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Review

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.

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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*. 2017*a*; 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 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; Paez *et al*. 2017; 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 pathogens, with only three coronavirus surveillance studies (Smith *et al*. 2016; Holz *et al*. 2018; Prada *et al*. 2019). Even though none of Australia's bat species have distributions overlapping with species that are known hosts of SARS-related viruses, most of the chiropteran genera in which zoonotic-related coronaviruses have been detected in China and 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).

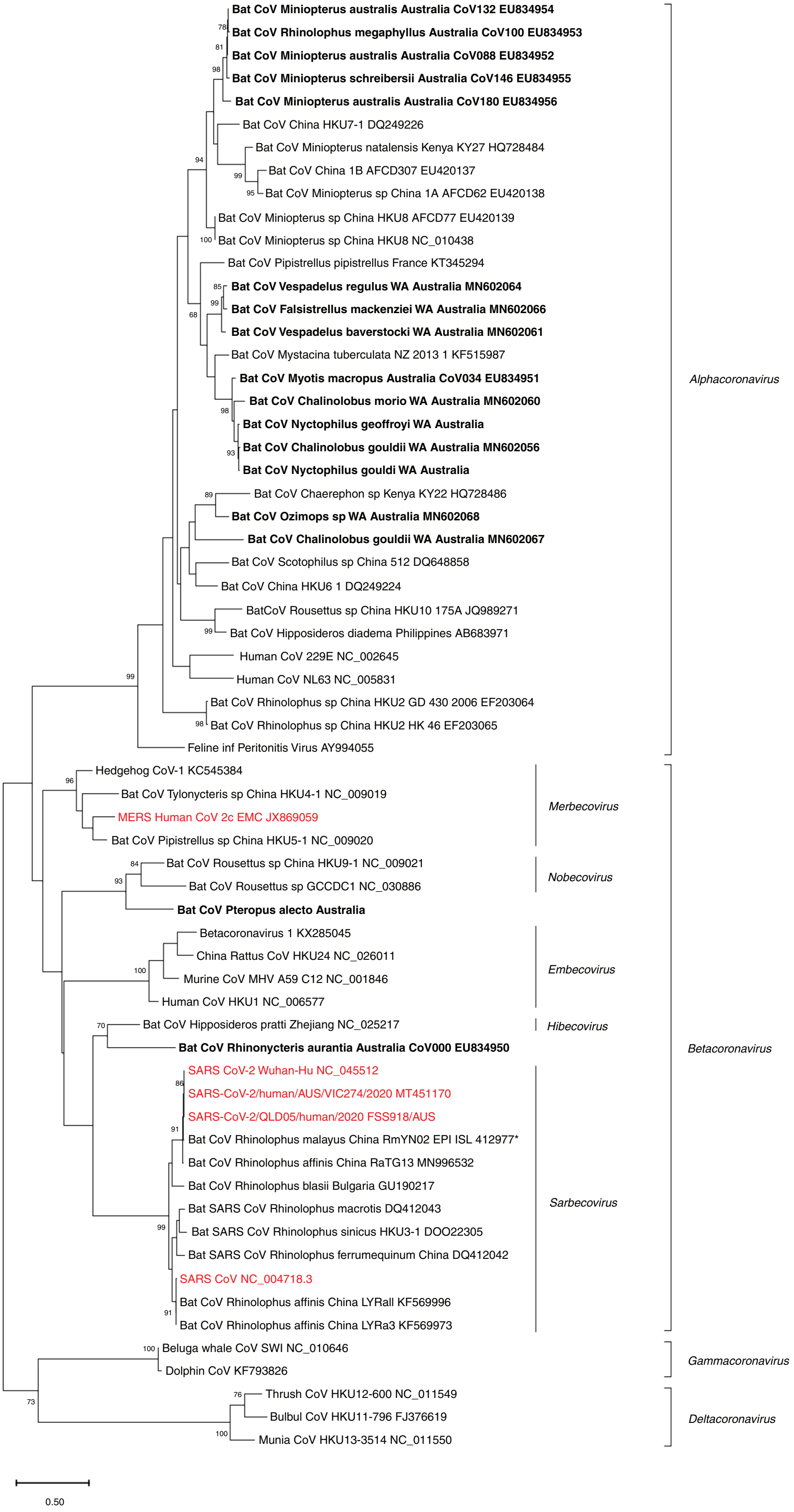
Against this background, we first seek to review the current state of knowledge of bat coronaviruses globally and within Australia, identifying key areas in need of further research. Second, we canvass the potential for spillover of endemic Australian bat coronaviruses to humans and the potential for 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 is the highest detected to date in any mammalian host group (Drexler *et al*. 2014). Empirical detections and estimates suggest the existence of 2–5 unique coronaviruses per bat species, and potentially up to 7000 coronaviruses worldwide when ~1400 bats species are considered (Anthony *et al*. 2017*a*; Willoughby *et al*. 2017; Latinne *et al*. 2020; Simmons and Cirranello 2020).

