions should be made if mixing these types of species (Boritt, 2008).

3. Enclosure design and husbandry management for mixing: As particular enclosure design features such as number of nest sites provided and presence of non-bird taxa have been highlighted as factors that could impact on bird breeding it may be important for collections that want to breed within a mixed enclosure to focus more on the design and planning of that enclosure. More consideration for the role of the enclosure and the features it provides for each species could be taken when designing and or managing mixed species enclosures. Based on the factors highlighted within this study some of the more prominent factors to consider are the number of species that are being mixed, how many nest sites are provided and the breeding sociality of the species. However, there does need to be more research into the reasons why these features were significant within this study, how exactly they are impacting on the breeding and also how this can be managed in the future. Additionally density of the species housed within an enclosure requires investigation and should be considered within any future collection planning.

As previously mentioned, the high number of species that were found to be housed in mixed settings and in many cases the low number of replicates for these species, there still remains a significant number of species that are yet to be investigated. Therefore it may be important to promote the completion of case studies either for species that could not be analysed within this study or those that have now been highlighted as having particular breeding issues. These case studies could be focused on specific-mixes and styles of enclosure, which may enable a better understanding of species compatibility, which remains a topic of interest within the zoo community. These types of project would require collaborative research across multiple collections and would need to be driven and managed as a collective to allow for useful results to be obtained. This could be a future direction for the BIAZA BWG Mixed Aviaries Focus Group to take following the completion of this research.

References

Alatalo, R.V. & Moreno, J. (1987) Body size, interspecific interactions and use of foraging sites in tits (*Paridae*). *Ecology* 68.6: 1773-1777.

Anderson, N., Andrews, L., Evans, K., Flessness,N., Hiddinga, B., Itoh, K., Iwata, T., Lacy, B., Lai, F., Lees, C., Leus, K., Manansang, J., Phillips, M., Popov, S., Schwartz, K.,Simmons, L., Skipper, G., Smrcek, M., Taggart, D., Traylor-Holzer, K., Tsao, E. and Wilkins, R. (2009) Ex-situ population management tools working group report. *CBSG News* 20.1: 1-7.

Anderson, R. M. & May, R. A. (1982) Coevolution of hosts and parasites. *Parasitology* 85.2: 411-426.

Archibald, G. W. & Meine, C.D. (1996) Family *Gruidea* (Cranes). In del Hoyo, J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 3: Hoatzin to Auks. Lynx Edicions, Barcelona, Spain.

AZA. (2005) *Wild Bird Acquisition Working Group Planning Workshop - Final Report*. IUCN/SSC Conservation Breeding Specialist Group, Minnesota, USA.

AZA. (2006) *Eastern Regional Sustainability Workshop*, 2006. Cited in Boritt, D.A.W. 2008. Small *Gruiformes* Usage in Mixed Species Exhibits. Proceedings of AZA *Gruiformes* Workshop: Alabama, USA.

AZA. (2014) *Animal record keeping systems*. [Online] https://www.aza.org/animal-data-and-records-software/. [Accessed: 10/02/2014].

Baker, A., (2007) *Animal ambassadors: an analysis of the effectiveness and conservation impact of ex-situ breeding efforts*. In Zimmerman, A., Hatchwell, M., Dickie, L. & West. C. (eds.). Zoos in the 21st century: catalysts for conservation. Cambridge University Press, Cambridge, UK.

Baratay, E. & Hardouin-Fugier, E. (2002) *Zoo: a history of zoological gardens in the west*. Reaktion Books, London, UK.

Beissinger, S.R. (2001) *Trade of live wild bird: potentials, principles and practices of sustainable use*. In Reynold, J.D. (Ed.). Conservation of Exploited Species. Cambridge University Press, Cambridge, UK.

Benson, G. & Holmberg, M. B. (1985) Validity of questionnaires in population studies on drug use. *Acta Psychiatrica Scandinavica* 71: 9–18.

BIAZA. (2014) *Animal records*. [Online] http://www.biaza.org.uk/members_home/http://www.biaza.org.uk/animal-management/animal-records-and-species. [Accessed: 15/09/2014].

BIAZA. (2012) *Top 10 species fighting extinction with the help of zoos*. [Online] http://www.theguardian.com/environment/gallery/2012/aug/15/top-10-species-extinction-zoos-in-pictures [Accessed: 30/12/2014].

BIAZA BWG (2006) unpublished. *1st Annual BIAZA Bird Working Group meeting*. London Zoo, London, UK.

BIAZA BWG (2009) *Proceedings of the 4th Annual BIAZA Bird Working Group Meeting*. Flamingo Land, Yorkshire, UK.

Birdlife International. (2013) *Datazone factsheets*. [Online] www.birdlife.org/datazone/sowb/state. [Accessed: 02/01/2014].

Birdtree.org. (2014) *A global phylogeny of birds*. [Online]. http://birdtree.org/. [Accessed: multiple dates in 2014 and 2015].

Blay, N. & Cote, I.M. (2001) Optimal conditions for breeding of captive Humboldt penguins (*Spheniscus humboldti*): A Survey of British Zoos. *Zoo Biology* 20: 545-555.

