Coronaviruses and Australian bats: a review in the midst of a pandemic

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Abstract. Australia’s 81 bat species play vital ecological and economic roles via suppression of insect pests and maintenance of native forests through pollination and seed dispersal. Bats also host a wide diversity of coronaviruses globally, including several viral species that are closely related to SARS-CoV-2 and other emergent human respiratory coronaviruses. Although there are hundreds of studies of bat coronaviruses globally, there are only three studies of bat coronaviruses in Australian bat species, and no systematic studies of drivers of shedding. These limited studies have identified two betacoronaviruses and seven alphacoronaviruses, but less than half of Australian species are included in these studies and further research is therefore needed. There is no current evidence of spillover of coronaviruses from bats to humans in Australia, either directly or indirectly via intermediate hosts. The limited available data are inadequate to determine whether this lack of evidence indicates that spillover does not occur or occurs but is undetected. Conversely, multiple international agencies have flagged the potential transmission of human coronaviruses (including SARS-CoV-2) from humans to bats, and the consequent threat to bat conservation and human health. Australia has a long history of bat research across a broad range of ecological and associated disciplines, as well as expertise in viral spillover from bats. This strong foundation is an ideal platform for developing integrative approaches to understanding bat health and sustainable protection of human health.

Introduction

The global COVID-19 pandemic resulting from the emergence of a novel coronavirus, SARS-CoV-2 in late 2019 (Zhu et al. 2020) has refocussed attention on coronaviruses of bat origin. Bats host a wide diversity of coronaviruses (Cui et al. 2007; Vijaykrishna et al. 2007; Drexler et al. 2014; Anthony et al. 2017a; Lacroix et al. 2017; Wong et al. 2019; Latinne et al. 2020), including viral species linked to emergent human respiratory syndrome coronaviruses (Cui et al. 2019). SARS-CoV-2 has close nucleotide sequence identity with coronaviruses isolated from bats in Yunnan Province in China (Hu et al. 2017; Zhou et al. 2020). The epidemiological link between early COVID-19 cases in Wuhan and a Wuhan wet market (Chen et al. 2020; Li et al. 2020) led to an initial hypothesis that transmission from bats and recombination in an unknown intermediate host sold in the market might be involved (Zhang et al. 2020); however, the links to intermediate hosts are unclear (Boni et al. 2020), and it is possible that the market was the site of a superspreading event after the emergence of SARS-CoV-2 elsewhere. This scenario parallels the emergence of severe acute respiratory syndrome (SARS) in China in 2002 (Ksiazek et al. 2003); the search for the origins of the aetiological coronavirus (SARS-CoV) of that pandemic (Guan et al. 2003; Tu et al. 2004; Kan et al. 2005; Poon et al. 2005; Tang et al. 2006) and the cluster of SARS-related betacoronaviruses subsequently described in Rhinolophus species in China (Lau et al. 2005; Li et al. 2005) provides the background for the current focus on bats in the search for the origins of SARS-CoV-2.

Australia has a diverse bat community, with 81 species representing both suborders and 9 families (Reardon et al. 2015). The majority of Australian species are smaller insectivorous bats with little public profile and generally limited public contact opportunity. In contrast, large, arboreal, colonially roosting...
pteropodid bats (commonly known as flying-foxes) are regularly present, and prominent, in eastern Australian cities and towns. This bat community has been the focus of a diverse range of research studies, including their genetic and evolutionary history (e.g. Godthelp et al. 1992; Webb and Tidemann 1996), ecology (e.g. McKenzie and Rolfe 1986; Lumsden and Bennett 2005; Eby and Law 2008), physiology (e.g. Hosken and Withers 1997; Welbergen et al. 2008), immunology (e.g. Zhang et al. 2013; Zhou et al. 2016; Schountz et al. 2017), and infectious disease emergence (Gould et al. 1998; Halpin et al. 2000; Barr et al. 2012; Kessler et al. 2018) and dynamics (e.g. Field et al. 2015; Plowright et al. 2015; Edson et al. 2019; Peel et al. 2019).

The vital ecosystem services provided by bats through insect pest control (e.g. Kolkert et al. 2020), pollination (e.g. Law and Lean 1999; Eby and Law 2008) and seed dispersal (e.g. Moran et al. 2009) are often overshadowed in public perception by their potential to act as reservoirs of zoonotic viruses, such as Hendra virus, Australian bat lyssavirus and Menangle virus. Most research on bat-borne viruses in Australia (~200 papers to date) has focussed on these lyssavirus and Menangle virus. Most research on bat-borne public perception by their potential to act as reservoirs of dispersal (e.g. Moran et al. 2009) are also seen and dynamics (e.g. Field et al. 2015; Plowright et al. 2015; Edson et al. 2019; Peel et al. 2019).

Against this background, we first seek to review the current state of knowledge of bat coronaviruses globally and within Australia, identifying key areas in need of further research. Second, we canvass the potential for spillover of endemic Australian bat coronaviruses to humans and the potential for transmission of SARS-CoV-2 from infected humans into Australian bat populations.

**Coronaviruses in bats worldwide**

Bats naturally host viruses from two of the four genera of coronaviruses: alpha- and betacoronaviruses – the other two (delta- and gammacoronaviruses) are predominantly found in birds (Woo et al. 2009, 2010; Su et al. 2016) (Fig. 1). The diversity of coronaviruses circulating in bat populations in China has been detected in infected humans and Australia elsewhere are represented in Australia (e.g. Rhinolophus spp., Hipposideros spp., Chaerophon spp., Pipistrellus spp.) (Tang et al. 2006; Pfefferle et al. 2009; Tong et al. 2009).

