A Review of Chlamydial Infections in Wild Birds

Helena S. Stokes *, Mathew L. Berg and Andrew T. D. Bennett

Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Geelong, VIC 3216, Australia; mathew.berg@deakin.edu.au (M.L.B.); andy.bennett@deakin.edu.au (A.T.D.B.)
* Correspondence: helena.stokes@birdlife.org.au

Abstract: The Chlamydiae are a globally distributed genus of bacteria that can infect and cause disease in a range of hosts. Birds are the primary host for multiple chlamydial species. The most well-known of these is Chlamydia psittaci, a zoonotic bacterium that has been identified in a range of wild and domesticated birds. Wild birds are often proposed as a reservoir of Chlamydia psittaci and potentially other chlamydial species. The aim of this review is to present the current knowledge of chlamydial infections in wild avian populations. We focus on C. psittaci but also consider other Chlamydiaceae and Chlamydia-related bacteria that have been identified in wild birds. We summarise the diversity, host range, and clinical signs of infection in wild birds and consider the potential implications of these infections for zoonotic transmission and avian conservation. Chlamydial bacteria have been found in more than 70 species of wild birds, with the greatest chlamydial diversity identified in Europe. The Corvidae and Accipitridae families are emerging as significant chlamydial hosts, in addition to established wild hosts such as the Columbidae. Clarifying the effects of these bacteria on avian host fitness and the zoonotic potential of emerging Chlamydiales will help us to understand the implications of these infections for avian and human health.

Keywords: Chlamydia; Chlamydia psittaci; psittacosis; chlamydiosis; birds; Chlamydiales; bacteria; zoonoses

1. Introduction

The Chlamydiae are a diverse genus of gram-negative, intracellular bacteria in the family Chlamydiaceae and order Chlamydiales, which share a unique biphasic development cycle of replication [1–3]. To date, 14 species have been proposed or formally classified, with four additional uncultured candidate species also proposed [4–6]. They have varying degrees of host specificity: some chlamydial species (‘chlamydial’ hereafter referring to any species within the order Chlamydiales) have only been reported in one host species, whereas others have been documented in multiple species of wild and domestic hosts, including humans [1].

One of the most well-documented zoonotic Chlamydia species, for which birds are the primary host, is Chlamydia psittaci [4,7]. C. psittaci is a zoonotic species that can infect and cause a severe disease in humans, termed psittacosis, which can result in pneumonia in up to 83% of cases and significant mortality if untreated [8,9]. C. psittaci is a globally distributed pathogen, to which more than 450 bird species from 30 different orders are known to be susceptible [10]. C. psittaci infection is particularly common in captive parrots and cockatoos (order Psittaciformes), where prevalence is between 16% and 81%, and in captive doves and pigeons (order Columbiformes), where prevalence is between 13% and 95% [7]. C. psittaci is also often found in poultry and is considered endemic in the turkey industry [11]. Additional orders of infected wild birds include the Lariformes (gulls) and Anseriformes (ducks and geese) [12]. Signs of disease in infected birds (termed psittacosis or avian chlamydiosis) can include lethargy, respiratory disease, anorexia, and conjunctivitis [13–15], although infection can also be subclinical [7]. C. psittaci strains tend to be
host-specific [7], with pathogenicity dependent on host species as well as individual condition [14]. In humans, the pathogenicity of C. psittaci infection is also highly variable: symptoms can range from mild, non-specific illness (such as chills and a headache) to severe systemic illness [16,17]. Subclinical infection is also common, and it is likely that many human cases remain unreported or are misdiagnosed [15]. Most reported cases of human psittacosis are thought to result from direct contact with wild or captive birds or bird material, such as through handling infected birds or inhalation of respiratory secretions or faecal particles [15].

Wild birds have long been proposed as a natural reservoir of C. psittaci infection [18]. However, direct evidence to support this hypothesis has been lacking. There has been relatively little targeted surveillance undertaken of wild bird populations, despite evidence supporting links between infections and mass mortality events [19] as well as zoonotic transmission to humans [9]. With the recent characterisation of several new avian Chlamydia species (namely C. gallinacea, C. avium, and C. buteonis) [4,5] as well as the proposition of novel transmission routes (specifically, transmission from wild birds to horses and then to humans) [20,21] the role of wild birds in chlamydial epidemiology warrants further discussion.

In this review, we present the current knowledge of chlamydial infections in wild birds worldwide. Our review addresses an important gap in the literature, as previous reviews of avian chlamydial infections have focused primarily on a captive bird or human disease perspective (e.g., [11,15]) or are confined to one geographic region or host species (e.g., [22]). We primarily discuss C. psittaci, as this is the most studied species; however, we also review the available data on other Chlamydiaceae and Chlamydia-related bacteria. We discuss the diversity, host range, and clinical signs of chlamydial infections in wild birds, and we consider the potential implications for zoonotic transmission and avian conservation.

2. Chlamydial Diversity in Wild Birds—the Known and the Novel

2.1. Chlamydia psittaci

C. psittaci is the best-studied avian Chlamydia species and has been isolated from several specimens across multiple host species (section 3 ‘Host Range of Chlamydial Infections in Wild Birds’) and locations (section 4 ‘Global Chlamydial Distribution’). C. psittaci is genetically variable, and genotypes have been designated based on outer membrane protein A (ompA) sequences. Genotypes A to F, E/B, M56, and WC were the first to be described [23–25], with further ompA genotypes proposed using newer sequencing techniques [26]. Genotypes A to F and E/B are primarily avian strains [24], whereas genotypes M56 and WC have been isolated from mammals [25]. Genotypes A and F are generally associated with psittacine birds, genotype B with pigeons, genotypes C and E/B with waterfowl, genotypes D and C with turkeys (Meleagris gallopavo), and genotype E has been isolated from a variety of bird species [7]. More recent genomic analysis has shown that genotype A strains belong to a lineage termed the 6BC clade, which is generally considered the most pathogenic [27,28]. While many of the avian C. psittaci genotypes were initially isolated from captive populations, several of these genotypes have also been found in wild birds [28–30]. Genotypes E and B are particularly common in feral pigeons (Columbia livia domestica) [30,31]. Genotype A has been isolated from a diverse range of wild hosts, including parrots (e.g., crimson rosellas (Platycercus elegans) and galahs (Eolophus roseicapillus)) [32,33], passerines (including robins (Erithacus rubecula), dunnocks (Prunella modularis) and great tits (Parus major)), raptors (including Eurasian sparrowhawks (Accipiter nisus) and common buzzards (Buteo buteo)) [34], and fulmars (Fulmarus glacialis) [30,35]. The more recently proposed genotype 1V appears to be associated with the Corvidae family [34,36]. Interestingly, genotype M56 (originally associated with mammals) has recently been found in association with wild raptors [34,37] in Switzerland and the USA.
2.2. Other Chlamydia and Chlamydia-Related Bacteria (CRB)

Since the identification of *C. psittaci*, several new *Chlamydia* species have been described in birds, and it is likely that some older reports of *C. psittaci* infections are actually infections with other *Chlamydia* species, particularly studies based only on serology [7]. Here we briefly describe the other chlamydial species that have been isolated from wild birds, with information available from captive birds for context where appropriate. *C. gallinacea* was first reported in domestic chickens (*Gallus gallus domesticus*) in 2009 [38] and was formally characterised in 2014 [39]. *C. gallinacea* has to date primarily been associated with poultry, having been detected in chickens and other poultry species in several countries globally [40–44], although it has been reported in one captive Passeriformes bird in Argentina [45]. Within the last four years, *C. gallinacea* has also been identified in wild birds, in two parrot species in Australia [33,46] and woodcock (*Scolopax rusticola*) in South Korea [36]. *C. avium* was also originally identified in captive birds, namely parrots and pigeons [39] with more recent isolation from wild Columbiformes [47,48] and a wild ring-necked parakeet (*Psittacula krameri*) [49]. Other recently described avian *Chlamydia* species include *C. buteonis*, isolated from a red-shouldered hawk (*Buteo lineatus*) [5], and a Candidatus species, Ca. *C. ibidis*, isolated from sacred ibises (*Threskiornis aethiopicus*) [50] and crested ibises (*Nipponia nippon*) [51]. Several chlamydial species primarily associated with human and other mammalian hosts have also been identified in wild birds, including *C. trachomatis* and *C. abortus* [29,52], as well as additional *Chlamydiaceae* which could not be defined to species level [29].

In addition to the *Chlamydiaceae*, there are several other related families within the *Chlamydiaceae* order, often described as ‘*Chlamydia*-related bacteria’ (CRB) [1]. There are eight additional families currently described. CRB are increasingly being identified in mammalian hosts [53–55] and have also been identified in birds, specifically poultry [56], and among wild birds, seabirds [57], and parrots [46]. Many of these emerging CRB are thought to cause disease in their respective hosts or humans [1,58], so the presence of these bacteria in wild hosts may be of zoonotic significance.

3. Host Range of Chlamydial Infections in Wild Birds

3.1. Parrots

The parrots and cockatoos (comprising the order Psittaciformes; hereafter referred to as parrots) consist of around 400 species [59], and in captivity they are frequently infected with *C. psittaci* [7]. The published studies of *Chlamydia* species in wild parrots are listed in Table 1. Most studies of wild parrots, as with other taxa, have focused on *C. psittaci* [7]. However, because some of the diagnostic methods described are not species-specific, they may have detected DNA from other chlamydial species or antibodies against other chlamydial species [33]. Apart from a few reports (e.g., [60,61]), chlamydial prevalence in wild parrots is usually below 10% (Table 1) and therefore much lower than the prevalence reported in captive parrots, which can be as high as 80% [7]. Reported prevalence estimates can vary depending on the sample type or diagnostic method used. For instance, in wild hyacinth macaw (*Anodorhynchus hyacinthinus*) nestlings, *C. psittaci* prevalence was 27% in cloacal swabs but only 9% in tracheal swabs in the same individuals [62]. In two other studies of wild parrots, a lower *C. psittaci* prevalence was identified from PCR analysis compared to sequencing [33,63].

Molecular analyses have demonstrated that the majority of *C. psittaci* strains identified in wild Australian parrots are in the 6BC clade [28,32,63]. Successful sequencing of *C. psittaci* strains has not, to our knowledge, been carried out for other wild parrot populations. The identification of the 6BC clade in wild Australian parrots suggests that wild hosts could be a reservoir of this clade, which is highly virulent in humans and has potential public health implications [28]. Other chlamydial species identified in wild parrots include *C. avium* in a single wild ring-necked parakeet in France [49] and *C. gallinacea* and
other Chlamydiales (e.g., Parachlamydiaceae) in crimson rosellas and galahs in Australia [46,64].

3.2. Pigeons

The pigeons and doves (order Columbiformes) are a major host of C. psittaci infections, with genotype B considered to be endemic in this order [7,65]. Consequently, several populations of feral pigeons have been tested for C. psittaci (and more recently, other chlamydial species) worldwide [22,66,67]. A 2009 review of European studies reported evidence of C. psittaci infection in feral pigeons in 11 countries [22]. C. psittaci has since been identified in European feral pigeon populations in further studies [47,48]. Surveillance of feral pigeon populations for C. psittaci has also been carried out outside Europe, in countries including Brazil [68,69], Japan [67], and Thailand [70,71]. In Australia, C. psittaci has been isolated from an individual spotted dove (Streptopelia chinensis), and a strain primarily associated with Columbiformes was also isolated from infected equine samples [72].

The majority of C. psittaci strains identified in wild pigeons and doves across Europe are in genotypes B and E [30,31,47], and genotype B has also been identified in pigeons in Thailand [71]. C. avium has now also been identified in several feral pigeon populations in Europe [39,47,48] at prevalences ranging from 0.9% to 36.6% [47,48], with one study in the Netherlands detecting C. avium at a higher prevalence than C. psittaci [48]. Other chlamydial species have also been identified in feral pigeon populations, such as C. pecorum in Japan [67] and C. pecorum, C. abortus, and C. trachomatis in Germany [66]. While the majority of studies only report C. psittaci and C. avium infections, this may simply reflect testing protocols, as pigeons have been tested for these chlamydial species most frequently (Table 1).

3.3. Other Wild Bird Species

Chlamydiaceae have been found in a wide variety of other wild bird species and appear to be fairly prevalent in birds in the Anatidae (duck) family (19.7–58.0%), where Chlamydiaceae have been identified in at least five different species [12,29,73] and the Corvidae (crow) family (13.4–23.7%) where Chlamydiaceae have been isolated from at least six species [29,34,36]. Many seabirds are also infected, with Chlamydiaceae detected in at least seven different species from three different families, including the Laridae (gulls; prevalence of up to 13.6% in European herring gull (Larus argentatus)), Sulidae (gannets and boobies; up to 41.3% in the Northern gannet (Morus bassanus) [12]) and the Procellariidae (fulmars; where prevalence is up to 21% according to location [74]). Both the Anatidae and Corvidae families can have C. psittaci infections [12,29], and several seabird species, including fulmars, black-headed gulls (Chroicocephalus ridibundus), and Northern gannets, have been found infected with C. psittaci and C. psittaci related strains [12,57,74]. The Anatidae, Corvidae, and Laridae have also been reported with C. abortus and non-classified Chlamydia infections [29,34], and the Gruiformes (specifically, Eurasian coots (Fulica atra)) have tested positive for C. trachomatis [52]. Raptors within the Accipitridae family are increasingly being tested for chlamydial bacteria and have tested positive for C. psittaci, the novel C. buteonis, and for novel CRB [5,75,76]. Further host species are increasingly being found with other Chlamydia species, such as woodcock with C. gallinaceae [36]. Gulls have been found harbouring novel Chlamydiaceae outside the Chlamydia genus [57,77]. Recently, wild greater flamingos (Phoenicopterus roseus) in France have been found harbouring two newly proposed Chlamydiaceae species within a newly proposed genus, Chlamydiiifrater gen. nov. [78]. It is likely that a wide variety of wild bird species are carrying other known and novel Chlamydiaceae [79], which may become evident with increased testing and molecular analyses.