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), or the *Merbecovirus* subgenus (MERS-CoV) (Fig. 1). Although the specific conditions resulting in the spillover of 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*. 2020*a*). 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*. 2020*b*) 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*. 2017*a*). 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*. 2017*a*; 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*. 2017*a*). 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 Miniopteridae, Vespertilionidae and Pteropodidae in Asia), but bat family did not influence rate of detection in Latin America (Anthony *et al*. 2017*a*).


Bat CoV Miniopterus australis Australia CoV132 EU834954
78
Bat CoV Rhinolophus megaphyllus Australia CoV100 EU834953
81
Bat CoV Miniopterus australis Australia CoV088 EU834952
98
Bat CoV Miniopterus schreibersii Australia CoV146 EU834955
Bat CoV Miniopterus australis Australia CoV180 EU834956
Bat CoV China HKU7-1 DQ249226
Bat CoV Miniopterus natalensis Kenya KY27 HQ728484
94
Bat CoV China 1B AFCD307 EU420137
99
95
Bat CoV Miniopterus sp China 1A AFCD62 EU420138
Bat CoV Miniopterus sp China HKU8 AFCD77 EU420139
100
Bat CoV Miniopterus sp China HKU8 NC_010438
Bat CoV Pipistrellus pipistrellus France KT345294
85
Bat CoV Vespadelus regulus WA Australia MN602064
99
Bat CoV Falsistrellus mackenziei WA Australia MN602066
68
Bat CoV Vespadelus baverstocki WA Australia MN602061
Bat CoV Mystacina tuberculata NZ 2013 1 KF515987
Bat CoV Myotis macropus Australia CoV034 EU834951
Bat CoV Chalinolobus morio WA Australia MN602060
98
Bat CoV Nyctophilus geoffroyi WA Australia
Bat CoV Chalinolobus gouldii WA Australia MN602056
93
Bat CoV Nyctophilus gouldi WA Australia
89
Bat CoV Chaerephon sp Kenya KY22 HQ728486
Bat CoV Ozimops sp WA Australia MN602068
Bat CoV Chalinolobus gouldii WA Australia MN602067
Bat CoV Scotophilus sp China 512 DQ648858
Bat CoV China HKU6 1 DQ249224
BatCoV Rousettus sp China HKU10 175A JQ989271
99
Bat CoV Hipposideros diadema Philippines AB683971
Human CoV 229E NC_002645
99
Human CoV NL63 NC_005831
Bat CoV Rhinolophus sp China HKU2 GD 430 2006 EF203064
98
Bat CoV Rhinolophus sp China HKU2 HK 46 EF203065
Feline inf Peritonitis Virus AY994055
Alphacoronavirus
Hedgehog CoV-1 KC545384
96
Bat CoV Tylonycteris sp China HKU4-1 NC_009019
MERS Human CoV 2c EMC JX869059
Bat CoV Pipistrellus sp China HKU5-1 NC_009020
Merbecovirus
84
Bat CoV Rousettus sp China HKU9-1 NC_009021
93
Bat CoV Rousettus sp GCCDC1 NC_030886
Bat CoV Pteropus alecto Australia
Nobecovirus
Betacoronavirus 1 KX285045
China Rattus CoV HKU24 NC_026011
100
Murine CoV MHV A59 C12 NC_001846
Human CoV HKU1 NC_006577
Embecovirus
70
Bat CoV Hipposideros pratti Zhejiang NC_025217
Hibecovirus
Bat CoV Rhinonycteris aurantia Australia CoV000 EU834950
Betacoronavirus
SARS CoV-2 Wuhan-Hu NC_045512
86
SARS-CoV-2/human/AUS/VIC274/2020 MT451170
SARS-CoV-2/QLD05/human/2020 FSS918/AUS
91
Bat CoV Rhinolophus malayus China RmYN02 EPI ISL 412977*
Bat CoV Rhinolophus affinis China RaTG13 MN996532
Bat CoV Rhinolophus blasii Bulgaria GU190217
Sarbecovirus
Bat SARS CoV Rhinolophus macrotis DQ412043
99
Bat SARS CoV Rhinolophus sinicus HKU3-1 DOO22305
Bat SARS CoV Rhinolophus ferrumequinum China DQ412042
SARS CoV NC_004718.3
Bat CoV Rhinolophus affinis China LYRall KF569996
91
Bat CoV Rhinolophus affinis China LYRa3 KF569973
100
Beluga whale CoV SWI NC_010646
Dolphin CoV KF793826
Gammacoronavirus
76
Thrush CoV HKU12-600 NC_011549
73
Bulbul CoV HKU11-796 FJ376619
100
Munia CoV HKU13-3514 NC_011550
Deltacoronavirus
0.50