Bockheim, G. & Congdon, S. (2001) *The Sturnidae Husbandry Manual and Resource Guide*. Disney's Animal Kingdom, Florida, USA.

Boritt, D.A.W. (2008) *Small Gruiformes Usage in Mixed Species Exhibits*. Proceedings of AZA *Gruiformes* Workshop: Alabama, USA.

Bracko, A. & King, C.E. (2014) Advantages of aviaries and the Aviary Database Project: a new approach to an old housing option for birds. *International Zoo Yearbook* 48: 1-18.

Bratton, D. & Dimeo-Ediger, N. (1993) Displacement rates at food bowls in a mixed African species aviary. *International Zoo News* 247: 14-20.

Brazill-Boast, J., van Rooji, E., Pryke, S.R. & Griffith, S.C. (2011) Nest-site utilisation and niche overlap in two sympatric, cavity-nesting finches. *Journal of Animal Ecology* 80.1:39-48.

Broom, D.M. (1991) Animal welfare: concepts and measurement. *Journal of Animal Science* 69:4167-4175.

Brouwer, K., Jones, M.L. King, C.E & Schifter, H. (1992) Longevity and breeding records of storks *Ciconidae* in captivity. *International Zoo Yearbook* 31: 131-139.

Brouwer, K., Jones, M.L. King, C.E & Schifter, H. (2000) Longevity records for *Psittaciformes* in captivity. *International Zoo Yearbook* 37: 299–316.

Brown, J.H. & Maurer, B.A. (1986) Body size, ecological dominance and Cope's rule. *Nature* 324: 248-250.

Buchanan-Smith, H. (2012) Mixed species exhibition of Neotropical primates: an analysis of species combination success. *International Zoo Yearbook* 46:150-163.

Burger, J., Caldwell Hahn, D. & Chase, J. (1979) Aggressive interactions in mixed-species flocks of migrating shorebirds. *Animal Behaviour* 27.2: 459-469.

Burgess, T.F. (2001) *A general introduction to the design of questionnaires for survey research*. [Online] http://www.leeds.ac.uk/iss/documentation/top/top2/index.html. [Accessed: 27/08/2013].

Carboneras, C. (1992) Family *Anatidae* (Ducks, geese and Swans). In del Hoyo, J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona, Spain.

Carroll, J.P. (1994) Family *Odontophoridae* (New World Quails). In del Hoyo, J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 2New World Vultures to Guineafowl. Lynx Edicions, Barcelona, Spain.

Carlstead, K., Fraser, J., Bennett, C., & Kleiman, D. G. (1999) Black rhinoceros (*Diceros bicornis*) in US zoos: II Behavior, breeding success and mortality in relation to housing facilities. *Zoo Biology* 18.1: 35-52.

Carrete, M., Lambertucci. S. A., Speziale, K., Ceballos O., Travaini, M., Delibes, F., Hiraldo, J. & Don´azar, A. (2010) Winners and losers in human-made habitats: interspecific competition outcomes in two Neotropical vultures. *Animal Conservation* 13.4: 390-398.

Cheng, M. & Balthazart, J. (1982) The role of nest-building activity in gonadotropin secretions and the reproductive success of ring doves (*Streptopelia risoria*). *Journal of Comparative and Physiological Psychology* 96. 2: 307-324.

Clubb, R., Rowcliffe, M., Lee, P., Mar K.U., Moss, C. & Mason G.J. (2009) Fecundity and population viability in female zoo elephants: problems and possible solutions. *Animal Welfare* 18:237–247.

Cockle, K, L., Martina, K, & Drevera, M.C. (2010) Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation* 143.11: 2851–2857.

Cody, M.L. (1985) *Habitat selection in birds*. Academic Press Inc, London, UK.

Coe, J. C. (2001) *Mixed-species exhibits*. In Bell, C. E. & Coe, J.C. (Eds.). Encyclopaedia of the World's Zoos 2, Fitzroy Dearborn Publishers. Chicago, USA.

Collar, N.J., Gardener, L., Jeggo, D., Marcordes, B., Owen, A., Pagel, T., Pes, T., Vaidl, A., Wilkinson, R. & Wirth, R. (2012) Conservation breeding and the most threatened birds in Asia. *Birding Asia* 18: 50-57.

Collar, N.J. & Butchart, S.H.M. (2014) Conservation breeding and avian diversity: Chances and challenges. *International Zoo Yearbook* 48: 1- 22.

Conde, D.A., Flesness, N., Colchero, F., Jones, O.R. and Scheuerlein, A. (2011) An emerging role of zoos to conserve biodiversity. *Science* 331:1390-1391.

Conway, W.G. (2000) The changing role of zoos in the 21st century. *EAZA News* 29:8-13.

Conway, W.G. (2003) The role of zoos in the 21st century. *International Zoo Yearbook* 38: 7–13

Conway, W.G. (2011) Buying time for wild animals within zoos. *Zoo Biology* 30.1: 1-8.