All of the known zoonotic coronaviruses with origins in bats are betacoronaviruses, belonging either to the Sarbecovirus subgenus (i.e. the SARS-related coronaviruses [SARSr-CoV]: SARS-CoV-1, SARS-CoV-2, and MERS-CoV remain unresolved, the closest evolutionary relatives to these viruses have been identified in bat hosts. Viruses with 88–91% nucleotide identity to SARS-CoV-1 have been amplified from horseshoe bat species (Rhinolophus sinicus, R. ferrumequinum, R. macrotis and R. pearsoni), supporting Rhinolophus bats as the ancestral reservoir origin of SARS (Lau et al. 2005; Li et al. 2005; He et al. 2014; Zhou et al. 2020; Zhou et al. 2020a). The viruses most closely related to SARS-CoV-2 identified so far include lineages of sarbecoviruses circulating in bat populations in China: RaTG13 CoV isolated from Rhinolophus affinis (Zhou et al. 2020b) and RmYN02 CoV detected in Rhinolophus malayanus (Zhou et al. 2020).

Beyond Rhinolophidae, SARS-related coronaviruses have also been detected in bats from the Hipposideridae and Vespertilionidae in Europe and Asia, and the Molossidae in Asia (Drexler et al. 2014; Fan et al. 2019; Wong et al. 2019). At least three bat families have been identified as hosts of Merbecoviruses to date, though most detections have been in bats from the Vespertilionidae (reviewed in Wong et al. 2019).

Existing bat coronavirus studies demonstrate several factors with apparent influence on coronavirus detectability and diversity. Coronavirus detection rates are statistically significantly higher in specimens collected from bats in human-altered landscapes (e.g. particularly associated with animal usage in hunting, trade, etc), compared with those from undisturbed environments, suggesting the influence of environmental conditions on bat–coronavirus interactions (Anthony et al. 2017a). Coronavirus diversity is higher where bat diversity is also high, suggesting an intimate and long evolutionary history of interactions. This is evident at the continental scale (bat coronavirus diversity is highest in South-east Asia, northern Latin America, and south-west, equatorial and east Africa) and also within continents (Anthony et al. 2017a; Wong et al. 2019; Joffrin et al. 2020). Phylogenetic analyses of bat coronavirus genetic sequences show that closely related coronaviruses are commonly shared among closely related bat families (Drexler et al. 2014). For instance, in Mexico, coronaviruses in vespertilionid bats cluster together with coronaviruses in molossid bats (Anthony et al. 2013). This relationship supports an influence of cospeciation and host-switching in the ecology and evolution of bats and their coronaviruses (Cui et al. 2007; Joffrin et al. 2020; Latinne et al. 2020). Both alpha- and betacoronaviruses have been detected across all continents occupied by bats, yet in North America, betacoronaviruses have been detected in Mexico but are notably absent in bats in the USA and Canada (Anthony et al. 2013; Wong et al. 2019). It is important to note that sampling efforts are not globally uniform, and therefore such absences may not necessarily represent true diversity and abundance of circulating coronaviruses (Anthony et al. 2017a). This may also affect analyses that indicate that the number of coronavirus species detected per bat family varies by continent in Africa and Asia (with high rates of detection in Pteropodidae in Africa; high rates of detection in Miniopterae, Vespertilionidae and Pteropodidae in Asia), but bat family did not influence rate of detection in Latin America (Anthony et al. 2017a).
Coronaviruses in Australian bats

Coronavirus diversity and antibody prevalence in Australian bats is known from two cross-sectional studies on bat faeces or rectal swabs, encompassing 35 Australian bat species across 17 genera and 8 families (Smith et al. 2016; Prada et al. 2019) (Table 1, Fig. 2). Based on PCR amplification and sequencing of a 396–440 bp fragment of the RNA-dependent RNA polymerase (RdRp) gene, Smith et al. (2016) and Prada et al. (2019) detected two betacoronaviruses (exclusively from pteropodiformes) and seven alphacoronaviruses (mainly from vespertilionid bats) across 15 Australian bat species. Full genome sequences from four of the seven alphacoronaviruses amplified from host species have been subsequently obtained and made publicly available (Prada et al. 2019). To date, there is no evidence of any SARS-like viruses (Sarbecoviruses) or MERS-like viruses (Merbecoviruses) in any Australian bat species, though cross-reactive antibodies have been detected (Smith et al. 2016; W. Boardman, pers. comm.) and further surveillance is currently underway.

In agreement with other studies globally (Drexler et al. 2014; Lacroix et al. 2017), strains amplified from Australian bats have strong host associations, with sequences clustering within these genera is the small number of strains and lack of representative Australian betacoronavirus strains very low (1.5%; 95% CI = 0.2–8.3%). Equally surprising as the single detection in this species suggests that this target sample number must be replicated across sites and seasons before firm conclusions are drawn on a species’ viral diversity.