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 alphaviruses 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 by host taxonomic affinity instead of sampling site (Fig. 1). For example, betacoronaviruses amplified from *Pteropus alecto* and *Rhinonicteris aurantia* were more similar to other sequences amplified from Asian bats of the same taxonomic order than to each other.

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*. 2017*a*). 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

Fig. 1. Maximum-likelihood coronavirus consensus tree based on a 394-bp fragment of the RdRp gene. Representative coronavirus strains amplified from Australian bats are shown in bold and coronavirus sequences associated with emergent pandemics (MERS, SARS-CoV-1, SARS-CoV-2) are highlighted in red in the online version of this article. GenBank accession numbers are shown at the end of each sequence; the sequence indicated with an asterisk shows its GISAID accession reference. The tree was constructed with MegaX (Kumar *et al*. 2018) using a General Time Reversible evolutionary model, a Gamma distribution and 1000 bootstrap replication. Bootstrap values above 70% are indicated on the tree branches. Branch lengths reflect the number of substitutions per site. Aligned sequences are included as a supplementary material file.

Table 1. Evidence of coronavirus infection in Australian bats across existing studies, and antibodies cross-reactive with SARS-coronavirus antigen

Geographic location of sampling: FNQ, far-north Queensland; CQ, central Queensland; SEQ, south-east Queensland; NT, Northern Territory; WA, Western Australia; SE-AUST, south-eastern Australia; SW-WA, south-west Western Australia; SA, South Australia; Vic., Victoria. PCR and Antibody results are represented as: no. of positive individuals/no. tested (proportion). Blank cells = not tested