Cornelius,C., Cockle, K., Politi, N., Berkunsky, N., Sandoval, N., Ojeda, V., Rivera, L., Hunter, O. & Martin, K. (2008) Cavity-nesting birds in neotropical forests: cavities as a potentially limiting resource. *Ornithlogia Neotropical* 19 (Suppl.): 253–268.

Crockett, C.M. & Ha, R.R. (2010) *Data collection in the zoo setting, emphasizing behavior*. In Kleiman D.G., Thompson, K.V. & Baer, C.K. (Eds.) Wild mammals in captivity: principles and techniques for zoo management. University of Chicago Press, USA.

Crosta, L, & Timossi, L. (2009) *The management of a multi-species bird collection in a zoological park. Handbook of Avian Medicine, 2nd Edition*. Saunders Publishing, California, USA.

Crotty, M.J. (1981) Mixed species exhibits at the Los Angeles Zoo. *International Zoo Yearbook* 21.1: 203-206.

Curio, E. (1998) *Behaviour as a tool for management intervention in birds*. In Caro, R. (ed.). Behavioural Ecology and Conservation Biology. Oxford University Press, Oxford UK: 163 -187.

Dalton, R & Buchanan-Smith, H.M. (2005) A mixed-species exhibit of Goeldi's Monkeys *Callimico goeldii* and pygmy marmosets *Cebuella pygmaea* at Edinburgh Zoo. *International Zoo Yearbook* 39 .1: 176-184.

Davis, N.J. (2009) *Social and environmental influences on the welfare of zoo-housed spider monkeys (Ateles geoffroyi rufiventris*). PhD Thesis, University of Liverpool, UK.

DEFRA. (2004) *Secretary of State's Standards for Modern Zoo Practice*. DEFRA, London, UK.

del Hoyo, J. (1994) Family *Cracidae* (Chachalacas, Guans and Curassows). In del Hoyo,J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 2: New World vultures to Guineafowl. Lynx Edicions, Barcelona, Spain.

del Hoyo,J., Elliott, A. & Christie, D. (2011) *Handbook of the Birds of the World – Volume 16: Tanagers to New World Blackbirds*. Lynx Edicions, Barcelona, Spain.

Dick, G. & Gusset, M. (2010) The global reach of zoos and aquariums in visitor numbers and conservation expenditures. *Zoo Biology* 30.5: 566-569.

Dick, P. (2012) Keeping different species in mixed collections. *Just Finches and Softbills* 30: 37-39.

Dickie, L.A. (2009) The sustainable zoo: an introduction. *International Zoo Yearbook* 43.1, 1-5.

Donázar, J.A, & Feijóo, J.E. (2002) Social structure of Andean condor roosts: influence of sex, age and season. *The Condor* 104.4: 832-837.

Dorman, N. & Borne, D. (2010) Canids and ursids in mixed-species exhibits. *International Zoo Yearbook* 44.1: 75-86.

Dube, C., Mehren, K.G., Barker, I.K., Peart, B.L. & Balachandran, A. (2006). Retrospective investigation of chronic wasting disease of cervids at the Toronto Zoo: 1973–2003. *Canadian Veterinary Journal* 47:1185-1193.

Earnhardt, J.M., Thompson, S.D. & Willis, K. (1995). ISIS Database: An evaluation of records essential for captive management. *Zoo Biology* 14: 493 – 508.

EAZA. (2013) *List of managed breeding programmes*. EAZA Executive Office, Amsterdam, Netherlands.

EAZA. (2014) *Using records in husbandry management*. [Online] http://www.eaza.net/. [Accessed. 15/07/2014].

Elliot, A. (1992) Family *Scopidae* (Hamerkop) and Family *Ciconiidae* (Storks). In del Hoyo, J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona, Spain.

Ellis, J.C. & Good, T.P. (2006) Nest attributes, aggression and breeding success of gulls in single and mixed species sub-colonies. *The Condor* 108: 211-219.

European Council Directive 1999/22/EC. (2002). [online] http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=URISERV:l28069 [Accessed: 07/07/2015].

Fargallo, J.A., Blanco, G. Potti, J. and Vinuela, J. (2001) Nestbox provisioning in a rural population of Eurasian Kestrels: breeding performance, nest predation and parasitism. *Bird Study* 48: 236–244.

Faust, L.J. & S.D. Thompson. (2000) Birth sex ratio in captive mammals: Patterns biases, and the implications for management and conservation. *Zoo Biology* 19:11-25.

Fiby, M. (2008) Trends in zoo design-Changing needs in keeping wild animals for a visiting audience. *Topos: The International Review of Landscape Architecture and Urban Design*. Munich, Germany.

Fidgett, A.L., Pullen, P.K. & Brunger, D. (2008) *Zoo Research Guidelines: Research Using Zoo Records*. BIAZA, London, UK.

Finch, D.M. (1990) Effects of predation and competitor interference on nesting success of house wrens and tree swallow. *The Condor* 92:674-687

Flesness, N.R. (2003) International Species Information System (ISIS): over 25 years of compiling global animal data to facilitate collection and population management. *International Zoo Yearbook* 38:53–61.