Estimates of chlamydial prevalence have varied greatly between studies, even within the same host lineages (family or order). For example, among the Passeriformes, Chlamydiaceae prevalence was only 0–0.4% in some European surveillance studies [30,31]. In con-
contrast, chlamydial prevalence has also been reported at 23% (5/22 positive) in the Passeriformes [52] and prevalence as high as 54% reported within the Paridae family [80]. Additionally, a retrospective study in the U.K. found several passerine birds (including dunnocks, great tits, and blue tits (Cyanistes caeruleus)), which tested positive for C. psittaci [81]. There are several reasons why infection levels may fluctuate within a family, species, or population; seasonal variation in prevalence or seroprevalence has been found in gannets and crimson rosellas [12,46], with inter-annual variation reported in pigeons [66]. A limitation of studies to date that have tested wild species other than Columbiformes and Psittaciformes is that they are largely opportunistic, for instance, carried out on veterinary submissions or hunted birds (e.g., [32,52]) or as part of a sampling program for other diseases (e.g., [30]). This often results in a large total number of individuals being tested, but often only a small number of each species, limiting the scope of intra-species or other intra-taxon comparisons of prevalence or chlamydial diversity.

3.4. Studies Where Chlamydia Have Not Been Found

While C. psittaci and other chlamydial species have been detected across a wide host range, there are host species and studies in which very few or no birds have tested positive (Table 1). In two of the larger surveillance studies carried out in the last five years (in Switzerland and Australia), less than 1% of wild birds tested positive for C. psittaci or other Chlamydia [31,32]. Each study tested more than 40 different species from more than 20 families, a combined total of more than 600 individuals [31,32].

Early psittacosis outbreaks in Europe and the USA were attributed to the import of wild South American parrots [7]. However, of five studies of wild South American parrots, only two found evidence of C. psittaci infection ([62,82]; Table 1). While some of these South American studies were of nestlings [62,82,83] that may have limited exposure to C. psittaci, it is interesting that neither of the two studies of adults found any positive individuals [84,85].

There are many potential reasons for why some host species or populations are less likely to suffer chlamydial infections. These include host species variation in susceptibility to infection and disease, as well as seasonal or inter-annual variation and geographic variation in infection rates, as described above [12,66,69]. Alternatively, C. psittaci and other Chlamydia may not be detected in wild birds if a host species or population suffers severe acute disease, resulting in rapid death and so making detection unlikely [86].
Table 1. Studies of wild birds summarized in this review. Where a study included both captive and wild birds, we only report prevalence in wild birds. We have excluded case studies involving a single individual bird.

| Host Species | Family | Location | Sample Source | Sample Size | Detection Method(s) | Chlamydia Species Tested For | Key Findings | Disease Signs Reported? | Reference |
|--------------|--------|----------|---------------|-------------|---------------------|-----------------------------|--------------|------------------------|-----------|
| Seabirds; 13 species, 4 orders* | Anatidae, Alcidae, Laridae, Procellaridae, Sulidae | France | Rehabilitation centre | 195 | PCR (cloacal swabs) Sequencing Multilocus sequence typing (MLST) | C. psittaci Chlamydiaceae | • 18.5% Chlamydiaceae prevalence (prev.)  
• Prev. varied between host spp; Northern gannets Morus bassanus had higher prev. compared to European herring gulls Larus argentatus and common murres Uria aalge  
• Seasonal variation in prev. (in Northern gannets)  
• C. psittaci identified in Northern gannets and herring gulls  
• Unclassified Chlamydiaceae also identified | N | Aaziz et al., 2015 [12] |
| 48 species from 11 orders* | Psittacidae, Cacatuidae, Podargidae (…)* | Australia | Rehabilitation centre | 229 | PCR (live birds: choanal/cloacal swabs; dead birds: swabs from trachea and intestine/caecum) MLST | C. psittaci | • 1 crimson rosella Platycercus elegans and 1 superb lyrebird Menura novaehollandiae tested positive (0.7%)  
• All other wild birds tested negative | Y | Amery-Gale et al. 2020 [32] |
| Great white pelicans (Pelecanus onocrotalus) | Pelecanidae | South Africa | Live trapping | 50 | PCR (tracheal and cloacal swabs) | C. psittaci | • 0% C. psittaci prevalence | N/A | Assunção et al., 2007 [87] |
| Songbirds (Passeriformes); Pigeons and doves (Columbiformes)* | Paridae, Prunellidae, Turdidae (…)* | U.K. | Necropsy (selected based on clinical signs) | 40 | PCR (liver and spleen) Histology Immunohistochemistry | C. psittaci | • 53% C. psittaci prevalence  
• Nonspecific clinical signs observed (lethargy, fluffed up plumage) and emaciation  
• Concurrent disease in >50% cases  
• Genotype A present in all passerine cases | Y | Beckmann et al., 2014 [81] |
| 16 species from 5 orders* | Cacatuidae, Psittacidae, Columbidae (…)* | Australia | Trapping and community submissions | 278 | Isolation (from liver) and inoculation Serology (Complement Fixation Test (CFT)) | C. psittaci (methods not spp. specific) | • 10.6% prevalence (Psittaciformes)  
• 0.7% prevalence (all other species; 1 house sparrow Passer domesticus tested positive) | NR | Beech and Miles 1953 [60] |
| Peregrine falcons (Falco peregrinus) and white-tailed sea eagles (WTSE) (Haliaeetus albicilla) | Falconidae, Accipitridae | Sweden | Nestlings (breeding monitored; 108 falconets and 191 museum submissions) | 319 (299 nestlings; 108 falconets and 191 museum submissions; WTSE, and 20 WTSE adults) | PCR (cloacal swabs ompA sequencing | C. psittaci Chlamydia | • 1.3% C. psittaci prev. (n = 2 falcons, n = 2 eagles)  
• New strains of C. psittaci identified | NR | Blomqvist et al., 2012 [76] |
| Pathogens | Isolation and inoculation methods | Feral pigeons \((Columba livia domestica)\), ring-necked parakeets \((Psittacula krameri)\), crows \((Corvus splendens)\) |
|---|---|---|
| Psittacidae, Columbidae, Corvidae | India | Trapping | 85 (55 pigeons, 19 parakeets, 11 crows) |
| Isolation and inoculation (faecal swabs/intestinal and visceral organs) Serology (indirect immunofluorescence test \((IMIFT)\) and ELISA) C. psittaci (methods not spp.-specific) | C. psittaci | 26.3% prev. in ring-necked parakeets 16.4% prev. in pigeons 18.2% prev. in crows |
| Seabirds; 22 species* | Laridae, Alcidae | Bering Sea | NR | 722 | PCR (faeces) ompA, mPB, and 16S sequencing | C. psittaci Chlamydiales | 0.1% C. psittaci prev. (\(n = 1\) black-headed gull \((Larus ridibundus)\)) |
| Blue-fronted Amazon parrot \((Amazona aestiva)\) and hyacinth macaw \((Anodorhynchus hyacinthinus)\) | Psittacidae | Brazil | Nestlings (breeding monitoring) | 77 (32 Amazon parrots nestlings, 45 macaw nestlings) | PCR (tracheal and cloacal swabs) Serology (CFT) C. psittaci (methods not spp.-specific) | 6.3% prevalence in Amazon parrots (cloacal swabs) 26.7% prevalence in hyacinth macaws (cloacal swabs) 8.9% (tracheal swabs), 4.8% (CFT) |
| Feral pigeons | Columbidae | Brazil | Live trapping | 238 | PCR (cloacal and tracheal swabs) C. psittaci | 16.8% C. psittaci prev. Prev. ranged from 6.1% to 37.8% according to location |
| Blue-fronted Amazon parrot | Psittacidae | Bolivia | Live trapping | 34 | Serology (CFT) C. psittaci (method not species-specific) | 0% prevalence |
| Canada goose \((Branta canadensis)\) | Anatidae | Belgium | Culling program | 81 | Serology (rMOMP-based ELISA) Inoculation and culture (pharyngeal swabs) C. psittaci | 93.6% seropositive 58% of swabs were culture positive, but low culture score \((\text{low no. of viable organisms})\) |
| Rosy-faced lovebirds \((Agapornis roseicollis); 15 other species, including Passeriformes and Columbiformes*\) | Psittaculidae, Columbidae, Leptidae, Troglohydidae \((…)\)* | USA | Live trapping | 188 (46 lovebirds; 142 birds of other species) | PCR (conjunctival/choanal and cloacal swabs) C. psittaci | 93% C. psittaci prev. and 76% seroprevalence in lovebirds 10% C. psittaci prev. and 7% seroprevalence \((\text{in all other bird species combined})\) |
| Feral pigeons | Columbidae | Brazil | Live trapping | 240 | PCR (cloacal swabs) C. psittaci | 13% C. psittaci prevalence |
| New Zealand bellbirds \((Aotearoa melanura); \(n = 4\)\); rifleman \((Acathisis chloris); \(n = 3\)\); hihi \((Notiotyges cineta); \(n = 2\)\); whitehead \((Mohoua albicilla); \(n = 1\)\) | Meliphagidae, Notiomystidae, New Acathistidae, Zealand Mohouidae | Live trapping | 10 | PCR (cloacal swabs) Sequencing C. psittaci | 10% C. psittaci prevalence; one bird identified positive \((\text{a hihi})\) First report of C. psittaci detection from a wild native bird in New Zealand |

*NR = not reported

---

Chahota et al., 1997 [61]; Christerson et al., 2010 [57]; de Freitas Raso et al., 2006 [62]; de Lima et al., 2010 [69]; Deem et al., 2005 [84]; Dickx et al., 2013 [73]; Dusek et al., 2018 [88]; Ferreira et al., 2016 [68]; Gartrell et al., 2012 [89]
Dusky-headed parakeets (Aratinga weddellii) and Tui parakeets (Brotogetis sanctithomae) | Psittacidae | Peru | Live trapping | 48 (35 dusky-headed parakeets, 13 Tui parakeets) | Serology (CFT, Latex agglutination, EBA) | C. psittaci (methods not spp-specific) • 0% seroprevalence using any method | N/A | Gilardi et al., 1995 [85]  
Fulmars (Fulmarus glacialis) | Procellaridae | Faroe Islands | Non-flying juveniles sampled | 431 (juveniles) | PCR (cloacal swabs) ompA sequencing | C. psittaci • 10% C. psittaci prevalence (range from 7% to 21% between locations) • 6BC strain identified in all positive samples | NR | Hermann et al., 2006 [74]  
Great tits (Parus major; n = 318), blue tits (Parus caeruleus; n = 43), marsh tits (Parus palustris; n = 32), coal tits (Parus ater; n = 3), willow tits (Parus montanus; n = 3) | Paridae | Germany | Live trapping (n = 389), necropsy (n = 6) | 395 | Inoculation and culture (cloacal and pharyngeal swabs)  
Organ tissues (necropsied birds) | Chlamydia • 54.3% Chlamydia prevalence  
• Shedding varied according to swab site  
• Prevalence varied between host species; highest prevalence in blue tits, followed by great tits, then marsh tits  
• Repeated sampling of n = 38 individuals; 60.5% changed in Chlamydia status | N | Holzinger-Umlauf et al., 1997 [80]  
Chinstrap penguins (Pygoscelis antarctica) and Magellanic penguins (Spheniscus magellanicus); seabirds* | Spheniscidae, Stercorariidae, Laridae, Procellariidae, Chionidae | Antarctic, Chile | Live trapping (penguins), fresh faeces (seabirds) | 527 (264 penguins; 263 seabirds) | PCR (cloacal swabs and faeces)  
Sequencing | C. psittaci | 18% Chlamydia prevalence (Antarctica)  
• No C. psittaci detected in birds in Antarctica  
• 10% C. psittaci prevalence (Chile) | NR | Isaksson et al., 2015 [77]  
43 species; 14 different orders* | Corvidae, Scolopacidae, Columbidae (…)* | South Korea | Rehabilitation centres | 225 | PCR (tracheal swabs and tissues) ompA sequencing | C. psittaci | 1.8% C. psittaci prev. (rook (Corvus frugilegus), Korean magpie (Pica serica), feral pigeon)  
• 0.9% C. gallinacea prev. (woodcock (Scolopax rusticola)) | NR | Jeong et al., 2017 [36]  
Raptors: osprey (Pandion haliaetus); great horned owl (Bubo virginianus); red-tailed hawk (Buteo jamaicensis) (others not listed) | Accipitridae, Pandionidae, Strigidae (others not listed) | USA | Rehabilitation centres | 82 | PCR (oral and cloacal swabs)  
Sequencing | C. psittaci | 1 osprey was C. psittaci-positive  
1 red-tailed hawk was Ca, Rhabdochlamydia spp. positive | NR | Jouffroy et al., 2016 [75]  
35 species; 15 orders* | Anatidae, Accipitridae, Passeridae (…)* | Poland | Hunting, culling programs, fishing bycatch, wildlife rehabilitation centres, community submissions | 369 | PCR (combined tissues and conjunctival swabs)  
Sequencing | Chlamydia (all species) • 7.3% Chlamydia prevalence  
• C. psittaci and C. trachomatis identified  
• Chlamydia positive birds identified across eight orders | N | Krawiec et al., 2015 [52]
| Pathogen Species | Host Family | Country | Sampling Method | Sample Size | Pathogen Detection | Prevalence/Results |
|------------------|-------------|---------|-----------------|-------------|--------------------|--------------------|
| Hawks, *Buteo* genus | Accipitridae | USA | Live trapping | 297 | PCR (conjunctival, choanal, and cloacal swab) Serology (EBA) | Chlamydiaceae | 14% Chlamydia prev. (2 positive red-tailed hawks, 2 positive Swainson's hawks (*Buteo swainsoni*)) 0% seroprevalence |
| Feral pigeons; house sparrows | Columbidae | Iran | NR | 150 (75 pigeons; 75 house sparrows) | PCR (cloacal swabs) ompA sequencing | C. psittaci | 25.3% C. psittaci prev. in pigeons 18.6% C. psittaci prev. in house sparrows Genotypes A and B identified |
| Feral pigeons, Eurasian collared doves (*Streptopelia decaocto*), wood pigeon (*Columba palumbus*) | Columbidae | Switzerland | Pigeon lofts, re-habilitation centres, culling programs | 431 | PCR (choanal/cloacal swabs and liver samples) DNA microarray assay 16S sequencing MLST | C. psittaci Chlamydiaceae | 14.1% Chlamydiaceae prev. (feral pigeons) 5.1% Chlamydiaceae prev. (collard dove) 5.7% Chlamydiaceae prev. (wood pigeon) Prevalence in feral pigeons varied by location 57.6% positive samples were C. psittaci, 5.4% of positive samples were C. avium |
| 7 species, order Psittaciformes, Anseriformes, Passeriformes* | Cacatuidae, Anatidae, Rallidae, Artamidae | Australia | NR | 124 | PCR (conjunctival, choanal, and cloacal swabs) Cell culture | C. psittaci | 0% prevalence; no wild birds tested positive |
| Galapagos doves (*Zenaida galapagoensis*) and feral pigeons | Columbidae | The Galapagos Islands, Ecuador | Live trapping | 133 (105 Galapagos doves, 28 feral pigeons) | PCR (cloacal swabs) | C. psittaci | 6% C. psittaci prev. (Galapagos doves) 0% C. psittaci prev. (feral pigeons) Geographic variation in prev. (all positive cases occurred on one island) |
| Ring-necked parakeet | Psittacidae | France | Live trapping | 85 | PCR (cloacal swabs) | C. psittaci C. avium Chlamydiaceae | 7.1% Chlamydiaceae prevalence The chlamydial species was only identified to species level in one individual (C. avium) |
| Red-tailed Amazon parrot (*Amazona brasiliensis*) | Psittacidae | Rasa Island, Brazil | Nestlings (breeding monitoring) | 117 (nestlings) | PCR (tracheal and cloacal swabs) | C. psittaci (method not spp specific) | 1.2% prevalence (one positive sample identified) |
| Feral pigeons | Columbidae | Germany | Management project | 570 | PCR (cloacal swabs and faeces) DNA microarray ompA sequencing | C. psittaci Chlamydiaceae | 14.6% Chlamydiaceae prev. (swabs) and 10.4% C. psittaci prev. (swabs) Faecal prev. higher than swabs Temporal variation in Chlamydiaceae prev.; 9.3% prev. in 2009, compared to 19.3% in 2010 C. pecorum, C. abortus, C. trachomatis, and unclassified Chlamydiaceae also identified |
| Feral pigeons | Columbidae | Thailand | NR | 407 | PCR (tracheal and cloacal swabs), ompA sequencing | C. psittaci | 10.8% C. psittaci prev. Genotype B identified |