Genus and higher taxa	Species	Common name	Location	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[C]	Smith *et al.* (2016)
			WA		0/31 (0%)	Smith *et al.* (2016)
Rhinonicteris	*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)
			WA		17/21 (81%)	Smith *et al.* (2016)
Pteropodidae						
Pteropus	*alecto*	Black flying-fox	SEQ	4/33 (12%)	9/34 (26.5%)	Smith *et al.* (2016)
Pteropus	*conspicillatus*	Spectacled flying-fox	FNQ		6/40 (15%)	Smith *et al.* (2016)
Pteropus	*poliocephalus*	Grey-headed flying-fox	SEQ	0/27 (0%)	12/73 (16.4%)	Smith *et al.* (2016)
Pteropus	*scapulatus*	Little red flying-fox	NT		3/40 (7.5%)	Smith *et al.* (2016)
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						
Saccolaimus	*flaviventris*	Yellow-bellied sheath-tailed bat	WA		0/18[C]	Smith *et al.* (2016)
Taphozous	spp.	Tomb bats	WA		8/38 (38%)	Smith *et al.* (2016)
Miniopteridae						
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)
			WA		1/1[C]	Smith *et al.* (2016)
Miniopterus	*orianae*[D]	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)
		Eastern/large bent-wing bat (*Miniopterus orianae oceanensis*)	Vic.	0/26 (0%)		Holz *et al.* (2018)
		Southern bent-wing bat (*Miniopterus orianae bassanii*)	Vic.	0/32 (0%)		Holz *et al.* (2018)
		Southern bent-wing bat (*Miniopterus orianae bassanii*)	SA	0/155 (0%)		Holz *et al.* (2018)
Molossidae						
Astronomus	*australis*	White-striped free-tailed bat	SW-WA	0/9[C]	1/11[C]	Prada *et al.* (2019)
Chaerephon	*jobensis*	Northern free-tailed bat	WA		2/4[C]	Smith *et al.* (2016)
Ozimops[E]	*lumsdenae*[F]	Northern free-tailed bat	SEQ	0/3[C]	40/41 (97.6%)	Smith *et al.* (2016)
Ozimops[E]	*norfolkensis*	East coast free-tailed bat	SEQ	0/1[C]		Smith *et al.* (2016)
Ozimops[E]	spp.	Molossid bats	SW-WA	1/3[C]	0/1[C]	Prada *et al.* (2019)
Vespertilionidae						
Chalinolobus	spp.	Long-tailed bats	WA		2/4[C]	Smith *et al.* (2016)
Chalinolobus	*gouldii*	Gould's wattled bat	SW-WA	59/232 (25.4%)	2/62 (3.0%)	Prada *et al.* (2019)
Chalinolobus	*morio*	Chocolate wattled bat	SW-WA	17/45 (37.8%)	4/59 (6.8%)	Prada *et al.* (2019)
Myotis	*macropus*	Southern myotis	FNQ	0/31 (0%)	18/31 (58.1%)	Smith *et al.* (2016)
			SEQ	13/64 (20.3%)		Smith *et al.* (2016)
Nyctophilus	*bifax*	Eastern long-eared bat	SEQ	0/6[C]		Smith *et al.* (2016)
Nyctophilus	*gouldi*	Gould's long-eared bat	SEQ	0/7[C]		Smith *et al.* (2016)
			SW-WA	2/56 (3.5%)	7/67 (10.4%)	Prada *et al.* (2019)
Nyctophilus	*geoffroyi*	Lesser long-eared bat	SW-WA	2/51 (3.9%)	0/27 (0%)	Prada *et al.* (2019)
Nyctophilus	*major*	Western long-eared bat	SW-WA	0/10[C]	2/5[C]	Prada *et al.* (2019)
Scotorepens	*greyii*	Little broad-nosed bat	SEQ	0/1[C]		Smith *et al.* (2016)
Scotorepens	*rueppellii*	Greater broad-nosed bat	SEQ	0/1[C]		Smith *et al.* (2016)
Scotorepens	spp.	Broad-nosed bats	SEQ		24/24 (100%)	Smith *et al.* (2016)
			WA		0/1[C]	Smith *et al.* (2016)
Scotorepens	*balstoni*	Inland broad-nosed bat	SW-WA	0/9[C]	0/2[C]	Prada *et al.* (2019)
Vespadelus	*finlaysoni*	Finlayson's cave bat	WA		0/1[C]	Smith *et al.* (2016)
Vespadelus	*pumilus*	Eastern forest bat	SEQ	1/4[C]		Smith *et al.* (2016)
Vespadelus	*troughtoni*	Eastern cave bat	FNQ	0/31 (0%)	5/31 (16.1%)	Smith *et al.* (2016)
Vespadelus	*baverstocki*	Inland forest bat	SW-WA	2/4[C]	0/1[C]	Prada *et al.* (2019)
Vespadelus	*regulus*	Southern forest bat	SW-WA	17/141 (12.1%)	9/150 (6.0%)	Prada *et al.* (2019)
Falsistrellus	*mackenziei*	Western false pipistrelle	SW-WA	2/11[C]	0/7[C]	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 oceanensis* 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 genus *Ozimops* was formerly recognised as *Mormopterus* (as identified in Smith *et al.* 2016).