Forshaw, J.M. (1981) *Parrots of the World: 2nd Edition*. David and Charles Publishing, Newton Abott, UK.

Foulds, Y. (2008) Preliminary survey of mixed species bird enclosures in British zoos. *BIAZA Research Newsletter* 9.1:8

Foulds, Y. (2011) unpublished. *Online survey of research priorities for mixed species enclosures in Europe*. Chester Zoo, UK.

Frankham, R. (2008) Genetic adaptation to captivity in species conservation programs. Molecular *Ecology* 17. 1: 325–333.

Gause, G.F. (1934) The struggle for existence. Baltimore, MD: Williams & Wilkins. Cited in: Hardin, G. (1960). The Competitive Exclusion Principle. *Science* 131, 1292-1297.

Gautschi, B., Jacob, G., Negro, J.J., Godoy, J.A., Müller, J.P. & Schmidt, B. (2003) Analysis of relatedness and determination of the source of founders in the captive bearded vulture, *Gypaetus barbatus*, population. *Conservation Genetics* 4.4: 479-490.

Gendall, P. (1998). Framework for questionnaire design: Labaw revisited. *Marketing Bulletin* 9.3: 28-39.

Gochfeld, M. & Berger, J. (1996) Family *Laridae* (Gulls). In del Hoyo,J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 3: Hoatzin to Auks. Lynx Edicions, Barcelona, Spain.

Griffin, A.S., Savani, R.S., Hausmanis, K. & Lefebvre, L. (2005) Mixed-species aggregations in birds: zenaida doves, *Zenaida aurita*, respond to the alarm calls of carib grackles, *Quiscalus lugubris*. *Animal Behaviour* 70.3: 507-515.

Hardin, G. (1960) The Competitive Exclusion Principle. *Science* 131, 1292-1297.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K. Braun, E.L., Braun, M.J., Chojnowski, J.L, Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., and T. Yuri. (2008) A phylogenomic study of birds reveals their evolutionary history. *Science* 320: 1763-1768.

Hammer, G. (2002) *Mixed species exhibits involved mammals: stock report and problems*. PhD Thesis, Naturwissenschaftliche Fakulat Univesitat Salzburg, Austria.

Hankerson, S.J., Deitz, L.M. & Raboy, B.E. (2006). Associations Between Golden-Headed Lion Tamarins and the Bird Community in the Atlantic Forest of Southern Bahia. *International Journal of Primatology* 27.2: 487-495.

Hartt, E.W., Harvey, N.C., Leete, A.J. & Preston, K. (1994). Effects of age at pairing on reproduction in captive Californian condors (*Gymnogyps californianus*). *Zoo Biology* 13: 3-11.

Hatchwell, B.J., Russell, A.F., Fowlie, M.K. & Ross, D.J. (1999). Reproductive success and nest-site selective in a cooperative breeder: effect of experience and a direct benefit of helping. *Auk* 116: 355-363.

Hawkins, R. (1970) *Notes of bird ecology as applied to planted aviaries*. In Rugers, L. & Norris, B. (Eds) Encycldpeia of Avicultural Volume 1. Blanford Press, London, UK.

Haythorpe, K.M., Sulikowski, D. & Burke, D. (2012). Relative levels of food aggression displayed by common mynas when foraging with other bird species in suburbia. *Emu* 2012: 129-136.

Hediger, H. (1950) *Wild Animals in Captivity*. Butterworths Scientific. London , UK.

Heymann, E.W. & Buchanan-Smith, H.M. (2000) The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Review* 75: 169–190.

Hino, T. (1998) Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest of western Madagascar. *Journal of Avian Biology* 29.1: 17-24.

Hosey, G., Hill, S. & Lherbier, M. (2012) Can zoo records help answer behavioural research questions? The case of the left-handed lemurs (*Lemur catta*). *Zoo Biology* 31: 189-196

Hosey, G, Melfi, V. & Pankhurst, S. (2013) *Zoo Animals: Behaviour, Management, and Welfare* 2nd Edition. Oxford University Press, Oxford, UK.

Hunt, E. (2008) *ZIMS outshines ARKS*. [Online] http://zimsblog.isis.org/2008/05/zims-outshines-arks.html. [Accessed: 24/10/2012].

ISIS. (2014) *ISIS species holdings*. [online] https://zims.isis.org/. [Accessed: multiple dates in 2014].

IUCN. (2007) *IUCN Habitats Classification Scheme Version 3.0*. [Online] http://www.iucnredlist.org/technical-documents/classification-schemes/habitats-classification-scheme-ver3. [Accessed: 15/06/2012].

IUCN. (2012) *IUCN Red List of Threatened Species*. [Online] http://www.iucnredlist.org/. [Accessed: multiple dates in 2012].

IUCN. (2013) *IUCN Red List of Threatened Species*. [Online] http://www.iucnredlist.org/. [Accessed: multiple dates in 2013].

