

**Population Dynamics of the Critically Endangered,
Southern Bent-winged Bat *Miniopterus orianae
bassanii***

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Abstract

Bats comprise a significant component of global biodiversity and contribute to a range of ecosystem services; but, more than half of the world's bat species assessed for conservation status have declining or unknown population trends. In this study, I investigated the population dynamics of the critically endangered, southern bent-winged bat *Miniopterus orianae bassanii*, a cave-dwelling taxon in south-eastern Australia. The southern bent-winged bat has experienced severe historical population decline but the current population trajectory is uncertain. Over three years, I tagged 2966 southern bent-winged bats with passive integrated transponder (PIT) tags. Large antennas were used to create vertical detection planes exceeding 8 m² to detect PIT-tagged bats in flight at a major maternity cave and a non-breeding cave in south-east South Australia. Fifty-two bats recaptured after PIT-tagging had their physical condition reassessed. PIT-tagging procedures were not associated with lowered body mass, infection, or irritation. Subsequent detection rates of the free-flying bats were high, with 97% of PIT-tagged individuals being detected, resulting in over 1.4 million unique detections. Apparent seasonal survival rates were lowest in summer and autumn, particularly for juveniles and lactating females. Lowest survival during the study coincided with severe drought conditions in early 2016. Bats congregated at the maternity cave for most of the year, although there were different movement and migration patterns among sex and age classes, including a previously undescribed migration event occurring over March each year. Overall, the population was more mobile than expected, with bats flying the 72 km between the two roosting caves in just a few hours. Population modelling predicts continued population decline. This study demonstrates that large PIT antennas can be used to safely and successfully detect small volant species, extending the scope for use of PIT-tag technology in wildlife research. Critically, the findings highlight the need for urgent recovery action to reduce extinction risk in the southern bent-winged bat.

Statement of authorship

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis accepted for the award of any other degree or diploma. No other person's work has been used without due acknowledgment in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Emmi van Harten

22 December 2020

Preface

This thesis consists of series of publications, with a thesis introduction and discussion as framing material. Each chapter is therefore written as a self-contained manuscript, set out in the style of the respective journal or publisher, and presented in this thesis in full. All publication details, and the nature of the candidate and co-author contributions for each jointly authored chapter, are outlined below. This research was conducted in accordance with the La Trobe University Animal Ethics Committee (AEC15-67) and under a permit provided by the South Australian Department of Environment and Water (permit U26453). The capture data and PIT-tag numbers for all the animals tagged in this study have been made accessible at OPAL doi:10.26181/5fe163436b704.

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E.v.H., R.L., L.F.L., N.M. and T.R. conceived and designed the study; E.v.H. led the trapping and tagging field work with assistance from L.F.L., T.R. and R.L.; E.v.H. and T.R. installed the RFID systems, troubleshooted system problems and downloaded data; E.v.H., T.A.A.P., T.R. and J.W. manipulated, explored and analysed the data; all authors contributed to data interpretation; E.v.H. drafted the paper; and all co-authors contributed to revising the manuscript.

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E.v.H. proposed the study; E.v.H. collected the data with assistance from L.F.L., P.H.H., T.R. and R.L.; E.v.H. analysed the data with assistance from T.A.A.P.; E.v.H. wrote the manuscript; and all authors contributed to revising the manuscript.

Chapter 5, in preparation for submission to *Journal of Animal Ecology*

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E.v.H., R.L., L.F.L., and T.R. designed the study; E.v.H. collected the data with assistance from T.R., L.F.L. and R.L.; E.v.H. and T.A.A.P analysed the data. E.v.H. interpreted the data and wrote the manuscript; all authors contributed critically to the manuscript and assisted with revision.

Chapter 6, in preparation for submission to *Wildlife Research*

van Harten, E., Lawrence, R., Lumsden, L. F., Reardon, T., and Prowse, T. A. A. (2020). Seasonal population dynamics and movement patterns of a critically endangered, cave-dwelling bat.

E.v.H, R.L., L.F.L. and T.R. designed the study; E.v.H. collected the data, with assistance from T.R., L.F.L. and R.L.; E.v.H. analysed the data with assistance from T.A.A.P; E.v.H. interpreted the data and wrote the manuscript; all authors contributed critically to the manuscript and assisted with revision.