[F] The species *Ozimops lumsdenae* was formerly recognised as *Mormopterus beccarii* (identified as *M. beccarii* in Smith *et al.* 2016).

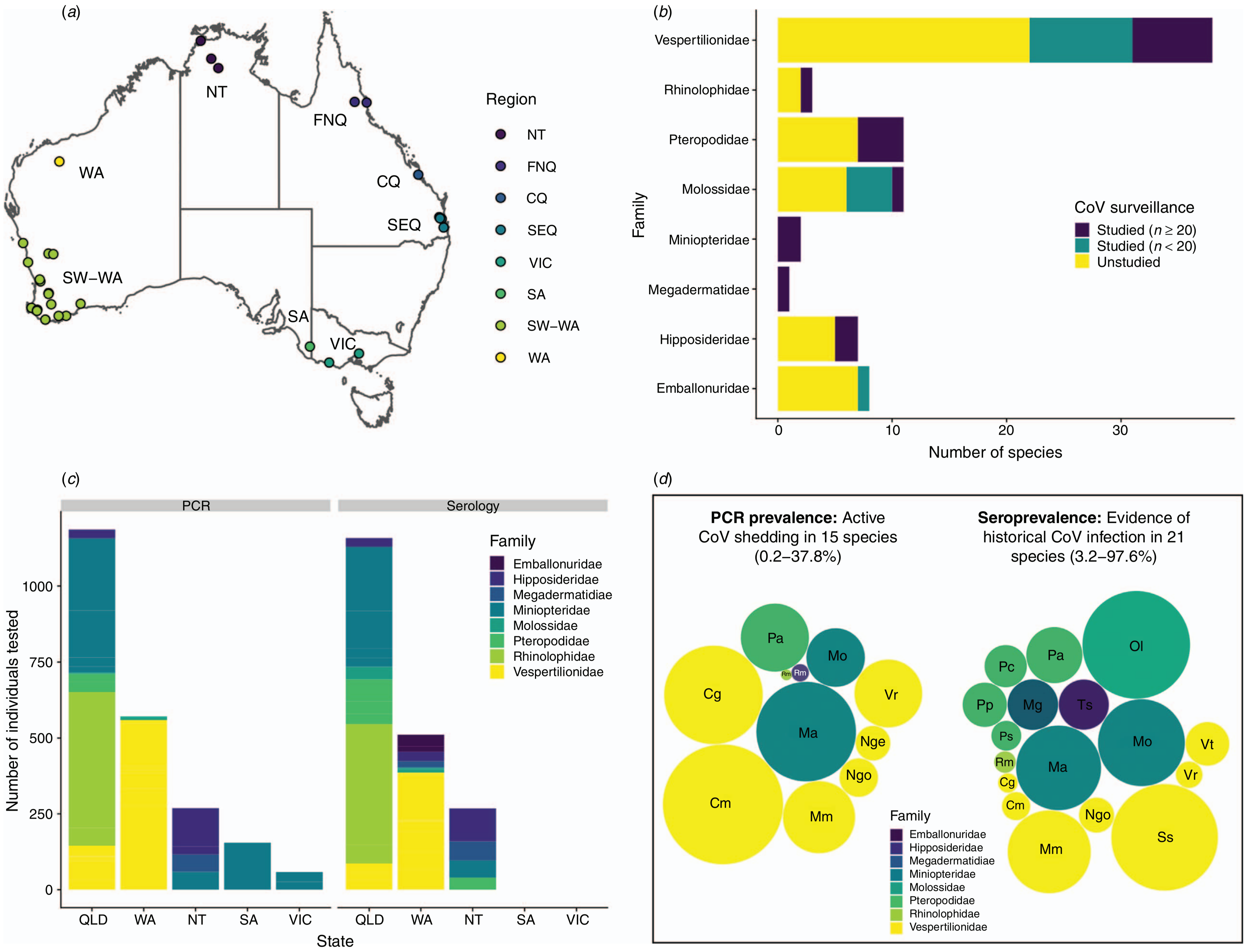


Fig. 2. (*a*) Map of sampling locations in Australian bat coronavirus studies. (*b*) Number of Australian species for which coronavirus surveillance has been undertaken, using either PCR or serology and noting whether data were derived from more or less than 20 individuals of each species. (*c*) Number 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*; Mm, *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 aurantia*; Ss, *Scotorepens* spp.; Ts, *Taphozous* spp.; Vr, *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 kapalgensis	Arnhem sheath-tailed bat	n.a.
Taphozous troughtoni	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 semoni	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 orianae[A]	Large bent-winged bat	Smith *et al*. (2016) and Holz *et al*. (2018)
Molossidae		
Austronomus australis	White-striped free-tailed bat	Prada *et al*. (2019)
Chaerephon jobensis	Greater northern free-tailed bat	Smith *et al*. (2016)
Ozimops cobourgianus	Northern coastal free-tailed bat	n.a.
Ozimops eleryi	Bristle-faced free-tailed bat	n.a.
Ozimops halli	Cape York free-tailed bat	n.a.
Ozimops kitcheneri[B]	Western free-tailed bat	Prada *et al*. (2019)
Ozimops lumsdenae[C]	Northern free-tailed bat	Smith *et al*. (2016)
Ozimops norfolkensis	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.
Macroglossus minimus	Northern blossom bat	n.a.
Nyctimene robinsoni	Eastern tube-nosed bat	n.a.
Pteropus alecto	Black flying-fox	Smith *et al*. (2016)
Pteropus brunneus	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 australis	Eastern blossom bat	n.a.
Rhinolophidae		
Rhinolophus megaphyllus	Eastern horseshoe bat	Smith *et al*. (2016)
Rhinolophus robertsi	large-eared horseshoe bat	n.a.
Rhinolophus sp.	Intermediate horseshoe bat	n.a.
Rhinonycteridae		