Jeggo, D., Young, G.H. & Darwent, M. (2001) The design and construction of the Madagascar teal aviary at Jersey Zoo. *Dodo* 37: 50-59.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Redding, D. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature* 491: 444–448.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Redding, D. & Mooers, A.O. (2014) Distribution and conservation of global evolutionary distinctness in birds. *Current Biology* 24:1-12.

Kaiser, S. & Sachser, N. (2005) The effects of prenatal social stress on behaviour: mechanisms and function. *Neuroscience & Biobehavioral Reviews* 29. 2: 283–294.

Kerth, G., Weissmen., K. & Konig, B. (2001) Day roost selection in female Bechstein's bats (*Myotis bechsteinii*): a field experiment to determine the influence of roost temperature. *Oecologia* 126:1–9.

King, C.E. (1998) *What can zoos contribute to aviculture*? Proceedings of the fourth International Parrot Conference. Loro Parque, Tenerife, Spain.

Klasing, K.C. (1998) *Comparative avian nutrition*. Cabi Publishing, Oxon, UK.

Krebs, J.R. & Davies, N. B. (1997) *Behavioural ecology: an evolutionary approach*, 4th Edition. Blackwell Science, Cambridge, UK.

Krebs, K., Rimlinger, D. & Mace, M. (2002)*Husbandry Guidelines for Apodiformes-Hummingbirds*. San Diego Wild Animal Park, California, USA.

Krüger, O. (2002) Analysis of nest occupancy and nest reproduction in two sympatric raptors: common buzzard *Buteo buteo* and goshawk *Accipiter gentilis*. *Ecogeography* 25: 523-532.

Labaw, P.J. (1981) Advanced Questionnaire Design. Abt Books, Cambridge, Mass. Cited in: Gendall, P. (1998) Framework for questionnaire design: Labaw revisited. *Marketing Bulletin* 9.3: 29.

Lauer, J. (1976) *Saqqara: The royal cemetery of Memphis, evacuations and discoveries since 1850*, London, UK. Cited in Hosey, G., Melfi, V., and Pankhurst, S. (2013). Zoo Animals: Behaviour, management and welfare. Oxford University Press, Oxford, UK.

Lees, C & Wilcken, J. (2009) Sustaining the ark: the challenges faced by zoos in maintaining sustainable populations. *International Zoo Yearbook* 43: 6-18.

Leonardi, R., Buchanan-Smith, H., Dufour, V., MacDonald, C. & Whiten, A. (2010) Living together: behaviour and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology* 72.1:33-47.

Leus, K & Bingaman-Lackey, L. (2008a) Diverse bird populations in EAZA institutions; to be or not to be? *EAZA News* 62: 22-23

Leus, K. & Bingaman Lackey, L. (2008b) *EAZA bird populations – to be or not to be*? Technical Report, EAZA, Amsterdam, Netherlands.

Leus, K., Bingaman Lackey, L., van Lint, W., de Man, D., Riewald, S., Veldkam, A. & Wijmans, J. (2011) Sustainability of European Association of Zoos and Aquaria Bird and Mammal Populations. *WAZA Magazine* 12, 11-14.

Lišková, S. & Frynta, D. (2013) What determines bird beauty in Human eyes? *Anthrozoos: A Multidisciplinary Journal of the Interactions of People & Animals* 26.1: 27-41.

Mallinson, J.C. (2003) A Sustainable Future for Zoos and Their Role in Wildlife Conservation. Human dimensions of wildlife: *An International Journal* 8.1: 59-63.

Martin, T.E. (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* 18: 453-487.

Martinez-Vilalta, A. & Motis, A. (1992) Family *Ardeidae* (Herons). In del Hoyo,J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona, Spain.

Mascarelli, A. (2013) Conservation in captivity. *Nature* 498: 261-263.

Mason, G. (2010) Species differences in response to captivity: stress, welfare and the comparative method*. Trends of Ecology and Evolution* 25.12: 713-721.

Matheu, E. & del Hoy, J. (1992) Family *Threskiornithidae* (Ibises and Spoonbills). In del Hoyo,J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona, Spain.

Mcgowan, P.J.K. (1994) Family *Phasianidae* (Pheasants and Partridges). In del Hoyo,J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 2: New World vultures to Guineafowl. Lynx Edicions, Barcelona, Spain.

Melfi, V.A., Bowkett, A., Plowman, A.B. & Pullen, K. (2007) *Do zoo designers know enough about animals?* In Plowman, A.B. and Tonge, S. (eds.) Innovation or replication: Proceedings of the Sixth International symposium on zoo design. Devon, UK.

Melfi, V.A. & Hosey, G.R. (2012) *Zoo Research Guidelines: Multi-zoo research.* BIAZA, London, UK.

Mellen, J.D. (1991) Factors influencing reproductive success in small captive exotic felids (Felis Spp.) – A multiple regression analysis. *Zoo Biology* 10.2: 95-100.

Millam, J. R., Kenton, B., Jochim, L., Brownback, T. & Brice, A. T. (1995) Breeding orange-winged Amazon parrots in captivity. *Zoo Biology* 14.3: 275–284.

Miller, A. (2015) *Best Practices in Animal Records Keeping Using the ZIMS Application*. ISIS Publication.