Notable differences are also evident in Australian bat coronavirus studies; for example, despite high viral prevalences of betacoronaviruses in rhinolophid bats in China (e.g. 39%: Lau et al. 2005) and elsewhere (e.g. 32%: Drexler et al. 2010), no betacoronaviruses have been detected in Australian rhinolophids. Despite an extensive sampling effort of Rhinolophus megaphyllus (n = 506), only one bat tested positive by PCR and cross-regional seroprevalence was low (6.7%; 95% CI = 4–9%) (Smith et al. 2016). The single positive result was an alphacoronavirus with 99% nucleotide sequence identity with Miniopterus bat coronavirus HKU8 and which was widespread in concurrently sampled Miniopterus australis and M. schreibersii (now renamed M. orianae), suggesting that R. megaphyllus may not be the primary reservoir host for this viral species. Similarly, there has been no detection of betacoronaviruses in Australian Hipposideros species, even though SARSr-CoV have been amplified from this genera in Africa (Pfefferle et al. 2009; Quan et al. 2010). In Australia, no active viral shedding was detected in Hipposideros ater (n = 56), and seroprevalence was very low (1.5%; 95% CI = 0.2–8.3%). Equally surprising as the lack of representative Australian betacoronavirus strains within these genera is the small number of strains and lack of host-specific alphacoronaviruses detected within the broader Pteropodiformes group, since alphacoronaviruses generally have greater detection rates and a widespread global distribution (Wong et al. 2019).

Sample sizes and the employed primer set are congruent with global studies (Tsuda et al. 2012; Moreira-Soto et al. 2015; Lacroix et al. 2017; Joffrin et al. 2020), but broader sampling would help determine how representative these existing studies are, and how sample sizes, sample type, number of sampling sites, sampling season, number of bat species surveyed, or the implemented PCR assay have affected detection rates. For example, an additional study focussed in Australian populations of Miniopterus orianae yielded no coronavirus detections from oropharyngeal swabs (Holz et al. 2018). This lack of detection is likely due to decreased sensitivity of coronavirus detection in oropharyngeal swabs, because the route of coronavirus shedding in bats is predominantly through faeces (Wacharapluesadee et al. 2013; Wong et al. 2019). By comparison, rectal swabs collected from the same species in south-east Queensland and the Northern Territory were positive for coronavirus RNA in 26.5% and 10.2% of individuals, respectively (Smith et al. 2016) (Table 1). Only small numbers of individuals of several Australian bat species have been screened for coronaviruses, and an additional 46 species have not yet been screened at all (Table 2). A meta-analysis of bat coronavirus studies globally identified that a sampling effort of ~400 individuals per species is required to capture the full diversity of coronaviruses present in each species (Anthony et al. 2017a). Only one Australian species has been sampled to this intensity (R. megaphyllus, n = 506), and the single detection in this species suggests that this target sample number must be replicated across sites and seasons before firm conclusions are drawn on a species’ viral diversity.

Spillover potential of Australian bat-borne coronaviruses

Various processes must align in space and time for viruses to successfully spill over from a natural reservoir host to alternative hosts (Plowright et al. 2017). The viruses must be circulating within reservoir host populations, be shed and survive within the environment at a time and place where novel hosts may be exposed, and, finally, overcome any structural or immune barriers to infection and replication within that host. These cross-species transmission events can involve one-directional transmission from one species to another (e.g. bat to civet to human, as is suspected for SARS-CoV-1), or circular transmission between two or more host species (e.g. a shared virus between two bat host species; conceptually illustrated in Fig. 3). While coronaviruses are known to be circulating within Australian bat populations, there have been no reports of their spillover to humans, either directly or via an
### Table 1. Evidence of coronavirus infection in Australian bats across existing studies, and antibodies cross-reactive with SARS-coronavirus antigen