NR = Not Reported
| Pathogens | 2021, 10, 948 | 10 of 26 |
|-----------|--------------|----------|
| **Raptors; 15 species*** | 
| Accipitridae, Falconidae, Tytonidae, Strigidae, Pandionidae | Germany | Veterinary submissions | 39 | PCR (lung and spleen) | C. psittaci | 74% C. psittaci prevalence | No association of infection with sex, age, or year | NR | Schettler et al., 2003 [93] |
| **Raptors; 346 diurnal birds of prey; 55 owls)** | 
| Accipitridae, Pandionidae, Strigidae, Tytonidae, Falconidae | Germany | Rehabilitation centres | 428 | Serology (ELISA) | C. psittaci | 63% seropositivity | Age association with seroprevalence; older birds more likely to test seropositive | NR | Schettler et al., 2001 [94] |
| **10 species* majority of birds tested were Columbiformes** | 
| Columbidae, Turdidae, Anatidae (…*) | U.K. | Rehabilitation centre | 43 | PCR (cloacal swabs) | C. psittaci | 11.6% C. psittaci prevalence | All positive birds were Columbiformes | Y | Sharplees and Baines, 2009 [95] |
| **42 species*** | 
| Columbidae, Passeridae, Fringillidae (…)* | Switzerland | Rehabilitation centre | 339 | PCR (choanal and cloacal swabs, faecal swabs) ompA sequencing | C. psittaci Chlamydiaceae | 0.9% Chlamydiaceae prev. (all Columbidae) | No other birds tested positive | NR | Stalder et al., 2020 [31] |
| **Raptors (16 species); corvids (six species)** | 
| Accipitridae, Falconidae, Strigidae, Tytonidae, Corvida | Switzerland | Rehabilitation centres, community submissions, culling programs | 594 (341 raptors, 253 corvids) | PCR (choanal and cloacal swabs, faecal swabs) ompA and 16S sequencing | C. psittaci Chlamydiaceae C. buteonis | 23.7% Chlamydiaceae prev. (corvids) | 5.9% Chlamydiaceae prev. (raptors) | N | Stalder et al., 2020 [34] |
| **Feral pigeons** | 
| Columbidae | Poland | NR | 101 | PCR (cloacal and pharyngeal swabs) ompA sequencing | C. psittaci | 3.9% C. psittaci prevalence | More pigeons were co-infected with C. psittaci and pigeon circovirus than with C. psittaci alone | N | Stenzel et al., 2014 [96] |
| **Crimson rosella** | 
| Psittacidae | Australia | Live trapping | 136 | PCR (cloacal swabs) Serology (ELISA) 16S sequencing | C. psittaci Chlamydiaceae C. gallinacea | 27.7% Chlamydiaceae prevalence | 6.2% C. psittaci prev. and 4.6% C. gallinacea prev. | N | Stokes et al., 2020 [46] |
| **7 species; order Psittaciiformes** | 
| Psittacidae, Cacatuida | Australia | Live trapping | 132 | PCR (cloacal swabs) Serology (ELISA) 16S and ompA sequencing | C. psittaci Chlamydiaceae C. gallinacea | Overall Chlamydiaceae prevalence was 39.8% | C. psittaci prevalence was 9.8%, and C. gallinacea prevalence was 0.8% | N | Stokes et al., 2020b [33] |
| **Long-billed corella (Cacatua tenuirostris), little** | 
| Cacatuida | Australia | Live trapping and rehabilitation centres | 55 | PCR (choanal/cloacal swabs) | C. psittaci | None PCR positive, but NGS identified C. psittaci in one little corella; hence, overall prevalence was 1.8% | Y | Sutherland et al. 2019 [63] |
| Species                                      | Family               | Country | Methodology                                      | Species Identified                  | Chlamydiaceae prev. (%) |
|----------------------------------------------|----------------------|---------|-------------------------------------------------|-------------------------------------|-------------------------|
| Corella                                      | Accipitridae, Anatidae, Corvida (…) | Poland | Rehabilitation centres; some free-living birds captured | PCR (cloacal or faecal swabs) ompA and rRNA sequencing | 14.8% C. abortus                  |
| Sulfur-crested cockatoo                      | Cacatua galerita     | Germany | Community veterinary submissions                | PCR (pooled organs)                | 19.7% C. abortus                  |
| Red-tailed Amazon parrot                     | Psittacidae          | Brazil  | Nestlings (breeding monitoring)                 | PCR (cloacal and oropharyngeal swabs) | 4% C. psittaci C. abortus intermediate isolates identified |
| African sacred ibis                          | Threskiornithidae    | France  | Culling program                                 | PCR (cloacal swabs) Culture and inoculation | 0% prevalence            |
| Greater flamingo                            | Phoenicopteridae     | France  | Live trapping                                   | PCR (cloacal swabs) Isolation and cell culture Sequencing | 30.9% (125/404) chlamydial positive, but not for known species |
| Feral pigeons                               | Columbidae           | Thailand| Live trapping (public locations)                | PCR (cloacal swabs) Isolation and inoculation | 1.3% C. psittaci prevalence    |
| Songbirds (n = 527; 11 families)             | Columbidae, Fringillidae, Turdidae (…) | Switzerland | Collected through avian influenza surveillance, live trapping (pigeons), and hunters (coromans) | PCR (cloacal swabs) 16S Sequencing | 3.3% C. psittaci prev. in feral pigeons |
| Pigeons (n = 84; Columbidae)                 | Columbidae, Fringillidae, Turdidae (…) | Switzerland | Live trapping (public locations)                | PCR (cloacal swabs) 16S Sequencing | 0.4% C. abortus                  |
| Waterfowl (n = 442; 5 families)              |                      |         |                                                 |                                     | 4% C. abortus                  |

*For the list of all species and families tested, refer to the publication. **Y indicates Yes; N indicates No; NR indicates Not Recorded.
4. Global Chlamydial Distribution

4.1. Europe

There have been studies of chlamydial presence and diversity in wild birds in several countries in Europe, with multispecies surveillance carried out to a larger degree in Switzerland and Poland (Table 1). Many reports from Europe are of feral pigeon populations, but there has also been testing of other avian taxa, including waterfowl [29], songbirds [81], corvids [29,34], raptors [34,93,94], seabirds [12,74], feral ibis [50] and ring-necked parakeets [49]. Indeed birds have been found positive for *Chlamydiales* in all these taxa, with a range of different chlamydial organisms identified. *C. psittaci* has also been identified in most of the taxa above. *C. avium* has been found in pigeons in Switzerland, Italy, and the Netherlands [47,48,97]. *C. avium* has also been isolated from a ring-necked parakeet in France [49] and from a single mallard (*Anas platyrhynchos*) in Poland [29]. *C. gallinacea*, although widespread in poultry across Europe [38,40,98], has not yet been identified in European wild bird populations, and neither has *C. buteonis*, a recently described species, although screening for *C. buteonis* has now been undertaken in Switzerland [34]. *C. c. ibidis*, the main other chlamydial species affecting birds, was first isolated from wild birds in Europe (specifically, feral sacred ibises [50]). Non-classified *Chlamydiaceae* have been found in waterfowl and corvids in Poland [29].

4.2. Asia

Across Asia, feral pigeons have been tested for *C. psittaci* in Thailand, India, Japan, Korea, and Iran, with prevalence ranging from 1% to 25% [36,61,70,71,90,99]. Other species testing positive for *C. psittaci* include ring-necked parakeets (26.3%) and crows (18%) (*Corvus splendens*) in India [61], house sparrows (*Passer domesticus*) (14.8%) in Iran [90], and rooks (*Corvus frugilegus*) and Korean magpies (*Pica serica*) in South Korea [36]. There is little evidence of large numbers of any other avian species being tested. Other chlamydial species have been identified in wild birds in Asia, including *C. pecorum* and *C. gallinacea* (in pigeons and woodcock, respectively) [36,67] and an uncharacterised chlamydial species closely related to *C. avium* (in pigeons) [71]. Interestingly, while there are numerous studies of *Chlamydia* in captive birds in China [42,100–102], there is little evidence of testing wild birds. Since a diverse range of *Chlamydia* has been identified in Chinese poultry [42], it is plausible that a diverse range of *Chlamydiales* both within and outside the *Chlamydia* genus are circulating in wild birds in China and in other countries across Asia.

4.3. North America

In the USA, there have been suspected epizootics of psittacosis, in juvenile white-winged doves (*Zenaida asiatica*) in Texas [103], and in California gulls (*Larus californicus*) and ring-billed gulls (*Larus delawarensis*) in North Dakota [19], with *C. psittaci* found in many of the birds sampled at necropsy [19,103]. In recent years, a mortality event in rose-faced lovebirds (*Agapornis roseicollis*) prompted screening of wild birds at feeders in Arizona, where several bird species (including feral pigeons, house sparrows, and Inca doves (*Columbina inca*)) tested positive for *C. psittaci* [88]. There has been some raptor surveillance in the USA; a *Chlamydiaceae* prevalence of 1.4% was found in wild hawks in the *Buteo* genus [37], with the chlamydial species identified later characterised as *C. buteonis* [5]. Additionally, *C. psittaci* and another member of the *Chlamydiaceae, Candidatus Rhabdochlamydia* spp., were identified in an osprey (*Pandion haliaetus*) and a red-tailed hawk (*Buteo jamaicensis*), respectively [75]. In Canada, feral pigeons have been found infected with *C. psittaci* [104]. To our knowledge, the other avian *Chlamydia* (*C. gallinacea* and *C. avium*) have not been found in wild birds in North America: given that *C. gallinacea* has been identified in free-ranging poultry in the USA [44], it is plausible that the absence of other avian *Chlamydia* in wild birds reflects a lack of testing, rather than true absence.
4.4. South America

In South America, at least five wild parrot species have been tested for chlamydial infection, with these species possibly targeted due to the high prevalence of *C. psittaci* in many captive parrots [7] and historical cases of human psittacosis being linked to the importation of South American parrots [15,105]. Wild red-tailed Amazon parrot (*Amazona brasilienensis*), blue-fronted Amazon parrot (*Amazona aestiva*), and hyacinth macaw nestlings have been tested in Brazil [62,82,83]. Prevalence was 0–1.2% in red-tailed Amazon parrot nestlings [82,83] compared to 6.3% and 26.7% prevalence in blue-fronted Amazon nestlings and hyacinth macaws, respectively [62]. There are few studies where wild adults have been sampled (Table 1). All adult studies included only serological testing; there was no evidence of chlamydial antibodies found in dusky-headed parakeets (*Aratinga weddellii*) or tui parakeets (*Brotogeris sanctithomae*) in Peru [85] or blue-fronted Amazon parrots in Bolivia [84]. There is thus little to no evidence of chlamydial infection in wild adult South American parrots, although *C. psittaci* has been identified in captive populations of adult Amazon parrots [106], including in birds recovered from the wildlife trade, where at the same location, *C. psittaci* caused up to 97% mortality in nestlings [107].

In Brazil, studies have tested feral pigeons for *C. psittaci*, with prevalence ranging between 11.7% and 16.8% [68,69,108]. There is substantial variation between study locations; in São Paulo prevalence of *C. psittaci* was 37.8% compared to only 6.1% in Botucatu [69]. Although there are several Columbiformes species present across South America, including introduced feral pigeons, there are few studies from other countries testing feral pigeons or other Columbiformes for *C. psittaci*. Interestingly, 5.9% (6/102) of Galapagos doves (*Zenaida galapagoensis*) tested positive for *C. psittaci* on the Galapagos Islands, Ecuador, although none of the 28 feral pigeons tested positive in the same study [92]. Considering birds outside the Psittaciformes and Columbiformes, *C. psittaci* has been identified in seabirds in Chile during screening carried out as a comparison with surveillance in Antarctica [77]. There is little to no evidence of testing for chlamydial species other than *C. psittaci* in South America or molecular sequencing of any chlamydial strains identified.