Mitchell, H & Nevison, C. (2006) *The effect of inter-zoo transport on reproductive success of three felid species*. In: Dow. S. & Clark. F. (eds). 8th Annual Symposium on Zoo Research. BIAZA, London, UK.

Moss, A & Esson, M. (2010) Visitor interest in zoo animals and the implications for collection planning and zoo education programmes. *Zoo Biology* 29: 715-731.

Muller, D.W.H. Laurie Bingaman Lackey, Streich, W.J. Hatt, J.M, Clauss, M. (2010) Relevance of management and feeding regimens on life expectancy in captive deer. *American Journal of Veterinary Research* 71: 275-280.

Munn, C.A. & Terborgh, J.W. (1979) Multi-species territoriality in Neotropical foraging flocks. *Condor* 81.4: 3338-347.

Newton, I (1998) *Population Limitation in Birds*. Academic Press, San Diego, California, USA.

Oliver, W.L.R. & Wilkinson, R. (2007) *Philippine Hornbills Conservation Programme*. In Kemp, A.C. & Kemp M.I. (Eds). The active management of hornbills and their habitats for conservation. Proceedings of the 4th International Hornbill Conference, Mabula Game Lodge, Bela-Bela , South Africa: 13-30.

Owen, A., Wilkinson, R. & Sozer, R. (2014) In situ conservation breeding and the role of zoological institutions and private breeders in the recovery of highly endangered Indonesian passerine bird. *International Zoo Yearbook*. 48.1:199-211.

Pankhurst, S. Hosey, G. & Melfi, V. (2008) *Mind the gap! Where are the main gaps in zoo-based research*? Proceedings of the 10th Annual BIAZA Research Symposium. BIAZA, London, UK.

Papini, R., Girivetto, M., Marangi, M., Mancianti, F. & Giangaspero, A. (2012) Endoparasite Infections in Pet and Zoo Birds in Italy. *The Scientific World Journal* 2012: 1-9.

Pattee, O.H., Carpenter, J.W., Fritts, S.H. Rattner, B.A., Wiemeyer, S.N., Royle, J.A. & Smith, M.R. (2006) Lead poisoning in captive Andean condors (*Vultur gryphus*). *Journal of Wildlife Diseases* 42.4: 772-779.

Pearce, D., Prkye, S.R. & Griffith, S.C. (2011) Interspecific aggression for nest sites: model experiments with long-tailed finches (*Peophila acuticuda*) and endangered Gouldian finches (*Erythrura gouliae*). *Auk* 128.3:497-505.

Perkins, L. A. (1992) Variables that influence the activity of captive organutans. *Zoo Biology* 11: 177-186.

Plowman, A., Hosey, G. & Stevenson, M. (2006) *Zoo Research Guidelines: Surveys and Questionnaires*. British and Irish Association for Zoos and Aquariums, London, UK.

Poling, T.D. & Haysette, S.E. (2006) Dietary overlap and foraging competition between mourning doves and Eurasian collared-doves. *Journal of Wildlife Management* 70.4:998-104.

Poot , H., ter Maat, A., Trost, L., Schwabl, I., Jansen, R.F. & Gahr, M. (2012) Behavioral and physiological effects of population density on domesticated zebra finches (Teaniopygia guttata) held in aviaries. *Physiology and Behavior* 105.3:821-8.

Pullen, P.K. (2004) The EEP studbook for the white faced saki monkey (*Pithecia pithecia*): a tool for interpreting minimum standards of welfare in zoological parks. *Folia Primatologica* 75 (supplement): 214.

Rahbek, C. (1993) Captive breeding – a useful tool in the preservation of biodiversity? *Biodiversity and Conservation* 2.4: 426-437.

Reading, R.P. & Miller, B.J. (2007) *Attitudes and attitude change among zoo visitors*. In Zimmerman, A., Hatchwell, M., Dickie, L. & West. C. (eds.) Catalysts for conservation: a direction for zoos in the 21st Century, London, UK: pp. 63-91.

Ricklefs, R. E. (2000) Intrinsic aging-related mortality in birds. *Journal of Avian Biology* 31:103-111.

Ricklefs, R.E., Scheuerlein, A. & Cohen, A. (2003) Age-related patterns of fertility in captive populations of birds and mammals. *Experimental Gerontology* 38: 741-745.

Rietkerk, F., Brouwer, K., Smits, S. & Damen, M. (1997) *The Future of Birds in European zoos. In EEP Yearbook 1996/97 and the Proceedings of the 14th EAZA/EEP Conference*. Alphen. EAZA Executive Office, Amsterdam. Netherlands.

Ripley, D.S. (1961) Aggressive neglect as a factor in interspecific competition in birds. *Auk* 78.3: 366-371.

Rogers, C.W. & Wylie S.R. (1975) Use of tropical plants in bird exhibits at the Philadelphia Zoo. *International Zoo Yearbook* 15: 252-255.

Rogers, C.W. (1984) *Jungle bird walk: an avian conservatory.* Association of Zoological Horticulture National Conference, 1983. American Association of Botanical Gardens and Arboreta, California. USA.