| Genus and higher taxa | Species | Common name | Geographic location of sampling | PCR\(^a\), +/n (%) | Antibody\(^b\), +/n (%) | Study |
|-----------------------|---------|-------------|--------------------------------|---------------------|--------------------------|-------|
| Pteropodiformes       | Hipposideridae | *Hipposideros ater* | Dusky leaf-nosed bat | FNQ 0/29 (0%) | 0/29 (0%) | Smith et al. (2016) |
|                       |         |             | NT 0/27 (0%) | 0/4\(^d\) | Smith et al. (2016) |
|                       |         |             | WA 0/31 (0%) | 0/1 (0%) | Smith et al. (2016) |
|                       | Rhinolophidae | *Rhinolophus aurantia* | Pilbara leaf-nosed bat | NT 1/126 (1%) | 0/105 (0%) | Smith et al. (2016) |
|                       | Megadermatidae | *Macroderma gigas* | Ghost bat | NT 0/57 (0%) | 1/63 (1.6%) | Smith et al. (2016) |
|                       | Pteropodidae | *Pteropus alecto* | Black flying-fox | SEQ 4/33 (12%) | 9/34 (26.5%) | Smith et al. (2016) |
|                       |         |             | SEQ 14/30 (46.7%) | 16/30 (53.3%) | Smith et al. (2016) |
|                       |         |             | SEQ 38/154 (24.7%) | 80/124 (64.5%) | Smith et al. (2016) |
|                       |         |             | WA 1/1\(^e\) | | Smith et al. (2016) |
|                       | *Pteropus conspicillatus* | Spectacled flying-fox | | | | |
|                       | *Pteropus poliocephalus* | Grey-headed flying-fox | | | | |
|                       | *Pteropus scapulatus* | Little red flying-fox | | | | |
|                       | Rhinolophidae | *Rhinolophus megaphyllus* | Smaller horseshoe bat | FNQ 1/58 (1.7%) | 5/61 (8.2%) | Smith et al. (2016) |
|                       |         |             | SEQ 0/448 (0%) | 13/399 (3.3%) | Smith et al. (2016) |
| Vespertilioniformes   | Emballonuridae | *Emballonura flaviventris* | Yellow-bellied sheath-tailed bat | WA 0/18\(^f\) | | Smith et al. (2016) |
|                       | Taphozous | *Taphozous australis* | Tomb bats | WA 8/38 (38%) | | Smith et al. (2016) |
|                       | Minioptera | *Miniopterus australis* | Little bent-wing bat | CQ 1/20 (5%) | 15/30 (50%) | Smith et al. (2016) |
|                       |         |             | FNQ 14/30 (46.7%) | 16/30 (53.3%) | Smith et al. (2016) |
|                       |         |             | SEQ 38/154 (24.7%) | 80/124 (64.5%) | Smith et al. (2016) |
|                       | *Miniopterus orianae*\(^b\) | Northern bent-wing bat (Miniopterus orianae orianae) | | | | |
|                       |         |             | NT 6/59 (10.2%) | 25/56 (44.6%) | Smith et al. (2016) |
|                       |         |             | SEQ 63/238 (26.5%) | 145/211 (68.7%) | Smith et al. (2016) |
|                       | *Miniopterus schreibersii* | Southen bent-wing bat (Miniopterus schreibersii bassanii) | | | | |
|                       |         |             | Vic. 0/32 (0%) | | Holz et al. (2018) |
| Molessidae             | *Astronomus australis* | White-striped free-tailed bat | | | | |
|                       | *Chalinolobus* | *Chalinolobus gouldii* | Gould’s wattled bat | SW-WA 59/232 (25.4%) | 2/6 (3.0%) | Prada et al. (2019) |
|                       | *Chalinolobus morio* | Chocolate wattled bat | | | | |
|                       | *Myotis macropus* | *Myotis macropus* | Northern free-tailed bat | SEQ 0/25 (0%) | 40/41 (97.6%) | Smith et al. (2016) |
|                       | *Ozimops lumsdenae* | Northern free-tailed bat | | | | |
|                       | *Ozimops norfolkensis* | East coast free-tailed bat | SEQ 0/1\(^g\) | | Smith et al. (2016) |
|                       | *Ozimops norfolkensis* | Northern bent-wing bat (Miniopterus orianae oceanaensis) | | | | |
|                       |         |             | Vic. 0/26 (0%) | | Holz et al. (2018) |
| Vespertilionidae       | *Nyctophilus* | *Nyctophilus bifass* | Eastern long-eared bat | SEQ 0/6\(^h\) | | Smith et al. (2016) |
|                       | *Nyctophilus* | *Nyctophilus gouldi* | Gould’s long-eared bat | SEQ 0/9\(^i\) | | Smith et al. (2016) |
|                       | *Nyctophilus* | *Nyctophilus greyii* | Lesser long-eared bat | SW-WA 2/56 (3.5%) | 7/67 (10.4%) | Prada et al. (2019) |
|                       | *Nyctophilus* | *Nyctophilus major* | Western long-eared bat | SW-WA 2/51 (3.9%) | 0/27 (0%) | Prada et al. (2019) |
|                       | *Scotorepus* | *Scotorepus rupPELLii* | Greater broad-nosed bat | SEQ 0/1\(^j\) | | Smith et al. (2016) |
|                       |         |             | WA 0/1\(^k\) | | Smith et al. (2016) |
|                       | *Scotorepus* | *Scotorepus balstoni* | Broad-nosed bats | SW-WA 9/9\(^l\) | 2/2 (100%) | Smith et al. (2016) |
|                       | *Vespudalas* | *Vespudalas finlaysoni* | Finlayson’s cave bat | WA 0/1\(^m\) | | Smith et al. (2016) |
|                       | *Vespudalas* | *Vespudalas pumilus* | Eastern forest bat | SEQ 1/4\(^n\) | | Smith et al. (2016) |
|                       | *Vespudalas* | *Vespudalas troglodytus* | Eastern cave bat | FNQ 0/31 (0%) | 5/31 (16.1%) | Smith et al. (2016) |
|                       | *Vespudalas* | *Vespudalas baverstockii* | Inland forest bat | SW-WA 2/4\(^o\) | 0/1\(^p\) | Prada et al. (2019) |
|                       | *Vespudalas* | *Vespudalas regulus* | Southern forest bat | SW-WA 11/141 (12.1%) | 9/150 (6.0%) | Prada et al. (2019) |
|                       | *Falisticrillus* | *Falisticrillus mackenziei* | Western false pipistrelle | SW-WA 2/11\(^q\) | 0\(^r\) | Prada et al. (2019) |

\(^a\)PCR results are based on detection of viral RNA via RdRp PCR on faecal samples or rectal swabs, except for results from *Miniopterus orianae oceanaensis* and *Miniopterus orianae bassanii*, which were based on oropharyngeal swabs.

\(^b\)Antibody results reflect detection of antibodies cross-reactive with SARS-coronavirus antigen via ELISA or microbead assay (refer to original studies for details).

\(^c\)Prevalence not calculated (for species/locations with total sample sizes below 20 individuals).

\(^d\)The species *Miniopterus orianae* was formerly recognised as *Miniopterus schreibersii* (identified as *M. schreibersii* in Smith et al. 2016).