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My supervisory team has been instrumental throughout the study. Dr Ruth Lawrence, my principal supervisor for much of my study, provided valuable guidance and support from the moment I knocked on her office door enthusiastically talking about caves and bats. Professor Noel Meyers assisted with getting the project on its feet. Dr Lindy Lumsden and Terry Reardon gave both in a supervisory capacity as well as assisting on countless field trips (including every trapping and tagging trip); their dedication to bat conservation continues to inspire me and I will always remain indebted to them. Dr Thomas Prowse came on board mid-way the project and provided much needed coding and modelling expertise (much to the relief of all of us involved). And thank you to Professor Andrew Bennett who took the reins as primary supervisor for the final year and a half of the project (after a university department restructure), providing much appreciated guidance, encouragement, and manuscript comments on the lead-up to submission.

Supervisory team aside, John (Exo) Weyland provided generous and critical assistance in the early analysis phase. Karl Pomorin provided patient advice on the RFID technology. Staff at Naracoorte Caves National Park provided knowledge, time and in-kind support throughout the project, with particular thanks to Andrew Hansford and Tom Shortt. Matt Seeliger and Ali Meyer obligingly gave continued access to their property and put up with car batteries being hauled through their dairy herd on more than one occasion. Steve Griffiths loaned equipment, and he and Lisa Godhino also taught me how to PIT-tag bats at the beginning of the study. Ian Lewis, Kevin Mott, Jake Manser and Steve Bourne assisted with a summer bat count across caves of the south-east. Steve also shared knowledge throughout the study, showed me cave locations, as well as giving permission to use photographs. Thank you also to Susan and Nicholas White for inviting me to write the book chapter presented in Chapter 2.

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Rose Thompson was my star volunteer, attending every trapping and tagging weekend, as well as assisting with data collection. Dennis Matthews gave generously in field time for trapping and technology wrangling. Amanda Bush, Yvonne Ingeme and Reto Zollinger were also dedicated volunteers throughout the trapping and tagging phase. Remaining field volunteers were numerous, with some assisting over multiple field trips and years. The effort involved was immense, including working through until sunrise, fuelled by little sleep but boundless enthusiasm and determination. It would therefore be remiss not to name them here individually (in alphabetical order): David Andrew, Aleksei Atkin, Peter Blyth, Amie Callaghan, Stacey Carter, Mary Chrichton, Evie Clarke, Clare Crane, Jemma Cripps, Celia Dickason, Cath Dickson, Danielle Eastick, Wendy Elsner, Tim Featonby, Joan Gibbs, Abby Goodman, Laura Harbridge, Bec Harmer, Cassie Hlava, Peter Holz, Jasmin Hufschmid, Carly Humphrys, Andrew Jakubowicz, Lauren Kent, Melissa Kent, Vivien Lee, Pia Lentini, Mary Long, Alex McLeod, Sonya Medhurst, Joe Miles, Tony Mitchell, Eridani Mulder, Clare Oakley, Chris O'Connell, Veronica Peric, Georgina Pritchard, Polina Rezoun, Leah Royle, Annette Scanlon, Armstrong Scherlies, Krissy Scherlies, Adrian Schoo, Madeleine Schoo-van Harten, Katrina Sofo, Emily Tomassian, Anita Torrance, Walter van Leeuwen, Anneke van Leeuwen, Cornelius van Leeuwen, Mark Venosta, Casey Visintin, Melanie Wells, Jess Whinfield, Stacy Whitehorse, Mon Winterhoff and Andrew Wurst.

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And finally, dear Krissy, after all your support to me and your grandchildren, I am still in disbelief that you are no longer here to see me submit. Your last words to me have repeated in my mind so often: ‘but now you have to finish!’. This thesis is dedicated in your memory.

Chapter 1. Introduction



Figure 1. The candidate, Emmi van Harten, preparing to descend into the major southern bent-winged bat maternity cave, Bat Cave, South Australia, to collect data during the study. Photo: Joe Miles.