Rubenstein, D.I., Barnett, R.J., Ridgely, R.S. & Klopfer, P.H. (1977) Adaptive advantages of mixed-species feeding flocks among seed-eating finches in Costa Rica. *Ibis* 119.1: 10-21.

Sachser, N. & Kaiser, S. (1996) Prenatal social stress masculinizes the females' behaviour in guinea pigs. *Physiology & Behavior* 60. 2: 589–594

Sánchez-Macouzet, O., Rodríguez, C. & Drummond, H. (2014). Better stay together: pair-bond duration increases individual fitness independent of age-related variation. *Proceedings of the Royal Society of Biology* 281: 20132843.

Schulte, A.I. & Mastromonaco, G.F. (2015) Integrating evolution in the management of captive zoo populations. *Evolutionary Applications*. Early view: DOI: 10.1111/eva.12258

Seal, U.S., Makey, D. & Murtle, L. E. (1976) ISIS: An animal census system. *International Zoo Yearbook* 16: 180-184.

Seddon, P.J., Armstrong, D.P. & Maloney, R.F. (2007) Developing the science of reintroduction biology. *Conservation Biology* 21.2: 303-312.

Senar, J.C., Camerino, M. and Metcalfe, N.B. (1990) Familiarity breeds tolerance: the development of social stability in flocking Siskins (*Carduelis spinus*). *Ethology* 85: 13–24.

Shepherdson, D. J., Carlstead, K.C. & Wielebnowski, N. (2004) Cross-institutional assessment of stress responses in zoo animals using longitudinal monitoring of faecal corticoids and behaviour. *Animal Welfare* 13: 105-113.

Sheppard, C. (1995) Propagation of endangered birds in US institutions: How much space is there. *Zoo Biology* 14: 197-210.

Snyder, N.F.R., Derrickson, S.R. & Beissinger, S.R. Wiley, J.W., Smith, T.B., Toone, W.D. & Miller, B. (1996). Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10.2: 338-348.

Swaisgood, R.R. (2007) Current status and future directions of applied behavioral research for animal welfare and conservation. *Applied Animal Behaviour Science* 102: 139-162.

Taylor, V.J. & Poole, T.B. (1998) Captive breeding and infant mortality in Asian elephants: A comparison between twenty western zoos and three eastern elephant centers. *Zoo Biology* 17.4: 311-332.

Taylor, P.B. (1996) Family *Rallidae* (Rails, Gallinules and Coots). In del Hoyo,J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 3: Hoatzin to Auks. Lynx Edicions, Barcelona, Spain.

Terborgh, J. (1990) Mixed flocks and polyspecific associations in birds and primates. *International Journal of Primatology* 21.2: 87-100.

Thiollay, J.M. (1994) Family *Accipitridae* (Hawks and Eagles).In del Hoyo,J., Elliott, A. and Sargatal, J. (eds.). Handbook of the Birds of the World – Volume 2: New World vultures to Guineafowl. Lynx Edicions, Barcelona, Spain.

Thomas, W. D. & Maruska, E. J. (1996) *Mixed-species exhibits with mammals.* In: Kleiman D.G., Thompson, K.V. & Baer, C.K. (Eds.). Wild mammals in captivity: principles and techniques. University of Chicago Press, USA. 204–211.

Tritto, A. & Barbon, A. R. (2012) *Atoxoplasmosis in captive blue-crowned laughingthrush (Dryonastes courtoisi) population*. Poster presented at EAZA Annual Conference, Innsbruck, Austria.

Veasey, J. & Hammer, G. (2010) *Managing captive mammals in mixed-species communities*. In: Kleiman, D.G. Thompson, K. & Baer, C.K. (Eds.) Wild Mammals in Captivity: Principles and Techniques for Zoo Management, Second Edition. University of Chicago Press, USA.

Vince, M. (2008) Making the case for off-exhibit bird facilities. *EAZA News* 64: 39-41.

Wagner, S.J. & Gauthreaux, I. (1990) Correlates of dominance in intraspecific and interspecific interactions of song sparrows and white-throated sparrows. *Animal Behaviour* 39.3: 522-527.

Walter, O., Ellis, J.A., & Bingaman-Lackey, L. (2009) Will the EU ban on bird imports mean the demise of bird populations in EAZA collections? *International Zoo Yearbook* 43.1, 19-28.

Ward, G. (2012) *Passerine focus group survey results*. Presented at 7th Annual BIAZA BWG Meeting. Marton Mere Nature Reserve, Lancashire, UK.

Ward, P. I., Kistler, C. & Fischer, O. (1998) The Relationship between Popularity and Body Size in Zoo Animals. *Conservation Biology* 12.6:1408-1411.

WAZA. (2005) *Building a Future for Wildlife: The World Zoo and Aquarium Conservation Strategy*. WAZA Executive Office, Berne, Switzerland.

Wilkinson, R, Fen-qi, H., Gardner, L. &Wirth, R. (2004) A highly threatened bird – Chinese yellow-throated laughingthrushes in China and in zoos. *International Zoo News* 51.8: 456-469.