\(^e\)The species *Ozimops lumsdenae* was formerly recognised as *Mormopterus beccarii* (identified as *M. beccarii* in Smith et al. 2016).
Fig. 2. (a) Map of sampling locations in Australian bat coronavirus studies. (b) Number of Australian species for which coronavirus surveillance has been undertaken, using either PCR or serology and noting whether data were derived from more or less than 20 individuals of each species. (c) Number of individuals tested by PCR or serology within each bat family, faceted by Australian state (Qld, Queensland; WA, Western Australia; NT, Northern Territory; SA, South Australia; Vic., Victoria). (d) Overall PCR prevalence and seroprevalence by species (n > 20), where circle area is proportional to prevalence (Cg, Chalinolobus gouldii; Cm, Chalinolobus morio; Mg, Macroderma gigas; Ma, Miniopterus australis; Mo, Miniopterus orianae; Mn, Myotis macropus; Nge, Nyctophilus geoffroyi; Ngo, Nyctophilus gouldi; Ol, Ozimops lumsdenae; Pa, Pteropus alecto; Pc, Pteropus conspicillatus; Pp, Pteropus poliocephalus; Ps, Pteropus scapulatus; Rm, Rhinolophus megaphyllus; Ra, Rhinonicteris auranta; Ss, Scotorepens spp.; Ts, Taphozous spp.; Vt, Vespadelus regulus; Vt, Vespadelus troughtoni.) A colour version of this figure is available online.
Table 2. List of Australian bat species (by family), including common names and inclusion in bat coronavirus surveillance studies

n.a., no data available (species not included in any previous coronavirus studies). ID, Identified. Smith et al. (2016) were not able to differentiate between the two species of Taphozous that have an over-lapping range at the Western Australian sampling location (T. georgianus and T. hilli), but 38 serum samples from Taphozous spp. were tested for CoV antibodies.

| Taxa | Common name | CoV surveillance |
|------|-------------|-----------------|
| *Emballonuridae* | | |
| Saccolaimus flaviventris | Yellow-bellied sheath-tailed bat | Smith et al. (2016) |
| Saccolaimus mixtus | Cape York sheath-tailed bat | n.a. |
| Saccolaimus saccolaimus | Bare-rumped sheath-tailed bat | n.a. |
| Taphozous australis | Coastal sheath-tailed bat | n.a. |
| Taphozous georgianus | Common sheath-tailed bat | n.a. |
| Taphozous hilli | Hill’s sheath-tailed bat | n.a. |
| Taphozous kugelgeni | Arnhem sheath-tailed bat | n.a. |
| Taphozous troughoni | Troughton’s sheath-tailed bat | n.a. |
| *Hipposideridae* | | |
| Hipposideros ater | Dusky leaf-nosed bat | Smith et al. (2016) |
| Hipposideros cervinus | Fawn leaf-nosed bat | n.a. |
| Hipposideros diadema | Diadem leaf-nosed bat | n.a. |
| Hipposideros inornatus | Arnhem leaf-nosed bat | n.a. |
| Hipposideros longicornis | Semon’s leaf-nosed bat | n.a. |
| Hipposideros stenotis | Northern leaf-nosed bat | n.a. |
| *Megadermatidae* | | |
| Macroderma gigas | Ghost bat | Smith et al. (2016) |
| *Miniopteridae* | | |
| Miniopterus australis | Little bent-winged bat | Smith et al. (2016) |
| Miniopterus aurita | Large bent-winged bat | Smith et al. (2016) and Holz et al. (2018) |
| *Molosidae* | | |
| Austronomus australis | White-striped free-tailed bat | Prada et al. (2019) |
| Chaerophon jobensis | Greater northern free-tailed bat | Smith et al. (2016) |
| Ozimops cobourginus | Northern coastal free-tailed bat | n.a. |
| Ozimops eurytis | Bristle-faced free-tailed bat | n.a. |
| Ozimops halli | Cape York free-tailed bat | n.a. |
| Ozimops kitcheneri | Western free-tailed bat | Prada et al. (2019) |
| Ozimops lumsdeni | Northern free-tailed bat | Smith et al. (2016) |
| Ozimops norfolcensis | Eastern coastal free-tailed bat | Smith et al. (2016) |
| Ozimops petersi | Inland free-tailed bat | n.a. |
| Ozimops planiceps | Southern free-tailed bat | n.a. |
| Ozimops ridei | Ride’s free-tailed bat | n.a. |
| *Pteropodidae* | | |
| Dobsonia magna | Bare-backed fruit bat | n.a. |
| Macroglossum minimus | Northern blossom bat | n.a. |
| Nyctimene robinsoni | Eastern tubo-nosed bat | n.a. |
| Pteropus alecto | Black flying-fox | Smith et al. (2016) |
| Pteropus brumus | Percy island flying-fox | n.a. |
| Pteropus conspicillatus | Spectacled flying-fox | Smith et al. (2016) |
| Pteropus macrotis | Large-eared flying-fox | n.a. |
| Pteropus natalis | Christmas island flying-fox | n.a. |
| Pteropus poliocephalus | Grey-headed flying-fox | Smith et al. (2016) |
| Pteropus scapulatus | Little red flying-fox | Smith et al. (2016) |
| Syconycteris aurita | Eastern blossom bat | n.a. |
| *Rhinolophidae* | | |
| Rhinolophus australis | Eastern horseshoe bat | Smith et al. (2016) |
| Rhinolophus robustus | large-eared horseshoe bat | n.a. |
| Rhinolophus sp. | Intermediate horseshoe bat | n.a. |
| *Rhinonycteridae* | | |
| Rhinonycteris aurantia | Orange leaf-nosed bat | Smith et al. (2016) |
| *Vesperilionidae* | | |
| Chalinolobus dwyeri | Large-eared pipistrelle | n.a. |
| Chalinolobus gouldii | Gould’s wattled bat | Prada et al. (2019) |
| Chalinolobus morio | Chocolate wattled bat | Prada et al. (2019) |
| Chalinolobus nigrogriseus | Hoary wattled bat | n.a. |
| Chalinolobus pictus | Little eared bat | n.a. |
| Fallopiiullac macquenizei | Western falsistrellae | Prada et al. (2019) |
| Fallopiiullac tasmaniensis | Eastern falsistrellae | n.a. |
| Murina florid | Flute-nosed Bat | n.a. |
| Myotis macropus | Large-footed myotis | Smith et al. (2016) |
| Nyctophilus arnhemensis | Arnhem long-eared bat | n.a. |
| Nyctophilus bifl | Eastern long-eared bat | Smith et al. (2016) |