4.5. Australasia/Oceania

Signs of psittacosis were reported in wild Australian parrots obtained from dealers as early as the 1930s [109] and again in wild parrots during the 1950s, at 10.6% prevalence, with prevalence varying between host species [60]. More recent estimates of *C. psittaci* prevalence in wild Australian parrots are often lower, usually ranging between 0% and 1.8% [32,63,91], although some studies have reported prevalence estimates between 6.2% and 9.8% in common species such as galahs and crimson rosellas [33,46]. While the majority of wild bird studies to date in Australia have focused on parrots (Table 1), waterfowl, and other host species have been sampled [32,91]. Where species other than parrots have been tested, no birds tested positive in either study except for a single superb lyrebird (*Menura novaehollandiae*) [32,91]. In New Zealand, *C. psittaci* has been identified in feral pigeons and other Columbiformes, in a native hihi (*Notiothyrsus cincta*) [89], and in two wild duck species sampled in a wildlife rehabilitation centre [110]. As in most other regions, the majority of Australasian studies have only tested for *C. psittaci*, without testing for other *Chlamydialiae*. However, two recent studies in Australia have reported a greater diversity of chlamydial organisms, including *C. gallinacea* in two wild parrot species [46,64], as well as *Chlamydialiae* from other orders including the *Parachlamydialiae* [33,46]. As next-generation sequencing (NGS) is increasingly used to test samples from wild Australian birds [28,63], it is likely that a greater diversity of *Chlamydialiae* may soon be described.

4.6. Africa and Antarctica

There are very limited data available on the distribution of chlamydial bacteria in wild birds in Africa. Surveillance of pelicans (*Pelecanus onocrotalus*) in South Africa found
no positive individuals [87]. There is limited evidence to suggest that Chlamydia are present in wild birds in Egypt [111]. However, we were unable to find any other studies of chlamydial infection in wild African birds. Interestingly, chlamydial organisms have been identified in chinstrap penguins (Pygoscelis antarcticus) and seabirds from Antarctica [77] with an 18% prevalence of order Chlamydiales, although C. psittaci was not identified.

5. Host Disease and Fitness

5.1. Signs of Disease and Survival

The impacts of C. psittaci infections in wild birds are rarely documented [79], with reported effects of other chlamydial species even rarer. Many wild bird populations are thought to harbour chlamydial infections without being visibly affected [7]. However, suspected epizootics have occurred, such as in white-winged doves and various gull species in the USA [19,103], suggesting that chlamydial disease can also impact wild populations [112]. For the majority of studies discussed in this review, signs of infection were not recorded (Table 1), and across the literature, the majority of reported clinical signs are from captive birds (principally poultry and parrots) [11,14]. However, there are some reports of clinical signs in wild individuals, primarily from birds tested at rehabilitation centres or wildlife rescue clinics [95,107]. Wildlife health centres in the U.K. and Australia have reported wild C. psittaci-positive birds (specifically pigeons, a crimson rosella parrot and a superb lyrebird) being ‘emaciated’ [32,95], with the crimson rosella also presenting with diarrhoea [32]. Surprisingly, neither of these studies reported overt signs of respiratory distress in infected birds, although these are among the main disease signs found in captive birds [13,14]. Infected parrots in other Australian studies have also been found emaciated with diarrhoea [28,113,114]. However, some of these reports [28,114] are case studies of individuals who presented with severe clinical signs and were subsequently specifically tested at veterinary clinics. As such, they are likely to be cases with a very high bacterial load, which may not be representative of naturally infected wild individuals. Contrasting to this, in recent studies of apparently healthy wild Australian parrots, there was no significant association found between infection and three indices of body condition across the four host species tested [33,46]. There are few observations of infected wild parrots elsewhere globally for comparison, but hyacinth macaw nestlings in Brazil, which had between 9% and 27% prevalence depending on sample type, also showed no clinical signs [62]. However, captive studies have demonstrated that the same host species can suffer both mild and severe consequences of chlamydial infection. For example, high rates of C. psittaci infection have been found in healthy captive Amazon parrots (Amazona genus) in breeder collections [106] but the same genus has also suffered mortality rates of up to 97% when infected under stressful conditions [107]. Indeed, in most cases where C. psittaci has caused acute death or severe disease, for parrots at least, affected individuals were already stressed or immunocompromised, with many having recently been captured from the wild [107,115] or being co-infected with other pathogens, such as beak and feather disease virus (BFDV) [32].

It is generally considered that wild pigeons are relatively unaffected by C. psittaci, because they excrete C. psittaci without showing signs of disease [7,66]; moreover, pigeons in captivity often harbour subclinical infections with periodic shedding [18,22]. Some feral pigeon populations have only been sampled indirectly through faecal sampling, which limits understanding of the links between individual infection and disease signs [48,67]. Where there has been direct sampling (i.e., through using cloacal or choanal swab sampling [47,71]), some studies specifically state that there were no signs of infection ([68]; studies described in [22]). In most reports, however, disease signs were not recorded, and the effects of chlamydial infection on feral pigeon populations have not, to our knowledge, been systematically investigated. It is plausible that signs of disease in feral pigeons are similar to in captive pigeons, which often show clinical signs only when concurrent infections are present [116].
In the rare instances where clinical signs have been reported for other orders or species (i.e., other than Psittaciformes and Columbiformes) findings vary widely between studies and study populations. For example, a retrospective study in the U.K. carried out post-mortem examination of Passeriformes with signs of chlamydiosis and found evidence of histological lesions in 42% (8/19) birds that were *C. psittaci*-positive [81], suggesting that *C. psittaci* may also cause disease in passerine species including great tits and dunnocks. On the other hand, Holzinger-Umlauf et al. (1997) reported a high prevalence in tits (Paridae; 54%) and great tits specifically (53%) with no clinical signs [80], and Krawiec et al. (2015) similarly identified *C. psittaci*-positive passerine birds without signs of chlamydial disease [52]. Several factors may cause variability in clinical signs between populations. Individual conditions can cause marked variation in the course of infection, as shown by captive studies [14], and host species can suffer different disease signs when infected with different strains. An additional consideration is that the authors who carried out the retrospective post-mortem analysis only targeted passerine birds with clinical signs of disease; they did not test any clinically healthy birds [81]. Considering post-mortem studies from other species, there have been variable findings at necropsy; organ inflammation and hepatitis have been reported in pigeons and gulls [19,104], whereas other studies reported no pathological changes [52].

Concurrent infections of *C. psittaci* with other pathogens have been observed repeatedly in wild birds. More than half of the *C. psittaci*-positive passerine birds examined by Beckmann et al. (2014) had concurrent infectious diseases, including avian pox and trichomonas [81]. In other hosts, *C. psittaci* has also been found occurring concurrently with other infections, such as with BFDV in wild Australian parrots [32,63] and pigeon circovirus in feral pigeons [96]. There is a lack of longitudinal data available from wild birds to test whether chlamydial infection may predispose individuals to other infections (i.e., whether birds are infected with *C. psittaci* first) or whether birds immunosuppressed by other infections are then more likely to become infected with *Chlamydia*. Indeed, any repeated capture and testing of wild birds for their chlamydial infection status is rare. However, repeated testing has been carried out on recaptured tit species (*Parus* genus; Passeriformes) in Germany [80] and recaptured parrots (cockatoos and rosella (*Platycercus*) species) in Australia [33]. In both studies, recaptured individuals frequently changed in their *Chlamydia* status, suggesting that wild birds may suffer persistent infections and shed *Chlamydia* intermittently or may suffer repeated infections [33,80]. Persistent infections have also been proposed in Canada geese (*Branta canadensis*), which were found to have a high antibody prevalence (93.8%) in conjunction with lower levels of bacterial shedding, and no clinical signs [73].

The limited data available on chlamydial species other than *C. psittaci* (i.e., *C. gallinacea, C. avium*, or *C. buteonis*) in wild birds means that their effects on host health and survival are unknown. Indeed, the effects of these infections remain largely unknown even in captive birds [4], although chickens experimentally infected with *C. gallinacea* showed reduced bodyweight gain [42], and *C. avium* is hypothesised to cause depression, respiratory disease, and subsequent mortality in parrots [117].

5.2. Reproduction and Fitness

There is little information on whether chlamydial infections affect reproductive success in wild birds. One study of crimson rosellas found that breeding birds were much less likely to be infected compared to non-breeding birds [46], which suggests that infection may reduce the likelihood of breeding in this species. However, further data quantifying the effects of chlamydial infection on this population are needed to test this hypothesis; it is possible that the different infection rates were instead due to seasonal effects such as changes in social behaviour or breeding stress. Alternatively, there could be sub-lethal population-level effects of chlamydial infections, in addition to the reported epizootics [19,103]. Sub-lethal population impacts of infection are much less likely to be detected; wildlife disease sampling is generally biased towards mass die-offs [118]; hence, more
subtle population-level effects are likely to be missed, as are sporadic cases with low-level mortality [13]. For instance, captive studies have shown that younger birds are generally more susceptible to C. psittaci infection than adults [14], with evidence to suggest that the same could be true in some wild bird populations [46,103]. A chlamydial epizootic affecting wild white-winged doves resulted in an apparent population reduction of approximately 75%, where juvenile white-winged doves were disproportionately affected [103]. Such events could affect recruitment and breeding in subsequent years and may result in an altered population age structure. However, apart from the two reports described above, we were unable to find any observations or discussion of whether chlamydial infections may affect reproduction and population size.

6. Conservation Implications

Since C. psittaci is known to cause severe disease in at least some avian hosts, it is plausible that it may result in population declines in wild bird populations, particularly when populations comprise highly susceptible hosts (such as immunocompromised or inbred individuals) or when combined with additional stressors or concurrent infections. The same may be true for other Chlamydiales species, although their pathogenicity remains to be investigated. Chlamydial infection in certain avian populations may therefore be of conservation concern, particularly in hosts such as parrots, which are one of the most highly threatened bird orders [59], are known to suffer frequent C. psittaci infections [7,33] and can subsequently suffer high mortality [107,115]. In parrots and other birds, small, highly threatened populations that may have lost endemic pathogens may be particularly at risk of infection via pathogen spill-over from sympatric species, as suggested recently with BFDV in the critically endangered orange-bellied parrot (Neophema chrysogaster) [119].

Conservation concerns may also arise from the host specificity in chlamydial strains, with some genotypes occurring more frequently in certain orders of birds, and varying in virulence [7]. Strains that cause no clinical signs in one bird species can potentially cause severe disease in other host species; for example, in captive turkeys in the USA, experimental inoculation with a turkey strain from the same region caused much less severe disease compared to a parrot strain, and even compared to a turkey strain from Europe [120]. Consequently, if chlamydial strains associated with particular hosts are introduced into naïve populations or alternative hosts, they could potentially cause severe disease and population declines. Invasive species and infectious diseases are well-known causes of species declines and extinctions [121], and if an invasive species has a high chlamydial infection rate, it is possible they could infect a naïve host population and cause severe population impacts. For example, feral Canada geese are a widespread invasive species in Europe [122], which have a C. psittaci prevalence of up to 58%, seroprevalence of 94%, and show no clinical signs [73]. Species such as this may thus represent a potential reservoir for other host species. A newly proposed chlamydial species, Ca. C. ibidis has been isolated from another highly invasive species, the sacred ibis [50]; it is plausible that novel chlamydial species from this host could be transmitted to naïve hosts.

In addition, human-induced habitat change can increase stress on wild populations [123]. When the availability of suitable habitat for birds is reduced (such as through urbanisation, agricultural development, or climate change), birds can be forced into closer proximity with conspecifics and other species, resulting in higher population densities and increased social interaction, as well as changes in food availability and nutritional deficiencies [123]. Increased stress can affect host condition and reduce tolerance of infection [124] and can make birds more susceptible to chlamydial disease [15]. Furthermore, as stress increases chlamydial shedding [14,15], stressed birds may shed Chlamydia more frequently, favouring further transmission and environmental contamination. Habitat destruction and other stressors (including human encroachment) are already suspected to exacerbate chlamydial infection and disease in koalas (Phascolarctos cinereus), which are
otherwise often asymptomatic, with little impact of chlamydial infection on wild populations [124,125]. The presence of additional stressors may similarly exacerbate impacts of chlamydial infection in wild bird populations.

7. The Role of Wild Birds in Zoonotic Transmission

7.1. Evidence and Risk Factors for Zoonotic Transmission

Most reported cases of human psittacosis result from direct contact with birds or bird material, such as through handling infected birds or inhalation of respiratory secretions or faecal particles [15]. Most cases of human psittacosis are suspected to be contracted through contact with captive birds [126–128]; however, there are suspected cases due to direct and indirect contact with wild birds; a systematic review of human psittacosis case-control studies revealed that 16% of the articles included considered that direct or indirect contact with wild birds was a potential source of infection [129]. There are several cases where human infection is suspected from environmental exposure to, or handling of, feral pigeons [22,130–133], although direct testing of feral pigeon populations within the same locality is rarely carried out to test this hypothesis.

Environmental exposure or direct contact with wild birds other than feral pigeons have been hypothesised sources of infection following case-control studies in Sweden and Australia. In Sweden, two studies identified cleaning wild bird feeders and exposure to bird faecal material to be risk factors for human psittacosis [134,135]. A few years prior to this, bird ringers in Sweden were tested for chlamydial antibodies; however, none showed evidence of seroconversion to C. psittaci, despite a history of directly handling birds [136]. In Australia, direct contact with wild birds (primarily parrots) and mowing lawns without a grass catcher were identified as risk factors for human infection [8,9,137]. In the Blue Mountains, a region of Australia where human psittacosis is considered endemic, the same strain of C. psittaci was identified in six humans and a wild crimson rosella parrot [28], and three humans working in a veterinary clinic contracted psittacosis following their handling of an infected parrot [114]. Studies from this region of Australia therefore provide some of the best evidence for possible zoonotic transmission of C. psittaci from wild birds to humans.