Wilkinson. R. (1987a) Consumers must become producers. *Cage and Aviary Magazine* 2.

Wilkinson, R. (1987b) Chester Zoo, U.K., A review of the 1985 and 1986 breeding season. *International Zoo News* 204.34/5:35-40.

Williams, S.E. & Hoffman, E.A. (2009) Minimizing genetic adaptation in captive breeding programs: A review. Biological Conservation 142: 2388–2400.

Wojeciechowski, S. (2004) Introducing a forth primate species into an established mixed species exhibits of African monkeys. *Zoo Biology* 23.2: 95-108.

Wolters, S. & Zuberbuhler, K. (2003) Mixed-species associations of Diana and Campbell's monkeys: the costs and benefits of a forest phenomenon. *Behaviour* 140: 371–385.

WWF. (2012) *Ecoregions* [Online] https://www.worldwildlife.org/biomes. [Accessed: 03/05/2012]

Zeng, X. H. & Lu, X. (2009) Interspecific dominance and asymmetric competition with respect to nesting habitats between two snowfinch species in a high-altitude extreme environment. *Ecological Research* 24.3:607-616.

Zimmerman, A., Hatchwell, M., Dickie, L. & West. C. (2007) *Zoos in the 21st century: catalysts for conservation*. Cambridge University Press, Cambridge, UK.

Zoo Design Symposium. (2004) *Stakeholders in zoo enclosure design*. Cited in Melfi, V.A., Bowkett, A., Plowman, A.B. & Pullen, K. (2007) Doo zoo designers know enough about animals? In Plowman, A.B. and Tonge, S. (eds.) Innovation or replication: Proceedings of the Sixth International symposium on zoo design. Devon, UK.

ZooLex. (2011). *Zoo Design Organisation gallery*. [Online] http://www.zoolex.org/zoolexcgi/gallery.py. [Accessed: multiple dates in 2011].

Zoo Licencing Act (1981) [Online] http://www.legislation.gov.uk/ukpga/1981/37. [Accessed 23/11/2014].

ZSL. (2014) *Animal records*. [Online] http://www.zsl.org/education/animal-records [Accessed: 07/08/2014].

Appendices

Appendix A: Foulds, Y. (2008) Preliminary survey of mixed species bird enclosures in British zoos. *BIAZA Research Newsletter* 9.1:8.

Preliminary survey of mixed species bird enclosures within British Zoos

Yvette Foulds, Liverpool John Moores University and Blackpool Zoo

Within modern zoos it has become popular to house a variety of species together in one enclosure. This can include one or more taxonomic groups. At the 1st annual BIAZA Bird Working Group meeting in 2006 one of the issues raised was the perception of increased breeding problems and reduced welfare in mixed species bird exhibits and the lack of research evaluating addressing this.

After this meeting a questionnaire was devised to begin to assess mixed species bird enclosures found within British collections. The initial aim was to gain a general overview; including the prevalence of reported breeding problems and to identify key areas requiring further research. The results showed that 82% of the returned questionnaires had mixed species enclosures. This equated to 36 enclosures found within 14 zoos. A total of 158 different bird species were recorded, with 42% having reported breeding problems. The most prevalent perceived reasons for breeding problems were interference by other species and environmental factors. At this stage no statistical conclusions can be drawn due to the relatively low number of returned questionnaires and high number of variables, particularly the number of species listed. To further this research there needs to be a greater number of collections involved and a more narrow focus on species is required. The current results did highlighted seven species which were experiencing breeding problems in more than one collection and these species may be a starting point for the next stage in this ongoing project.

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Appenidx B: List of conference presentations.

Foulds, Y., Wilkinson, R. and Mettke-Hofmann, C. (2014) Mixed Aviaries Project: The results. [Oral Presentation] 9th Annual BIAZA Bird Working Group Meeting, The Hawk Conservancy Trust, UK.

Foulds, Y., Wilkinson, R., Dowell, S. and Mettke-Hofmann, C. (2013). Mixed Aviaries Project: Progress Update 2013. [Oral Presentation] 8th Annual BIAZA Bird Working Group Meeting, Chessington World of Adventures, UK.

Foulds, Y., Wilkinson, R., Dowell, S. and Mettke-Hofmann, C. (2013) To mix or not to mix? Evaluating breeding performance in mixed species bird enclosures within European zoological collections. [Poster Presentation] LJMU Faculty of Science Postgraduate Research Seminar, Liverpool, UK.

Foulds, Y., Wilkinson, R., Dowell, S. and Mettke-Hofmann, C. (2012) Mixed Aviaries Project: Progress Update 2012. [Oral Presentation] The 7th Annual BIAZA Bird Working Group Meeting, Marton Mere Nature Reserve, UK.

Foulds, Y., Wilkinson, R., Dowell, S. and Mettke-Hofmann, C. (2011) Evaluating the success of mixed species aviaries through assessment of species compatibility, enclosure design and

breeding productivity. [Oral presentation] The 6th Annual BIAZA Bird Working Group Meeting, Birdland, UK