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intermediate host. Some evidence exists for bat–bat cross-species transmission events between sympatric species within the studied communities (in fact, they appear to be somewhat common) (Fig. 3), yet sustained infection within the new host and further transmission within populations may be limited. For instance, high nucleotide similarity (100%) was detected between sequences amplified from *M. australis* and *R. megaphyllus*, yet marked differences existed between the species in the proportion of active infections (RNA detection; 46.7% versus 1.7%, respectively) and historical infections (coronavirus antibodies) (53% versus 8.2%, respectively) (Smith et al. 2016). These data are indicative of a cross-infection event from the vespertilionid bat *M. australis* into the pteropodiforme *R. megaphyllus* and warrant further investigation. Similarly, cross-infections were also detected in south-west Western Australian bat communities, with tree hollows proposed as a source of transmission between sympatric bat species (Prada et al. 2019). One alphacoronavirus strain detected in *Chalinolobus gouldii* had a spike protein with a higher sequence similarity to the coronavirus that causes Porcine Endemic Diarrhoea in pigs (Jung and Saif 2015) than to any other virus of bat origin (Prada et al. 2019). Since the spike protein determines host tropism, the ability of the spike protein to enter mammalian cells other than bat cells is currently under investigation (Haynes et al., unpubl. data). In general, however, the spatiotemporal shedding dynamics of Australian bat-borne coronaviruses and their capacity to infect cells and overcome immune systems of human or other animal species are unknown, making it challenging to assess whether spillover does not occur, or does not cause disease, or occurs but is simply not detected.

Insights from other bat–viral systems and geographic regions will be key in targeting further research in Australia. The origin of SARS-CoV-2, the chain of transmission to humans, and direct evidence for the involvement of an intermediate host are yet to be established. Pathogen transmission between species cannot occur without every condition, in a hierarchical series of events, lining up (Plowright et al. 2017). Hence, if intermediate hosts are required, then even if diverse viruses are present in bats and peaks of shedding generate pathogen pressure for bat-borne coronaviruses, spillover may not be able to occur without the presence of these competent intermediate hosts from which human exposure occurs. There are multiple reports of transmission of bat-borne coronaviruses to various laboratory animal species in experimental settings (Gretebeck and Subbarao 2015), domestic and wild felids across a range of settings (Shi et al. 2020; US Department of Agriculture Animal and Plant Health Inspection Service 2020), and to non-bat wildlife species utilised in wildlife farming and trade (Shi and Hu 2008; Gretebeck and Subbarao 2015). There are also

**Table 2.** (continued)

| Taxa                        | Common name                     | CoV surveillance |
|-----------------------------|---------------------------------|------------------|
| *Nyctophilus corbeni*       | Corben’s long-eared bat         | n.a.             |
| *Nyctophilus daedalus*      | Pallid long-eared bat           | n.a.             |
| *Nyctophilus geoffroyi*     | Lesser long-eared bat           | Prada et al. (2019) |
| *Nyctophilus gouldi*       | Gould’s long-eared bat          | Smith et al. (2016) and Prada et al. (2019) |
| *Nyctophilus howensis*      | Lord Howe long-eared bat        | n.a.             |
| *Nyctophilus major*         | Greater long-eared bat          | Prada et al. (2019) |
| *Nyctophilus sherrini*      | Tasmanian long-eared bat        | n.a.             |
| *Nyctophilus walkeri*       | Pymy long-eared bat             | n.a.             |
| *Phoniscus papuensis*       | Golden-tipped bat               | n.a.             |
| *Pipistrellus adamsi*       | Forest pipistrelle              | n.a.             |
| *Pipistrellus murrayi*      | Christmas island pipistrelle    | n.a.             |
| *Scotorepens sweppellii*    | Greater broad-nosed bat         | Smith et al. (2016) |
| *Scotorepens balstoni*      | Inland broad-nosed bat          | Prada et al. (2019) |
| *Scotorepens greyii*        | Little broad-nosed bat          | Smith et al. (2016) |
| *Scotorepens orion*         | Eastern broad-nosed bat         | n.a.             |
| *Scotorepens sanborni*      | Northern broad-nosed bat        | n.a.             |
| *Scotorepens sp.*           | Parnaby’s broad-nosed bat       | n.a.             |
| *Vespadelus baverstocki*    | Inland forest bat               | Prada et al. (2019) |
| *Vespadelus caurinus*       | Northern cave bat               | n.a.             |
| *Vespadelus darlingtoni*    | Large forest bat                | n.a.             |
| *Vespadelus douglasiroma*   | Yellow-lipped cave bat          | n.a.             |
| *Vespadelus finlaysoni*     | Finlayson’s cave bat            | Smith et al. (2016) |
| *Vespadelus pumilus*        | Eastern forest bat              | Smith et al. (2016) |
| *Vespadelus regulus*        | Southern forest bat             | Prada et al. (2019) |
| *Vespadelus troghtoni*      | Eastern cave bat                | Smith et al. (2016) |
| *Vespadelus valturnus*      | Little forest bat               | n.a.             |

The species *Miniopterus orianae* was formerly recognised as *Miniopterus schreibersii* (identified as *M. schreibersii* in Smith et al. 2016).