While most human cases of psittacosis with a confirmed association with wild birds have involved close contact with and handling of wild birds (e.g., wild birds brought into vet surgeries [109]), as discussed above, some cases have been linked to cleaning wild bird feeders [135] and mowing lawns without a grass catcher [9]. This highlights the potential benefits of greater public awareness and perhaps proactive human or wild bird surveillance in communities suspected at risk (such as the proactive surveillance described in [8]). This surveillance could target locations where humans come into close contact with birds through feeding, such as designated wildlife feeding areas or recreational sites where birds and humans congregate in close proximity [138,139]. Urbanisation can also increase the frequency of human-wildlife interactions [140]. In many countries, known chlamydial hosts such as feral pigeons and ring-necked parakeets thrive in city environments [141,142], and in Australia, the abundance of some native parrot species (such as rainbow lorikeets (Trichoglossus moluccanus) and sulfur-crested cockatoos (Cacatua galerita)) are also increasing in suburban areas [143,144]. At such locations where habitat change or urbanisation results in increased human presence and shifts in local bird abundance, there may be increased opportunities for zoonotic disease transmission, which may warrant targeted surveillance. An additional factor to consider when assessing zoonotic transmission risk is seasonality; only a few studies of wild birds investigate how chlamydial prevalence changes across seasons and years (Table 1; [10,43,63]), although temporal variation in host infection rates could affect the likelihood of zoonotic spill-over.
7.2. Transmission Involving Poultry and Agriculture

It is plausible that wild birds could be a reservoir for chlamydial infections in poultry, and subsequently of health concern to farm workers and consumers. Wild birds have previously been implicated in poultry infections [98,145], with transmission proposed via environmental contamination of feed or equipment [15]. On the other hand, serological analysis indicates that chlamydial exposure can be very high in poultry (90%–100%) [146], and infection is considered endemic in some poultry systems, such as in the turkey industry [11]. It is possible that poultry species are able to maintain chlamydial infection within a flock without the need for any maintenance reservoir host. Indeed, pathogen surveillance in sympatric wild and domesticated felid species in the USA suggests that inter-species transmission is relatively rare and that following sporadic cross-species transmission events, pathogen transmission becomes self-sustaining within the recipient host population [147]. Given that direct transmission is likely to be the most common route of chlamydial transmission and poultry are kept at relatively high densities (particularly at night, when kept in sheds), self-sustaining transmission is likely to facilitate rapid transmission and maintenance of chlamydial infection in poultry systems. Finally, while there is usually a focus on wildlife species being the reservoir host, it is also plausible that chlamydial bacteria are transmitted from poultry to wild birds, particularly on free-range farms where feeding stations are accessible to wild birds. For instance, C. gallinacea, a chlamydial species primarily associated with chickens, has been identified in two wild Australian parrot species [46,64].

There is evidence for C. psittaci spill-over from wild birds to horses and thereby to humans in Australia, with a highly virulent strain of C. psittaci associated with equine reproductive loss [148] and subsequently disease in humans [21]. This study provided the first evidence for mammal to mammal transmission of C. psittaci [149] and has since prompted further testing of horses in Australia [150,151].

8. Recommendations for Future Research

It is well established that C. psittaci is present in wild bird populations, is globally distributed with a broad host range, and that other chlamydial bacteria are likely to be similarly widespread. However, the true prevalence of chlamydial infections in wild bird populations is often unknown, particularly outside Europe, where less chlamydial surveillance has been carried out. Globally, there is a need for more proactive screening or active surveillance of wild bird populations, as opposed to convenience sampling through veterinary or community submissions, wildlife rehabilitation centres, or faecal sampling. Such methods can be biased and may only detect a subsample of wild bird populations. There are some avian taxa, specific examples including waterfowl, crows, and raptors [29,34,73], which are quite frequently found positive for chlamydial infection but have received less attention as chlamydial hosts compared to parrots and pigeons. It may be worth screening more of these birds from different regions to test whether this is a global occurrence. This surveillance may be of particular importance given the identification of new chlamydial species (e.g., C. buteonis) [5] of unknown pathogenicity. Additionally, while wild birds are increasingly being tested for multiple chlamydial species (examples including [28,30,49]), some studies still only carry out targeted screening for C. psittaci. To thoroughly investigate the diversity of Chlamydiales present within a host, it would be useful to use a broad spectrum pan-Chlamydiales PCR and a combination of either species-specific PCR protocols or sequencing. Such an approach has been used to successfully investigate the diversity of Chlamydiales present in wild ungulate populations [55].

Longitudinal studies are needed to investigate the potential impact of C. psittaci and other chlamydial infections on bird survival, reproduction, and so fitness. Although the non-specificity and variability of clinical signs make investigating the impacts of chlamydial infection challenging, it would be useful to test for an association of strains with clinical
signs in hosts of particular concern (for either zoonotic or conservation reasons) by recording clinical observations, taking relevant erythrocyte measures to assess haematological changes (for example, haematocrit) [14,152] and measuring changes in enzyme profiles and blood biochemistry [14]. These measures would be of greater value if individuals could be sampled more than once, in order to investigate pathological changes within the same individuals, and mark-recapture data could be used concurrently to assess survival [153]. Ideally, other pathogens would be screened for simultaneously to evaluate the impact of co-infections, particularly as evidence from several bird species indicates that chlamydial infections cause more severe disease in birds suffering concurrent infections [32,81,96]. It would be useful to measure indicators of breeding success and population health alongside this work, to evaluate the population-level impacts of infections. While such proposed investigations (particularly those involving recaptures) are logistically challenging in wild birds, they would provide useful insights into both individual and population effects of chlamydial infection, and such investigations would help to investigate any potential impact chlamydial infections may have on avian conservation.

Finally, in order to investigate suspected transmission pathways, including potential cases of zoonotic transmission, further phylogenetic comparisons are required, particularly of strains within and between hosts. NGS has greatly advanced the opportunities in this field. NGS techniques have already been employed to investigate potential sources of psittacosis outbreaks from wild birds in Australia [28,148] and were recently used to retrospectively investigate the C. psittaci strains present in fulmars following a human psittacosis epidemic that occurred several decades ago [35]. When zoonotic transmission is expected, ideally there should be a coordinated effort between health professionals, wildlife ecologists and veterinarians in order to carry out sampling of humans and wild birds within the same region and within a short time frame, with subsequent sequencing and phylogenetic analysis of any chlamydial strains identified.

9. Conclusions

Chlamydial bacteria have been found on every continent and have been isolated from at least 70 different species of wild bird. While the Psittaciformes and Columbiformes have long been known to harbour chlamydial infections, recent evidence suggests that families including the Corvidae and Accipitridae can also have a high prevalence, with a degree of host specificity in strains. Most chlamydial surveillance has been undertaken in Europe, which is reflected in the greater diversity of chlamydial organisms identified there; with increased surveillance carried out in other regions, it is likely that more chlamydial organisms will be identified and in a broader range of hosts. Most research has focused on zoonotic C. psittaci, but infections with Chlamydiaceae other than C. psittaci are proving to be more common than previously anticipated and sometimes more prevalent than C. psittaci. Increased understanding of the diversity and effects of these bacteria would be beneficial, including their zoonotic potential. Furthermore, although C. psittaci can cause disease in wild birds, there is scarce data on the effects of chlamydial infections on host fitness. It is possible that the majority of chlamydial infections in wild populations are commensal, at least for host-adapted strains, without negatively impacting either the host or sympatric species. However, the occurrence of epizootics, although rare, and the potential for severe disease suggests that chlamydial infections may also be relevant to avian conservation. As the world continues to be impacted by habitat destruction and environmental change, there is an urgent need to better understand fundamental disease ecology in wildlife hosts, particularly of pathogens that are known to be highly capable of host switching. Future surveillance of chlamydial infections in wild birds, such as the investigations outlined above, should offer benefits for wild birds, captive birds, and human health alike.
Author Contributions: Conceptualisation: H.S.S., M.L.B., and A.T.D.B. Original draft preparation: H.S.S. Review and editing: H.S.S., M.L.B., and A.T.D.B. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by Deakin University, the Australian Research Council (LP140100691 and DP180103949), the Holsworth Wildlife Research Endowment, and BirdLife Australia.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All publications or data cited in this review are already in the public domain.

Acknowledgments: We thank Johanne Martens, Yonatan Segal, Ken Walder, Amir Noormoham-madi, Hamish McCallum, Scott Carver and Adam Polkinghorne for useful advice and discussions relating to topics covered in this review.

Conflicts of Interest: The authors declare no conflict of interest.

References
1. Borel, N.; Polkinghorne, A.; Pospischil, A. A Review on Chlamydial Diseases in Animals: Still a Challenge for Pathologists? Vet. Pathol. 2018, 55, 374–390, doi:10.1177/0300985817751218.
2. Everett, K.; Bush, R.; Anderson, A. Emended description of the order Chlamydiales, proposal of Parachlamydiaceae fam. nov. and Simkaniaceae fam. nov., each containing one monotypic genus, revised taxonomy of the family Chlamydiaceae, including a new genus and five new species, and standards for the identification of organisms. Int. J. Syst. Bacteriol. 1999, 49, 415–440.
3. Knittler, M.R.; Sachse, K. Chlamydia psittaci: Update on an underestimated zoonotic agent. Pathog. Dis. 2015, 73, 1–15, doi:10.1093/femspd/ftu007.
4. Cheong, H.C.; Lee, C.Y.Q.; Cheok, Y.Y.; Tan, G.M.Y.; Looi, C.Y.; Wong, W.F. Chlamydiae: Diseases in Primary Hosts and Zoonosis. Microorganisms 2019, 7, 146, doi:10.3390/microorganisms7050146.
5. Laroucau, K.; Vorimore, F.; Aaziz, R.; Solomonson, L.; Hsia, R.C.; Bavoil, P.M.; Fach, P.; Holzer, M.; Wueneschmann, A.; Sachse, K. Chlamydia buteonis, a new Chlamydia species isolated from a red-shouldered hawk. Syst. Appl. Microbiol. 2019, 42, 125997, doi:10.1016/j.syapm.2019.06.002.
6. Laroucau, K.; Ortega, N.; Vorimore, F.; Aaziz, R.; Mitura, A.; Szymanska-Czerwinska, M.; Cicerol, M.; Salinas, J.; Sachse, K.; Caro, M.R. Detection of a novel Chlamydia species in captive spur-thighed tortoises (Testudo graeca) in southeastern Spain and proposal of Candidatus Chlamydia testudinis. Syst. Appl. Microbiol. 2020, 43, 126071.
7. Sachse, K.; Laroucau, K.; Vanrompay, D. Avian Chlamydiosis. Curr. Clin. Microbiol. Rep. 2015, 2, 10–21, doi:10.1007/s40588-014-0010-y.
8. Branley, J.; Weston, K.; England, J.; Dwyer, D.; Sorrell, T. Clinical features of endemic community-acquired psittacosis. New Microbes New Infect. 2014, 2, 7–12.
9. Telfer, B.; Moberly, S.; Hort, K.; Branley, J.; Dwyer, D.; Muscatello, D.; Correll, P.; England, J.; McNulty, J. Probable Psittacosis Outbreak Linked to Wild Birds. Emerg. Infect. Dis. 2005, 11, 391–397.
10. Kaleta, E.F.; Taday, E.M. Avian host range of Chlamyphila spp. based on isolation, antigen detection and serology. Avian Pathol. 2003, 32, 435–461, doi:10.1080/03079450310001593613.
11. Vanrompay, D. Avian Chlamydiosis. In Diseases of Poultry, 14th ed.; Swaine, D.E., Boulianne, M., Logue, C.M., McDougald, L.R., Nair, V., Suarez, D.L., de Wit, S., Grimes, T., Johnson, D.; Kromm, M.; et al., Eds.; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2020.
12. Aaziz, R.; Gourlay, P.; Vorimore, F.; Sachse, K.; Siarkou, V.I.; Laroucau, K. Chlamydiaceae in North Atlantic Seabirds Admitted to a Wildlife Rescue Center in Western France. Appl. Environ. Microbiol. 2015, 81, 4581–4590, doi:10.1128/AEM.00778-15.
13. Andersen, A.; Franson, J. Avian Chlamydiosis. In Infectious Diseases of Wild Birds, 1st ed.; Thomas, N., Hunter, D., Atkinson, C., Eds.; Blackwell Publishing Professional: Ames, IA, USA, 2007; pp. 303–316.
14. Gerlach, H. Chlamydia. In Avian Medicine: Principles and Application, Ritchie, B., Harrison, G., Harrison, L., Eds.; Wingers Publishing, Inc.: Lake Worth, FL, USA, 1994; pp. 984–996.
15. Harkinezhad, T.; Geens, T.; Vanrompay, D. Chlamyphila psittaci infections in birds: A review with emphasis on zoonotic consequences. Vet. Microbiol. 2009, 135, 68–77, doi:10.1016/j.vetmic.2008.09.046.
16. Longbottom, D.; Coulter, L. Animal Chlamydioses and Zoonotic Implications. J. Comp. Pathol. 2003, 128, 217–244.
17. Smith, K.A.; Campbell, C.T.; Murphy, J.; Stobierski, M.G.; Tengelsen, L.A. Compendium of Measures to Control Chlamyphila psittaci Infection Among Humans (Psittacosis) and Pet Birds (Avian Chlamydiosis), 2010 National Association of State Public Health Veterinarians (NASPHV). J. Exot. Pet Med. 2011, 20, 32–45, doi:10.1053/j.jemp.2010.11.007.
18. Andersen, A.A.; Vanrompay, D. Avian chlamydiosis. Scientific and Technical Review of the Office International des Epizooties 2000; 19,396–404.
19. Franson, J.C.; Pearson, J.E. Probable Epizootic Chlamydiosis in Wild California (Larus californicus) and Ring-Billed (Larus delawarensis) Gulls in North Dakota. J. Wildl. Dis. 1995, 31, 424–427.

20. Jelocnik, M.; Branley, J.; Heller, J.; Raidal, S.; Alderson, S.; Galea, F.; Gabor, M.; Polkinghorne, A. Multi locus sequence typing identifies an avian-like Chlamydia psittacci strain involved in equine placentitis and associated with subsequent human psittacosis. Emerg. Microbes Infect. 2017, 6, e7. doi:10.1016/j.emi.2016.135.