Rhinonicteris aurantia	Orange leaf-nosed bat	Smith *et al*. (2016)
Vespertilionidae		
Chalinolobus dwyeri	Large-eared pied bat	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 picatus	Little pied bat	n.a.
Falsistrellus mackenziei	Western falsistrelle	Prada *et al*. (2019)
Falsistrellus tasmaniensis	Eastern falsistrelle	n.a.
Murina florium	Flute-nosed Bat	n.a.
Myotis macropus	Large-footed myotis	Smith *et al*. (2016)
Nyctophilus arnhemensis	Arnhem long-eared bat	n.a.
Nyctophilus bifax	Eastern long-eared bat	Smith *et al*. (2016)

(continued next page)

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	Pygmy 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.
Pipistrellus westralis	Northern pipistrelle	n.a.
Scoteanax rueppellii	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 douglasorum	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 troughtoni	Eastern cave bat	Smith *et al*. (2016)
Vespadelus vulturnus	Little forest bat	n.a.

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

[B] Likely species identified as '*Ozimops* sp.' in Prada *et al*. (2019).

[C] The species *Ozimops lumsdenae* was formerly recognised as *Mormopterus beccarii* (identified as *M. beccarii* in Smith *et al*. 2016).

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

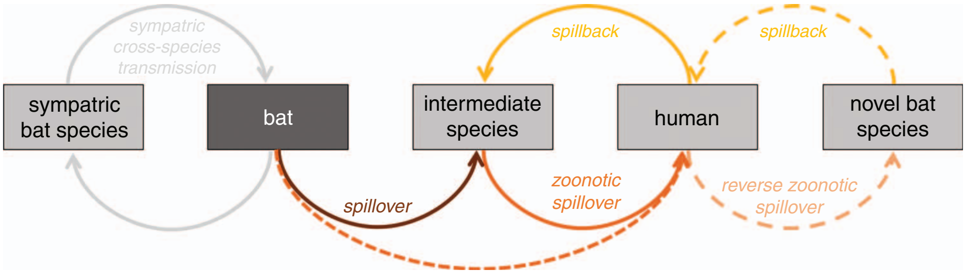


Fig. 3. Conceptual schematic representing terms for various forms of cross-species transmission of viruses associated with bats. Demonstrated transmission pathways for bat coronaviruses are shown in solid lines, hypothesised pathways are shown in dashed lines.

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*. 2017*b*), 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 endemically 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-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 care (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. orianae*) 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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