Likely species identified as ‘*Ozimops sp.*’ in Prada et al. (2019).

The species *Ozimops lamsdenae* was formerly recognised as *Mormopterus beccarii* (identified as *M. beccarii* in Smith et al. 2016).
Examples of spillover of coronaviruses from bats to livestock or farmed domestic species: in camels, associated with the emergence of MERS in 2012 in Saudi Arabia (Anthony et al. 2017b), and in pigs, associated with the emergence of Swine Acute Diarrhoea Syndrome (SADS) in 2016 in southern China that resulted in the deaths of ~25 000 pigs across four farms (Zhou et al. 2018). The novel SADS coronavirus detected in pigs that caused this outbreak shared 96–98% sequence identity with SADS-related bat coronaviruses present in ~10% of Rhinolophus spp. bats in the same region. This event was preceded by at least three other examples of bat–pig viral spillover: transmission of Nipah virus from Pteropus spp. flying foxes to pigs in Malaysia (Chua et al. 2000), Reston ebolavirus in pigs in the Philippines and China (Jayme et al. 2015), and Menangle virus from Pteropus poliocephalus to pigs in Australia (Philbey et al. 1998). The latter example highlights that bat–pig viral transmission events are feasible within an Australian context. Spillover events are more likely to succeed where susceptible intermediate hosts are stressed and immunocompromised and where ongoing transmission is facilitated by high-density cohousing and poor on-farm biosecurity (Lindahl and Grace 2015).

The potential for direct bat–human transmission of coronaviruses remains unclear (Fig. 3). There is no molecular evidence for direct spillover; however, Wang et al. (2018) found serological evidence of human exposure to SARS-related coronaviruses in 6 of 218 (2.7%) rural people living close to caves in which SARS-related coronaviruses had been identified in bats. None of the positive individuals had a history of exposure to SARS-CoV-1 virus during the 2002–03 outbreak and none could recall any clinical symptoms consistent with SARS-CoV-1 infection in the past 12 months, suggesting the possibility of subclinical or mild clinical infection. Uncertainty remains as to whether these findings could represent transmission via an intermediate host, but they are sufficient to warrant inclusion of direct bat–human transmission routes in coronavirus spillover risk assessments.

Several human–bat interaction scenarios could theoretically present the opportunity for spillover of bat coronaviruses to humans in Australia, including where people are occupationally exposed to bats and bat body fluids. Bat rescuers and rehabilitators would likely be at high risk of exposure because of the number of animals they handle, the length of time that animals are frequently in care, and the often physically close nature of contact between carer and bat (particularly orphan flying-foxes). Indeed, following the emergence of Hendra virus in 1994 (which spilled from flying-foxes to horses to humans), health authorities recognised that bat carers and others working with bats were an ideal sentinel group to screen for serological evidence of exposure to Hendra virus; however, no evidence of exposure was found (Selvey et al. 1996).

Given the tangible threats to human health and the unknown risks that emergent coronaviruses pose to wild bat populations, future surveillance efforts on bat taxa traditionally associated with zoonotic strains should prioritise species common to the human/urban interface. Additionally, the commonality and marked variability of alphacoronavirus infections among insectivorous bats, provide an opportunity to further investigate drivers of cross-species spillover, as well as pathogen persistence, viral shedding, transmission routes and their associations to the host ecology and health (Jeong et al. 2017; Smith 2015).

**Potential establishment of novel coronaviruses in Australian bat populations following human-to-bat transmission**

SARS-CoV-2 is expected to persist as the world’s fifth endemic circulating human coronavirus (Kissler et al. 2020), and it is unlikely to be the last novel coronavirus linked to bat origins. Widespread transmission within human populations of viruses that are either bat-borne, or whose progenitors originate in bats, raises the possibility of reverse zoonotic spillover (Fig. 3) of these viruses from humans into novel bat or other animal hosts that have no evolutionary association with the circulating strains. Bat organisations internationally have responded to this threat by advocating, at a minimum, for increased biosecurity protocols when handling bats for research or rehabilitation (IUCN Bat Specialist Group 2020; Olival et al. 2020; Runge et al. 2020). In some cases, this has extended to blanket bans on handling wild bats. Establishment of SARS-CoV-2, or other endemic human coronaviruses from people into Australian bat populations, could have serious public health implications, via establishment of an adjunct source of human infection (via ‘spillback’; Fig. 3) or via recombination events with endemic bat coronavirus strains. Bat welfare, conservation, and management, already contentious issues in Australia (Degeling and Kerridge 2012; Kung et al. 2015), would likely...
be further compromised. The likelihood of human-to-bat transmission of SARS-CoV-2 in Australia is likely to reflect levels of community transmission (at the time of writing (4 June 2020), there had been a total of ~7240 cases of COVID-19 in Australia (~28 per 100 000 individuals), and detection rates for new cases had dropped to an average of 13 per day: Australian Government Department of Health 2020). However, the likelihood of transmission would be expected to increase proportionately with increases in human cases, which has subsequently been observed in a ‘second wave’ in the State of Victoria (Australian Government Department of Health 2020). Given the dynamic nature of the COVID-19 pandemic, and the potentially serious consequences of a human–bat transmission event, now is an ideal time to be discussing practices to mitigate the risk of human-to-bat transmission of endemic and exotic coronaviruses more broadly.