21. Chan, J.; Doyle, B.; Branley, J.; Sheppeard, V.; Gabor, M.; Viney, K.; Quinn, H.; Janover, O.; McCready, M.; Heller, J. An outbreak of psittacosis at a veterinary school demonstrating a novel source of infection. One Health 2017, 3, 29–33, doi:10.1016/j.jonheli.2017.02.003.

22. Magnino, S.; Haag-Wackernagel, D.; Geigenfeind, I.; Helmecke, S.; Doce, A.; Pruken-Radovic, E.; Residbegovic, E.; Ilieski, V.; Laroucou, K.; Donati, M.; et al. Chlamydial infections in feral pigeons in Europe: Review of data and focus on public health implications. Vet. Microbiol. 2009, 135, 54–67. doi:10.1016/j.vetmic.2008.09.045.

23. Vanrompay, D.; Butaye, P.; Sayada, C.; Ducutelle, R.; Haesebrouck, F. Characterization of avian Chlamydia psittaci strains using ompl restriction mapping and serovar-specific monoclonal antibodies. Res. Microbiol. 1997, 148, 327–333.

24. Geens, T.; Desplanques, A.; Van Loock, M.; Bonner, B.M.; Kaleta, E.F.; Magnino, S.; Andersen, A.A.; Everett, K.D.; Vanrompay, D. Sequencing of the Chlamyphila psittaci ompA gene reveals a new genotype, E/B, and the need for a rapid discriminatory genotyping method. J. Clin. Microbiol. 2005, 43, 2456–2461. doi:10.1128/JCM.43.5.2456-2461.2005.

25. Andersen, A.A. Serotyping of Chlamydia psittaci Isolates Using Serovar-Specific Monoclonal Antibodies with the Microimmunofluorescence Test. J. Clin. Microbiol. 1991, 29, 707–711.

26. Sachse, K.; Laroucou, K.; Hotzel, H.; Schubert, E.; Ehrlich, R.; Slickers, P. Genotyping of Chlamydia psittaci using a new DNA microarray assay based on sequence analysis of ompA genes. BMC Microbiol. 2008, 8, 63. doi:10.1186/1471-2180-8-63.

27. Read, T.D.; Joseph, S.J.; Didelot, X.; Liang, B.; Patel, L.; Dean, D. Comparative analysis of Chlamydia psittaci genomes reveals the recent emergence of a pathogenic lineage with a broad host range. mBio 2013, 4, doi:10.1128/mBio.00642-13.

28. Branley, J.M.; Bachmann, N.L.; Jelocnik, M.; Myers, G.S.A.; Polkinghorne, A. Australian human and parrot Chlamydia psittaci strains cluster within the highly virulent 6BC clade of this important zoonotic pathogen. Sci. Rep. 2016, 6 1–8. doi:10.1038/srep30019.

29. Szymanska-Czwerwinska, M.; Mitura, A.; Niemczuk, K.; Zareba, K.; Jodko, A.; Pluta, A.; Scharf, S.; Vitek, B.; Aaziz, R.; Vorimore, F.; et al. Dissemination and genetic diversity of chlamydial agents in Polish wildfowl: Isolation and molecular characterisation of avian Chlamydia abortus strains. PLoS ONE 2017, 12, e0174599. doi:10.1371/journal.pone.0174599.

30. Zweifel, D.; Hoop, R.; Sachse, K.; Pospischil, A.; Borel, N. Prevalence of Chlamyphila psittaci in wild birds—potential risk for domestic poultry, pet birds, and public health? Eur. J. Wildl. Res. 2009, 55, 557–581. doi:10.1007/s10344-009-0275-2.

31. Stalder, S.; Marti, H.; Borel, N.; Mattmann, P.; Vogler, B.; Wolfurum, N.; Albini, S. Detection of Chlamydiaceae in Swiss wild birds sampled at a bird rehabilitation centre. Vet. Rec. 2020, 0, e000437. doi:10.1136/vetreco-2020-000437.

32. Amery-Gale, J.; Legione, A.R.; Marenda, M.S.; Owens, J.; Eden, P.A.; Konsak-Illieski, B.M.; Whiteley, P.L.; Dobson, E.C.; Browne, E.A.; Slocombe, R.F.; et al. Surveillance for Chlamydia spp. with Multilocus Sequence Typing Analysis in Wild and Captive Birds in Victoria, Australia. J. Wildl. Dis. 2020, 56, doi:10.7589/2018-11-281.

33. Stokes, H.S.; Martens, J.M.; Walder, K.; Segal, Y.; Berg, M.L.; Bennett, A.T.D. Species, sex and geographic variation in chlamydial prevalence in abundant wild Australian parrots. Sci. Rep. 2020, 10, 20478.

34. Stalder, S.; Marti, H.; Borel, N.; Sachse, K.; Albini, S.; Vogler, B.R. Occurrence of Chlamydiaceae in Raptors and Crows in Switzerland. Pathogens 2020, 9, 724. doi:10.3390/pathogens9070724.

35. Wang, H.; Jensen, J.K.; Olsson, A.; Vorimore, F.; Aaziz, R.; Guy, L.; Ellstrom, P.; Laroucou, K.; Herrmann, B. Chlamydia psittaci in fulmars on the Faroe Islands: A causative link to South American psittacines eight decades after a severe epidemic. Microbes Infect. 2020, 22, 356–359. doi:10.1016/j.micinf.2020.02.007.

36. Jeong, J.; An, I.; Oem, J.K.; Wang, S.J.; Kim, Y.; Shin, J.H.; Woo, C.; Kim, Y.; Jo, S.D.; Son, K.; et al. Molecular prevalence and genotyping of Chlamydia spp. in wild birds from South Korea. J. Vet. Med. Sci. 2017, 79, 1204–1209. doi:10.1292/jvms.16-0516.

37. Luján-Vega, C.; Hawkins, M.G.; Johnson, C.K.; Briggs, C.; Vennum, C.; Bloom, P.H.; Hull, J.M.; Cray, C.; Pesti, D.; Johnson, L.; et al. Atypical Chlamydiaceae in wild populations of hawks (Buteo spp.) in California. J. Zoo Wildl. Med. 2018, 49, 108–115.

38. Laroucou, K.; Vorimore, F.; Aaziz, R.; Berndt, A.; Schubert, E.; Sachse, K. Isolation of a new chlamydial agent from infected domestic poultry coincided with cases of atypical pneumonia among slaughterhouse workers in France. Infect. Genet. Evol. 2009, 9, 1240–1247. doi:10.1016/j.meegid.2009.08.005.

39. Sachse, K.; Laroucou, K.; Riege, K.; Wehner, S.; Dilcher, M.; Creasy, H.H.; Weidmann, M.; Myers, G.; Vorimore, F.; Vicari, N.; et al. Evidence for the existence of two new members of the family Chlamydiaceae and proposal of Chlamydiavium sp. nov. and Chlamydia gallinaeaca sp. nov. Syst. Appl. Microbiol. 2014, 37, 79–88. doi:10.1016/j.syapm.2013.12.004.

40. Heijne, M.; van der Goot, J.A.; Fijten, H.; van der Giessen, J.W.; Kuijt, E.; Maassen, C.B.M.; van Roon, A.; Wit, B.; Koets, A.P.; Roest, H.I.J. A cross sectional study on Dutch layer farms to investigate the prevalence and potential risk factors for different Chlamydia species. PLoS ONE 2018, 13, e0190774. doi:10.1371/journal.pone.0190774.

41. Zocevic, A.; Vorimore, F.; Marhold, C.; Horvatek, D.; Wang, D.; Slavec, B.; Prentza, Z.; Staviansis, G.; Pruken-Radovic, E.; Doce, A.; et al. Molecular characterization of atypical Chlamydia and evidence of their dissemination in different European and Asian chicken flocks by specific real-time PCR. Environ. Microbiol. 2012, 14, 2212–2222. doi:10.1111/j.1462-2920.2012.02800.x.

42. Guo, W.; Li, J.; Kaltenboeck, B.; Gong, J.; Fan, W.; Wang, C. Chlamydia gallinaeaca, not C. psittaci, is the endemic chlamydial species in chicken (Gallus gallus). Sci. Rep. 2016, 6, 19638. doi:10.1038/srep19638.
43. Ornelas-Eusebio, E.; Garcia-Espinosa, G.; Vorimore, F.; Aaziz, R.; Durand, B.; Laroucau, K.; Zanella, G. Cross-sectional study on Chlamydiaceae prevalence and associated risk factors on commercial and backyard poultry farms in Mexico. *Prev. Vet. Med.* 2020, 176, 104922, doi:10.1016/j.prevetmed.2020.104922.

44. Li, L.; Luther, M.; Macklin, K.; Pugh, D.; Li, J.; Zhang, J.; Roberts, J.; Kaltenboeck, B.; Wang, C. *Chlamydia gallinacea*: A widespread emerging *Chlamydia* agent with zoonotic potential in backyard poultry. *Epidemiol. Infect.* 2017, 145, 2701–2703, doi:10.1017/S0950268817001650.

45. Frutos, M.C.; Monetti, M.S.; Vaulet, L.G.; Cadario, M.E.; Fermepin, M.R.; Re, V.E.; Cuffini, C.G. Genetic diversity of *Chlamydia* among captive birds from central Argentina. *Avian Pathol.* 2015, 44, 50–56, doi:10.1080/03079457.2014.993593.

46. Stokes, H.S.; Martens, J.M.; Jelocnik, M.; Walder, K.; Segal, Y.; Berg, M.L.; Bennett, A.T.D. Chlamydial diversity and predictors of infection in a wild Australian parrot, the Crimson Rosella (*Platycercus elegans*). *Transbound. Emerg. Dis.* 2021, 68, 487–498, doi:10.1111/ted.13703.

47. Mattmann, P.; Marti, H.; Borel, N.; Jelocnik, M.; Albini, S.; Vogler, B.R. *Chlamydiaceae* in wild, feral and domestic pigeons in Switzerland and insight into population dynamics by *Chlamydia psittaci* multilocus sequence typing. *PLoS ONE* 2019, 14, e0226088, doi:10.1371/journal.pone.0226088.

48. Burt, S.A.; Roring, R.E.; Hejne, A. *Chlamydia psittaci* and *C. avium* in feral pigeon (*Columba livia domestica*) droppings in two cities in the Netherlands. *Vet. Q.* 2018, 38, 63–66, doi:10.1080/101652176.2018.1482028.

49. Pisanu, B.; Laroucau, K.; Aaziz, R.; Vorimore, F.; Le Gros, A.; Chapuis, J.-L.; Clergeau, P. *Chlamydia avium* Detection from a Ring-Necked Parakeet (*Psittacula krameri*) in France. *J. Exot. Pet Med.* 2018, 27, 68–74, doi:10.1053/j.jepm.2018.02.035.

50. Vorimore, F.; Hsia, R.C.; Huot-Creasy, H.; Bastian, S.; Deruyter, L.; Fasset, A.; Sachse, K.; Bavoil, P.; Myers, G.; Laroucau, K. Isolation of a New *Chlamydia* species from the Feral Sacred Ibis (*Threskiornis aethiopicus*): *Chlamydia ibidis*. *PLoS ONE* 2013, 8, e74823, doi:10.1371/journal.pone.0074823.

51. Li, Z.; Liu, P.; Hou, J.; Xu, G.; Zhang, J.; Lei, Y.; Lou, Z.; Liang, L.; Wen, Y.; Zhou, J. Detection of *Chlamydia psittaci* and *Chlamydia ibidis* in the Endangered Crested Ibis (*Nipponia nippon*). *Epidemiol. Infect.* 2020, 148, 1–5, doi:10.1017/S0950268819022331.

52. Krawiec, M.; Piatecki, T.; Wieliczko, A. Prevalence of *Chlamydia psittaci* and Other *Chlamydia* Species in Wild Birds in Poland. *Vector Borne Zoonotic Dis.* 2015, 15, 652–665, doi:10.1089/vbz.2015.1814.

53. Greub, G. *Parachlamydia acanthamoebae*, an emerging agent of pneumonia. *Clin. Microbiol. Infect.* 2009, 15, 18–28.

54. Wheelhouse, N.; Longbottom, D. Chlamydia-related Organisms: Infection in Ruminants and Potential for Zoonotic transmission. *Curr. Clin. Microbiol. Rep.* 2015, 2, 1–9, doi:10.1007/s40121-014-0011-x.

55. Jelocnik, M.; Taylor-Brown, A.; O’Dea, C.; Anstey, S.; Bomman, S.; Masters, N.; Katouli, M.; Jenkins, C.; Polkinghorne, A. Detection of a range of genetically diverse chlamydiala in Australian domesticated and wild ungulates. *Transbound. Emerg. Dis.* 2019, 66, 1132–1137, doi:10.1111/ted.13171.

56. Robertson, T.; Noormohammadi, A.H. Investigation of the Prevalence of Chlamydiosis in the Australian Chicken Meat Industry; Rural Industries Research and Development Corporation: Barton, ACT, Australia, 2011.

57. Christerson, L.; Blomqvist, M.; Grannas, K.; Thollesson, M.; Laroucau, K.; Waldenstrom, J.; Eliasson, I.; Olsen, B.; Herrmann, B. A novel *Chlamydiaceae*-like bacterium found in faecal samples from sea birds from the Bering Sea. *Environ. Microbiol.* Rep. 2010, 2, 605–610, doi:10.1111/j.1758-2229.2010.00174.x.

58. Taylor-Brown, A.; Vaughan, L.; Greub, G.; Timms, P.; Polkinghorne, A. Twenty years of research into *Chlamydia*-like organisms: A revolution in our understanding of the biology and pathogenicity of members of the phylum *Chlamydiae*. *Pathog. Dis.* 2015, 73, 1–15, doi:10.1093/femsdp/ftu009.

59. Collar, N. Globally threatened parrots: Criteria, characteristics and cures. *Int. Zoo Yearb.* 2000, 37, 21–35.

60. Beech, M.; Miles, J. Psittacosis among birds in South Australia I. A survey of infection in some common species in 1951 and 1952. *Aust. J. Exp. Biol.* 1953, 31, 473–480.