The risk of human-to-bat transmission will vary with the emergence of each new human-transmitted coronavirus, and also over space and time. Important human factors to consider in assessing this risk include prevalence in the human population and the proportion of asymptomatic carriers, as well as the likely transmission route, infectious period, and virus survival characteristics (Olival et al. 2020). Conditional on exposure of a bat to an infected human, successful human–virus survival characteristics (Olival et al. 2020). Conditional on exposure of a bat to an infected human, successful human-to-bat transmission will depend on individual bat and species susceptibility, which may be based on cross-reactive immunity to circulating bat coronaviruses, receptor sequence similarity across species, or alternative transmission mechanisms yet to be elucidated (Olival et al. 2020; Wildlife Health Australia, unpubl. data). Finally, the frequency and patterns of contact among people with different occupational or recreational exposure to bats (e.g. researchers, ecological consultants, bat rehabilitators, veterinary staff, and recreational cavers) and the different bat species they interact with, will determine groups at greatest risk of initiating or receiving spillover. Regardless, direct human-to-bat contact might not be necessary for spillover: since SARS-CoV-2 can be shed in faeces and may not be wholly inactivated by wastewater treatment processes, Franklin and Bevins (2020) have hypothesised that wastewater might be a potential route of transmission when human case numbers are high.

Discussion

Australian bats are not known to host Merbecoviruses or Sarbecoviruses with demonstrated zoonotic and pandemic potential. Nevertheless, the patchy coverage of coronavirus studies to date should alert us to the possibility that related viruses might be detected with increased sampling intensity. The wide variation in both viral RNA (0–46%) and antibody (0–100%) prevalence detected across species, space and time from existing cross-sectional studies also suggests that point-estimates of prevalence should be interpreted with caution (Becker et al. 2019). Such dynamic systems can be understood only through detailed spatiotemporal surveillance of coronaviruses in Australasian bat populations (Plowright et al. 2019).

Globally, coronaviruses are widely distributed across bat species and populations. Few studies, however, include sufficient spatial or temporal sampling design or host ecological factors to infer the drivers of transmission. Point prevalence of coronaviruses in wild bat populations varies considerably among sites, seasons, age categories and physiological stages of bats, with values of up to 60% of infected individuals (Montecino-Latorre et al. 2020). For instance, in a study in Pteropus lylei in Thailand, Wacharapluesadee et al. (2018) report higher prevalence of coronaviruses in juveniles than adults, with detections only in adults in January, only in juveniles in April and no differences among both age categories between May and October. Smith (2015) identified significantly higher anti-coronavirus antibody prevalence in M. schreibersii (now M. oriana) and R. megaphyllus in summer and in female adult bats. Comparable, but non-significant, trends were observed for PCR detection of coronaviruses. Similar age and seasonal effects have been reported for coronavirus shedding in other bat species: in some studies, juveniles present up to 16 times higher probability of shedding virus than adults, with a peak during the weaning season (Montecino-Latorre et al. 2020). These age, seasonal and physiologically related infection status and shedding patterns of coronaviruses show similarities to the dynamic of infections by Henipaviruses in Pteropus bats with seasons and life stages of high physiological stress playing a role in infection and shedding risk (Plowright et al. 2008; Field et al. 2015; Paez et al. 2017; Brook et al. 2019; Edson et al. 2019). These extensive data on the ecological drivers of Hendra virus shedding in Australia could provide a foundation upon which to base deeper investigations into the drivers of coronavirus shedding. An increase in coronavirus studies in Australian bats would provide an indication of the broad viral diversity, the potential for novel spillover risks, as well as a baseline comparison for efforts to detect human–bat transmission of CoV.

The current limited information and uncertainty about potentially zoonotic viruses, including coronaviruses, in Australian bats leaves openings for misinformation and fear. For example, in April 2020, a Victorian state member of Parliament called for the grey-headed flying-fox (P. poliocephalus) colony in Yarra Bend National Park to be removed because of a perceived disease threat, including COVID-19 (Rimmer 2020). Further investigations of the diversity, distribution, and zoonotic potential of coronaviruses in Australian bats are needed to allow a rational assessment of the risk, if any, of potential future spillover to humans or livestock, or spillback of SARS-CoV-2 to endemic bats.

Investigations of spillover potential of coronaviruses between Australian bats and humans should be framed in a broader ecological context. Describing the viruses that infect Australian bats is a first step, but without the ecological conditions that promote pathogen shedding, contact with susceptible hosts (intermediate or otherwise), and human behaviours that allow cross-species transmission, spillover may be unlikely. Landscape change is a key factor modulating all of these risk factors for disease emergence (Kessler et al. 2018; Johnson et al. 2020). The ecological integrity of landscapes affects bat distribution and health, and hence contact with other species and pathogen shedding dynamics. With increasing rates of emergence of pathogens from bats
associated with rapid environmental change (Johnson et al. 2020) and amplified stressors as a result of climate change, the links between environmental stress and spillover need more attention. Environmental changes not only drive bat virus emergence, they can decrease the ecosystem services that bats provide that directly benefit humans. Investigations of disease risk need to consider the holistic interaction of bats, their infections, and their environment.

Conclusion
Australia has a unique global advantage with its long history of bat research across a broad range of ecological and associated disciplines, as well as its expertise in viral spillover from bats. We must utilise this foundation to develop integrative approaches to understanding bat health and sustainable protection of human health.

Conflicts of interest
The authors declare no conflicts of interest.

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