61. Chahota, R.; Katroch, R.C.; Batta, M.K. Prevalence of *Chlamydia psittaci* among feral birds in Himachal Pradesh, India. *J. Appl. Anim. Res.* 1997, 12, 89–94, doi:10.1080/09712119.1997.9706190.

62. de Freitas Raso, T.; Seixas, G.H.; Guedes, N.M.; Pinto, A.A. *Chlamydophila psittaci* in free-living Blue-fronted Amazon parrots (*Amazona aestiva*) and Hyacinth macaws (*Anodorhynchus hyacinthinus*) in the Pantanal of Mato Grosso do Sul, Brazil. *Vet. Microbiol.* 2006, 117, 235–241, doi:10.1016/j.vetmic.2006.06.025.

63. Sutherland, M.; Sarker, S.; Vaz, P.K.; Legione, A.R.; Devlin, J.M.; Macwhirter, P.L.; Whiteley, P.L.; Raidal, S.R. Disease surveillance in wild Victorian cacatuids reveals co-infection with multiple agents and detection of novel avian viruses. *Vet. Microbiol.* 2019, 235, 257–264, doi:10.1016/j.vetmic.2019.07.012.

64. Stokes, H.S.; Martens, J.M.; Chaminos, A.; Walder, K.; Berg, M.L.; Segal, Y.; Bennett, A.T.D. Identification of *Chlamydia gallinacea* in a parrot and in free-range chickens in Australia. *Aust. Vet. J.* 2019, 97, 398–400, doi:10.1111/avj.12856.

65. Dicks, V.; Beeckman, D.S.; Dossche, L.; Tavernier, P.; Vanrompay, D. *Chlamydiaphila psittaci* in homing and feral pigeons and zoonotic transmission. *J. Med. Microbiol.* 2010, 59, 1348–1353, doi:10.1099/jmm.0.023499-0.

66. Sachse, K.; Kuehlewind, S.; Ruettger, A.; Schubert, E.; Rohde, G. More than classical *Chlamydia psittaci* in urban pigeons. *Vet. Microbiol.* 2012, 157, 476–480, doi:10.1016/j.vetmic.2012.01.002.

67. Tanaka, C.; Miyazawa, T.; Watarai, M.; Ishiguro, N. Bacteriological Survey of Feces from Feral Pigeons in Japan. *J. Vet. Med. Sci.* 2005, 67, 951–953.

68. Ferreira, V.L.; Dias, R.A.; Raso, T.F. Screening of Feral Pigeons (*Columba livia*) for Pathogens of Veterinary and Medical Importance. *Braz. J. Poult. Sci.* 2016, 18, 701–704, doi:10.1590/1806-9061-2016-0296.
69. de Lima, V.Y.; Langoni, H.; da Silva, A.V.; Pezerico, S.B.; de Castro, A.P.; da Silva, R.C.; Araujo, J.P., Jr. Chlamydiaphila psittaci and Toxoplasma gondii infection in pigeon (Columba livia) from Sao Paulo State, Brazil. Vet. Parasitol. 2011, 175, 9–14, doi:10.1016/j.vetpar.2010.10.006.

70. Wannaratanat, S.; Thontiravong, A.; Amonsin, A.; Pakpinyo, S. Persistence of Chlamydia psittaci in Various Temperatures and Times. Avian Dis. 2017, 61, 40–45, doi:10.1637/11475-072216-Reg.

71. Sariya, L.; Prompiram, P.; Tangsuadai, S.; Polpet, K.; Chamsai, T.; Mongkolphan, C.; Rattanavibul, K.; Sakdajavachareon, V. Detection and characterization of Chlamydiaphila psittaci in asymptomatic feral pigeons (Columba livia domestica) in central Thailand. Asian Pac. J. Trop. Med. 2015, 8, 94–97, doi:10.1016/s1995-7454(14)60195-4.

72. Jelocnik, M.; Jenkins, C.; O'Rourke, B.; Barnwell, J.; Polkinghorne, A. Molecular evidence to suggest pigeon-type Chlamydia psittaci in association with an equine foal loss. Transbound. Emerg. Dis. 2018, 65, 911–915, doi:10.1111/tbed.12817.

73. Dick, V.; Kalmar, I.D.; Tavernier, P.; Vanrompay, D. Prevalence and genotype distribution of Chlamydia psittaci in feral Canadian geese (Branta canadensis) in Belgium. Vector Borne Zoonotic Dis. 2013, 13, 382–384, doi:10.1089/vbz.2012.1131.

74. Hermann, B.; Persson, H.; Jensen, J.; Joensen, H.; Klint, M.; Olsen, B. Chlamydiaphila psittaci in Fulmars, the Faroe Islands. Emerg. Infect. Dis. 2006, 12, 330–332.

75. Jouffroy, S.J.; Schluter, A.H.; Bildfell, R.J.; Rockey, D.D. Rhabdochlamydia spp. in an Oregon raptor. J. Vet. Diagn. Invest. 2016, 28, 473–476, doi:10.1177/1040638716644608.

76. Blomqvist, M.; Christerson, L.; Waldenstrom, J.; Lindberg, P.; Helander, B.; Gunnarsson, G.; Herrmann, B.; Olsen, B. Chlamydia psittaci in birds of prey, Sweden. Infect. Ecol. Epidemiol. 2012, 2, doi:10.3402/iee.v2i10.8435.

77. Isaksson, J.; Christerson, L.; Blomqvist, M.; Wille, M.; Alladio, L.A.; Sachse, K.; Olsen, B.; González-Acuña, D.; Herrmann, B. Chlamydiaceae-like bacteria, but no new species isolated from flamingo (Phoenicopterus roseus): Chlamydiifilator phoenicopteri sp. nov. and Chlamydiifilator volucris sp. nov. Syst. Appl. Microbiol. 2021, doi:10.1016/j.syapm.2021.126200.

78. Burnard, D.; Polkinghorne, A. Chlamydial infections in wildlife-conservation threats and/or reservoirs of ‘spill-over’ infections? Vet. Microbiol. 2016, 196, 78–84, doi:10.1016/j.vetmic.2016.10.018.

79. Holzinger-Umlauf, H.A.; Marschang, R.E.; Gravendyk, M.; Kaleta, E.F. Investigation on the frequency of Chlamydia spp. infections in tits (Paridae). Avian Pathol. 1997, 26, 779–789, doi:10.1080/03079459708419252.

80. Beckmann, K.; Borel, N.; Pocknell, A.; Dagleish, M.; Sachse, K.; KJoh, S.; Pospichal, A.; Cunningham, A.; Lawson, B. Chlamydiosis in British Garden Birds (2005–2011): Retrospective Diagnosis and Chlamydia psittaci Genotype Determination. EcoHealth 2014, 11, 544–563.

81. Ribas, J.M.; Sipinski, E.A.B.; Serafini, P.P.; Ferreira, V.L.; De Freitas Raso, T.; Pinto, A.A. Chlamydiaphila psittaci assessment in threatened red-tailed Amazon (Amazona brasiliensis) parrots in Paraná, Brazil. Ornitologia 2014, 6, 144–147.

82. Vaz, F.F.; Serafini, P.P.; Locatelli-Dittrich, R.; Meurer, R.; Durigon, E.L.; de Araujo, J.; Thomazelli, L.M.; Ometto, T.; Sipinski, E.A.B.; Sezerban, R.M.; et al. Survey of pathogens in threatened wild red-tailed Amazon parrot (Amazona brasiliensis) nestlings in Rasa Island, Brazil. Braz. J. Microbiol. 2017, 48, 747–753, doi:10.1016/j.bjm.2017.03.004.

83. Deem, S.L.; Noss, A.J.; Cuellar, R.L.; Karesh, W.B. Health evaluation of free-ranging and captive blue-fronted Amazon parrots (Amazona aestiva) in the Gran chaco, Bolivia. J. Zoo Wildl. Med. 2005, 36, 598–605, doi:10.1638/04094.1.

84. Gilardi, K.V.K.; Lowenstein, L.J.; Gilardi, J.D.; Munn, C.A. A survey for selected viral, chlamydial, and parasitic diseases in wild dusky-headed parakeets (Aratinga weddelli) and tui parakeets (Brotogeris sanctithomae) in Peru. J. Wildl. Dis. 1995, 31, 523–528.

85. Tiyawattanaroj, W.; Lindenwald, R.; Mohr, L.; Günther, E.; Legler, M. Monitoring of the infectious agent Chlamydia psittaci in common swifts (Apus apus) in the area of Hannover, Lower Saxony, Germany. Berl. Münchener Tierärztliche Wochenschr. 2021, 134, 1–5, doi:10.1376/134-0299-2020-32.

86. Assunção, P.; de Ponte Machado, M.; De la Fe, C.; Ramírez, A.S.; Rosales, R.S.; Antunes, N.T.; Poveda, C.; Poveda, J.B. Prevalence of Pathogens in Great White Pelicans (Pelecanus onocrotalus) from the Western Cape, South Africa. J. Appl. Anim. Res. 2007, 32, 29–32, doi:10.1080/09712119.2007.9796841.

87. Dusek, R.J.; Justice-Allen, A.; Bodenstein, B.; Knowles, S.; Grear, D.A.; Adams, L.; Levy, C.; Yaglom, H.D.; Shearm-Bochsler, V.I.; Giembror, P.G.; et al. Chlamydiaphila psittaci in Feral Rosy-Faced Lovebirds (Agapornis Roseicollis) and Other Backyard Birds in Maricopa County, Arizona, USA. J. Wildl. Dis. 2018, 54, 248–260, doi:10.7589/2017-06-145.

88. Gartrell, B.D.; French, N.P.; Howe, L.; Nelson, N.J.; Houston, M.; Burrows, E.A.; Russell, J.C.; Anderson, S.H. First detection of Chlamydia psittaci from a wild native passerine bird in New Zealand. N. Z. Vet. J. 2013, 61, 174–176, doi:10.1080/00480169.2012.740656.

89. Mahzounieh, M.; Moloudidzargari, M.; Ghasemi Shams Abadi, M.; Baninameh, Z.; Heidari Khooei, H. Prevalence Rate and Phylogenetic Analysis of Chlamydiaphila psittaci in Pigeon and House Sparrow Specimens and the Potential Human Infection Risk in Chahmralah-va-Bakhtira, Iran. Arch. Clin. Infect. Dis. 2020, 15, doi:10.5812/archcid.67565.

90. McElnea, C.; Cross, G. Methods of detection of Chlamydia psittaci in domesticated and wild birds. Aust. Vet. J. 1999, 77, 516–521.

91. Padilla, L.R.; Santiago-Alarcon, D.; Merkel, J.; Miller, R.E.; Parker, P.G. Survey for haemoproteus spp., trichomonas gallinae, chlamydiaphila psittaci, and salmonella spp. in Galapagos Islands Columbiformes. J. Zoo Wildl. Med. 2004, 35, 60–64.
93. Schettler, E.; Fickel, J.; Hotzel, H.; Sachse, K.; Streich, W.J.; Wittstatt, U.; Frolich, K. Newcastle disease virus and Chlamydia psittaci in free-living raptors from eastern Germany. *J. Wildl. Dis.* 2003, 39, 57–63.

94. Schettler, E.; Langgemach, T.; Sommer, P.; Streich, J.; Frolich, K. Seroepizootiology of selected infectious disease agents in free-living birds of prey in Germany. *J. Wildl. Dis.* 2001, 37, 145–152, doi:10.7589/0099-3558-37.1.145.

95. Sharples, E.; Baines, S.J. Prevalence of *Chlamydophila psittaci*-positive cloacal PCR tests in wild avian casualties in the UK. *Vet. Rec.* 2009, 164, 16–17.

96. Stenzel, T.; Pestka, D.; Choszcz, D. The prevalence and genetic characterization of Chlamydia psittaci from domestic and feral pigeons in Poland and the correlation between infection rate and incidence of pigeon coccidiosis. *Poultry Sci.* 2014, 93, 3009–3016, doi:10.3382/ps.2014-04219.

97. Floriano, A.M.; Rigamonti, S.; Comandatore, F.; Scaltitri, E.; Longbottom, D.; Livingstone, M.; Laroucou, K.; Gaffuri, A.; Pongolini, S.; Magrino, S.; et al. Complete Genome Sequence of *Chlamydia avium* PV 4360/2, Isolated from a Feral Pigeon in Italy. *Microbiol. Resour. Announc.* 2020, 9, doi:10.1128/MRA.01509-19.

98. Hulin, V.; Oger, S.; Vorimore, F.; Aaziz, R.; De Barbeyrac, B.; Berrouch, J.; Sachse, K.; Laroucou, K. Host preference and zoonotic potential of *Chlamydia psittaci* and *C. gallinacea* in poultry. *Pathog. Dis.* 2015, 73, 1–11, doi:10.1093/femspd/ftv005.

99. Doosti, A.; Arshi, A. Determination of the Prevalence of *Chlamydia psittaci* by PCR in Iranian Pigeons. *Int. J. Biol.* 2011, 3, doi:10.5539/ijb.v3n4p79.

100. Zhang, N.Z.; Zhang, X.X.; Zhou, D.H.; Huang, S.Y.; Tian, W.P.; Yang, Y.C.; Zhao, Q.; Zhu, X.Q. Seroprevalence and genotype of *Chlamydia* in pet parrots in China. *Epidemiol. Infect.* 2015, 143, 55–61, doi:10.1017/S0950268814000363.

101. Cong, W.; Huang, S.Y.; Zhang, X.Y.; Zhou, D.H.; XU, M.J.; Zhao, Q.; Song, H.Q.; Zhu, X.Q.; Qian, A.D. Seroprevalence of *Chlamydia psittaci* infection in market-sold adult chickens, ducks and pigeons in north-western China. *J. Med. Microbiol.* 2013, 62, 1211–1214, doi:10.1099/jmm.0.059287-0.

102. Cong, W.; Huang, S.Y.; Zhang, X.X.; Zhou, D.H.; XU, M.J.; Zhao, Q.; AHN, Q.D.; Zhu, X.Q. Chlamydia psittaci exposure in pet birds. *J. Med. Microbiol.* 2014, 63, 578–581, doi:10.1099/jmm.0.070003-0.

103. Grimes, J.E. Recovery of Ornithosis Agent from Naturally Infected White-Winged Doves. *J. Wildl. Manag.* 1966, 30, 594–598.

104. Goltz, J.P.; Huiness, J.G. Psittacosis in Wild Rock Doves. In *Canadian Cooperative Wildlife Health Centre Newsletter*, Canadian Cooperative Wildlife Center, Canada, 2000; 9–10.

105. Hutchinson, R.; Rowlands, R.A.; Simpson, S.L. A study of psittacosis. *Br. Med. J.* 1930, 1, 633646.

106. de Freitas Raso, T.; Berchieri Júnior, A.; Augusto Pinto, A. Evidence of *Chlamydophila psittaci* infection in captive Amazon parrots in Brazil. *J. Zoo Wildl. Med.* 2002, 33, 118–121.

107. de Freitas Raso, T.; Godoy, S.N.; Milanelo, L.; Souza, C.A.I.; Matushima, E.R.; Araujo Jr, J.P.; Pinto, A.A. An outbreak of chlamydiosis in captive Blue-fronted Amazon parrots (*Amazona aestiva*) in Brazil. *J. Zoo Wildl. Med.* 2004, 35, 94–96.

108. Leal, D.C.; Negrão, V.B.; Santos, F.; Raso, T.F.; Barrouin-Melo, S.M.; Franke, C.R. Ocorrência de *Chlamyphila psittaci* em pombos (*Columba livia*) na cidade de Salvador, Bahia. *Arq. Bras. Med. Veterinária Zootec.* 2015, 67, 771–776, doi:10.1590/1678-4162-7919.

109. Burnet, F. Enzootic psittacosis amongst wild Australian parrots. *J. Hwgg.* 1935, 35, 412–420.

110. Gedye, K.R.; Fremaux, M.; Garcia-Ramirez, J.C.; Gartrell, B.D. A preliminary survey of *Chlamydia psittaci* genotypes from native and introduced birds in New Zealand. *N. Z. Vet. J.* 2018, 66, 162–165, doi:10.1080/00480169.2018.1439779.

111. El-Jakee, J.K.; Osman, K.M.; Ezzeldeen, N.A.; Ali, H.A.; Mostafa, E.R. Chlamydia species in free-living Cattle Egret (*Bubulcus ibis*) and Hoopoe (*Upupa epops*) in Egypt. *J. Int. Vet. Sci. Med.* 2014, 2, 1–6, doi:10.4172/2155-6110.100012.002.

112. Brand, C.J. Chlamydial infections in free-living birds. *J. Avian. Med. Vet. Assoc.* 1999, 15, 1531–1535.

113. Amery-Gale, J.; Marenda, M.S.; Owens, J.; Eden, P.A.; Browning, G.F.; Devlin, J.M. A high prevalence of beak and feather disease virus in non-psittacine Australian birds. *J. Med. Microbiol.* 2017, 66, 1005–1013, doi:10.1099/jmm.0.000516.

114. Branley, J.M.; Roy, B.; Dwyer, D.E.; Sorrell, T.C. Real-time PCR detection and quantitation of *Chlamydia psittaci* in human and avian specimens from a veterinary clinic cluster. *Eur. J. Clin. Microbiol. Infect. Dis.* 2008, 27, 269–273, doi:10.1007/s10096-007-0431-0.

115. Ornelas-Eusebio, E.; Sanchez-Godoy, F.D.; Chavez-Mayo, F.; De la Garza-Garcia, J.A.; Hernandez-Castro, R.; Garcia-Espinosa, G. First Identification of *Chlamydia psittaci* in the Acute Illness of Disease and Endemic of Endangered Psittacine Birds in Mexico. *Avian Dis.* 2016, 60, 540–544, doi:10.1637/11360-122915-Case.

116. Vanrompay, D.; Ducatellle, R.; Haesebrucker, F. *Chlamydia psittaci* infections: A review with emphasis on avian chlamydiosis. *Vet. Microbiol.* 1995, 45, 93–119.

117. Popelin-Wedlarski, F.; Roux, A.; Aaziz, R.; Vorimore, F.; Lagourette, P.; Crispo, M.; Borel, N.; Laroucou, K. Captive Psittacines with *Chlamydia avium* Infection. *Avian Dis.* 2016, 60, 542–546.

118. Wobeser, G. *Essentials of Disease in Wild Animals*, 1st ed.; Blackwell Publishing Professional: Ames, IA, USA, 2006; pp. 243.

119. Das, S.; Smith, K.; Sarker, S.; Peters, A.; Adriaanse, K.; Eden, P.; Ghorashi, S.A.; Forwood, J.K.; Raidal, S.R. Repeat Spillover of Beak and Feather Disease Virus into an Endangered Parrot Highlights the Risk Associated with Endemic Pathogen Loss in Endangered Species. *J. Wildl. Dis.* 2020, 56, doi:10.7589/2018-06-154.

120. Vanrompay, D.; Ducatellle, R.; Haesebrucker, F. Pathogenicity for turkeys of *Chlamydia psittaci* strains belonging to the avian serovars A, B and D. *Avian Pathol.* 1994, 23, 247–262, doi:10.1080/03079459408418993.

121. Crowe, T.A.; Crist, T.O.; Parmenter, R.R.; Belovsky, G.; Lugo, A.E. The spread of invasive species and infectious disease as drivers of ecosystem change. *Front. Ecol. Environ.* 2008, 6, 238–246, doi:10.1890/070151.
122. Brochner, B.; Vangeluwe, D.; van den Berg, T. Alien invasive birds. Rev. Sci. Tech. 2010, 29, 217–226.

123. Brearley, G.; Rhodes, J.; Bradley, A.; Baxter, G.; Seabrook, L.; Lunney, D.; Liu, Y.; McAlpine, C. Wildlife disease prevalence in human-modified landscapes. Biol. Rev. Camb. Philos. Soc. 2013, 88, 427–442, doi:10.1111/brv.12009.

124. McCallum, H.; Kerlin, D.H.; Ellis, W.; Carrick, F. Assessing the significance of endemic disease in conservation-koalas, chlamydia, and koala retrovirus as a case study. Conserv. Lett. 2018, 11, e12425, doi:10.1111/conl.12425.

125. Polkinghorne, A.; Hanger, J.; Timms, P. Recent advances in understanding the biology, epidemiology and control of chlamydial infections in koalas. Vet. Microbiol. 2013, 165, 214–223, doi:10.1016/j.vetmic.2013.02.026.

126. Vanrompuy, D.; Harkinezhad, T.; van de Walle, M.; Beecken, D.; van Droogenbroeck, C.; Verminnen, K.; Leten, R.; Martel, A.; Cauwerts, K. Chlamydiapila psittaci Transmission from Pet Birds to Humans. Emerg. Infect. Dis. 2007, 13, 1108–1110.

127. Larouche, K.; de Barbeyrac, B.; Vorimore; C.; Mair, A. Chlamydiial infections in duck farms associated with human cases of psittacosis in France. Vet. Microbiol. 2009, 135, 82–89.

128. Harkinezhad, T.; Verminnen, K.; Van Droogenbroeck, C.; Vanrompuy, D. Chlamydiapila psittaci genotype E/B transmission from African grey parrots to humans. J. Med. Microbiol. 2007, 56, 1097–1100, doi:10.1099/jmm.0.47157-0.

129. Nieuwenhuizen, A.A.; Dijkstra, F.; Notermans, D.W.; van der Hoek, W. Laboratory methods for case finding in human psittacosis outbreaks: A systematic review. BMC Infect. Dis. 2018, 18, 442, doi:10.1186/s12879-018-3317-0.

130. Levinson, D.C.; Gibbsm, J.; Bearwood, J.T. Ornithosis as a cause of sporadic atypical pneumonia. JAMA 1944, 126, 1079–1084.

131. Haag-Wackernagel, D.; Moch, H. Health hazards posed by feral pigeons. J. Infect. 2004, 48, 307–313, doi:10.1016/j.jinf.2003.11.001.

132. Henry, K.; Crossley, S. Wild-pigeon related psittacosis in a family. Chest 1986, 90, 708–710, doi:10.1378/chest.90.5.708.

133. Mair-Jenkins, J.; Lamming, T.; Dziadosz, A.; Flecknne, D.; Stibington, T.; Mentasti, M.; Muir, P.; Monk, P. A Psittacosis Outbreak among English Office Workers with Little or No Contact with Birds, August 2015. PLOS Curr. Outbreaks 2018, doi:10.1371/currents.outbreaks.b464c3b2b40e3397f183f1823becca6.

134. Rehn, M.; Ringberg, H.; Runehagen, A.; Herrmann, B.; Olsen, B.; Petersson, A.; Hjertqvist, M.; Küllmann-Berenzon, S.; Wallensten, A. Unusual increase of psittacosis in southern Sweden linked to wild bird exposure, January to April 2013. Eurosurveillance 2013, 18, 13–20.

135. Cheneau, F.; Rehn, M.; Pini, A.; Kuhlmann-Berenzon, S.; Ydring, E.; Ringberg, H.; Runehagen, A.; Ockborn, G.; Dotevall, L.; Wallensten, A. Wild and domestic bird faeces likely source of psittacosis transmission-A case-control study in Sweden, 2014-2016. Zoonoses Public Health 2018, 65, 790–797, doi:10.1111/zph.12492.

136. Olsen, B.; Persson, K.; Broholm, K.A. PCR detection of Chlamydia psittaci in faecal samples from passerine birds in Sweden. Epidemiol. Infect. 1998, 121, 481–484, doi:10.1017/S0950268898001320.

137. Williams, J.; Tallis, G.; Dalton, C.; Ng, S.; Beaton, S.; Catton, M.; Elliott, J.; Carrie, J. Community outbreak of psittacosis in a rural Australian town. Lancet 1998, 351, 1697–1699, doi:10.1016/S0140-6736(97)10444-5.

138. Parkin, D. Wildlife Feeding. National Park Policy and Visitor Practice: Where to from Here?; Brassall: Queensland, Australia, 2001; pp. 1–12.

139. Parsons, H.; Major, R.E.; French, K. Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. Austral Ecol. 2006, 31, 217–227, doi:10.1111/j.1442-9993.2006.01584.x.

140. Schell, C.J.; Stanton, L.A.; Young, J.K.; Angeloni, L.M.; Lambert, J.E.; Breck, S.W.; Murray, M.H. The evolutionary consequences of human-wildlife conflict in cities. Evol. Appl. 2021, 14, 178–197, doi:10.1111/eva.13131.

141. Isaksen, C. Impact of Urbanization on Birds. In Bird Species: How They Arise, Modify and Vanish; Tietze, D.T., Ed.; Springer International Publishing: Cham, Switzerland, 2018; pp. 235–257.

142. Strubbe, D.; Matthysen, E. Establishment success of invasive ring-necked and monk parakeets in Europe. J. Biogeogr. 2009, 36, 2264–2274, doi:10.1111/j.1365-2699.2009.01777.x.

143. Davis, A.; Taylor, C.E.; Major, R.E. Do fire and rainfall drive spatial and temporal population shifts in parrots? A case study using urban parrot populations. Landsc. Urban Plan. 2011, 100, 295–301, doi:10.1016/j.landurbplan.2010.12.017.

144. Davis, A.; Taylor, C.E.; Major, R.E. Seasonal abundance and habitat use of Australian parrots in an urbanised landscape. Landsc. Urban Plan. 2012, 106, 191–198.

145. Hulin, V.; Bernard, P.; Vorimore, F.; Aaziz, R.; Cleva, D.; Robineau, J.; Durand, B.; Angelis, L.; Siarkou, V.I.; Larouche, K. Assessment of Chlamydiapila psittaci Shedding and Environmental Contamination as Potential Sources of Worker Exposure throughout the Mule Duck Breeding Process. Appl. Environ. Microbiol. 2015, 82, 1504–1518, doi:10.1128/AEM.03179-15.

146. Verminnen, K.; Van Loock, M.; Hafez, H.M.; Ducatelle, R.; Haesebrouck, F.; Vanrompuy, D. Evaluation of a recombinant enzyme-linked immunosorbent assay for detecting Chlamydiapila psittaci antibodies in turkey sera. Vet. Res. 2006, 37, 623–632, doi:10.1051/vetres:2006023.

147. Carver, S.; Bevins, S.N.; Lappin, M.R.; Boydston, E.; Lyren, L.M.; Alldredge, M.; Logan, K.A.; Sweenor, L.L.; Riley, S.P.D.; Serieys, L.E.K.; et al. Pathogen exposure varies widely among sympatric populations of wild and domestic felids across the United States. Ecol. Appl. 2016, 26, 367–381.

148. Jenkins, C.; Jelocnik, M.; Micallef, M.L.; Galea, F.; Taylor-Brown, A.; Bogema, D.R.; Liu, M.; O’Rourke, B.; Chicken, C.; Carrick, J.; et al. An epizootic of Chlamydiapila psittaci equine reproductive loss associated with suspected spillover from native Australian parrots. Emerg. Microbes Infect. 2018, 7, 1–13, doi:10.1038/s41426-018-0089-y.

149. Polkinghorne, A.; Branley, J. New insights into chlamydial zoonoses. Microbiol. Aust. 2020, 41, 14–18.
150. Akter, R.; Stent, A.W.; Sansom, F.M.; Gilkerson, J.R.; Burden, C.; Devlin, J.M.; Legione, A.R.; El-Hage, C.M. *Chlamydia psittaci*: A suspected cause of reproductive loss in three Victorian horses. *Aust. Vet. J.* 2020, 98, 570–573, doi:10.1111/avj.13010.

151. Anstey, S.; Lizárraga, D.; Nyari, S.; Chalmers, G.; Carrick, J.; Chicken, C.; Jenkins, C.; Perkins, N.; Timms, P.; Jelocnik, M. Epidemiology of *Chlamydia psittaci* infections in pregnant Thoroughbred mares and foals. *Vet. J.* 2021, 273, doi:10.1016/j.tvjl.2021.105683.

152. Fudge, A.M. A Review of Methods to Detect *Chlamydia psittaci* in Avian Patients. *J. Avian Med. Surg.* 1997, 11, 153–165.

153. Buckland, S.T. A Mark-Recapture Survival Analysis. *J. Anim. Ecol.* 1982, 51, 833–847.