Context

Earth has entered a sixth mass extinction (Ceballos *et al.* 2015) and a new human-dominated geological epoch, the Anthropocene (Lewis and Maslin 2015). Current extinction rates are conservatively estimated to be up to one hundred times higher than the average rate over the last 10 million years (Ceballos *et al.* 2015; IPBES 2019). Projected habitat loss to 2040 is estimated to double the number of threatened vertebrates globally, with little overlap between predicted areas of extinction and the distribution of current protected areas (Gonçalves-Souza *et al.* 2020). More than 20% of mammal species assessed for conservation status are listed as threatened with extinction (IUCN 2020) and currently there are 515 vertebrates species, including 1.4% of the world's terrestrial mammals, on the brink of extinction with fewer than 1000 individuals remaining (Ceballos *et al.* 2020).

Australia has the highest extinction rate of mammals in the world (Woinarski *et al.* 2019), with the leading threats identified as being habitat loss, invasive species and change in fire regimes (Lamoreux and Lacher 2010). More than 10% percent of Australia's endemic terrestrial mammals have become extinct in the last ~200 years of European colonisation (Woinarski *et al.* 2014). Loss of mammal species has occurred at a rate of about one or two species per decade since the first known extinction (circa 1840) that occurred post-European settlement (Woinarski *et al.* 2015). The two most recent Australian mammalian extinctions were the Christmas Island pipistrelle *Pipistrellus murrayi*, an insectivorous bat, and the Bramble Cay melomys *Melomys rubicola*, a native rodent: both were probably preventable (Lunney *et al.* 2011; Martin *et al.* 2012; Woinarski *et al.* 2017). Of all Australian mammals, bats and rodents are the least studied despite comprising about 45% of the terrestrial mammal fauna (Fleming and Bateman 2016).

Among mammals, bats are distinctive in their ability to undertake sustained flight. They belong to the order Chiroptera, meaning 'hand wing' (Richards and Hall 2012). The Chiroptera is one of the most speciose mammalian orders in the world (second only to rodents), with the estimated number of species in the order of over 1300 (Taylor and Tuttle 2019) to more than 1400 species (Simmons and Cirranello 2020); and representing 20% of the global mammalian fauna (Teeling *et al.* 2005).

Traditionally, the order Chiroptera was separated into two suborders on the basis of

diet and body size (Dobson 1875). The frugivorous Megachiroptera ('megabats') encompass just one family, Pteropodidae, with some species being very large (e.g. wingspan exceeding a metre (Churchill 2008)). The Microchiroptera ('microbats') generally are insectivorous and typically are much smaller. Indeed, whilst bats are spectacularly diverse, half of all bat species weigh <14 g and most (~70%) are less than 30 g. More than 86% of the variation in body mass among bats is explained by Pteropodids (Moyers Arévalo *et al.* 2020). Microbats are capable of laryngeal echolocation, whereas megabats usually navigate by well-developed eyesight (Springer *et al.* 2001). An exception is *Rousettus*, a genus of fruit bats that uses a different form of echolocation, employing tongue clicks (Roberts 1975).

Following the discovery that the superfamily Rhinolophoidea (horseshoe bats) were more closely related to megabats than to other microbats (Teeling *et al.* 2000), phylogenetic and phylogenomic analyses have revealed more complex evolutionary relationships among the Chiroptera than originally described. Currently, two new suborders are recognised (superseding Megachiroptera and Microchiroptera): Yinpterochiroptera, including the previously described 'megabats' as well as horseshoe bats, leaf-nosed bats and false-vampire bats; and Yangochiroptera, including the numerous remaining families of bats previously classed as 'microbats' (Springer *et al.* 2001; Teeling *et al.* 2005; Tsagkogeorga *et al.* 2013). As a consequence of the revised suborder division in Chiroptera, the terms 'megabats' and 'microbats' are now less commonly used and are generally avoided herein.

Globally, bats provide critical ecosystem services (Kunz *et al.* 2011). For example, flying foxes and blossom bats are significant pollinators and seed dispersers (Fujita and Tuttle 1991; Law and Lean 1999; Ratto *et al.* 2018), with some species of flying foxes moving remarkably long distances (e.g. thousands of kilometres) unparalleled by other pollinators (Roberts *et al.* 2012; Welbergen *et al.* 2020). Insectivorous bats are important predators of a range of insects, including in agricultural systems (Maine and Boyles 2015; Puig-Montserrat *et al.* 2015; Kolkert *et al.* 2019). Recent declines of bat species in North America are estimated to have cost more than \$3.7 billion US in agricultural losses per year (Boyles *et al.* 2011). The Mexican free-tailed bat *Tadarida brasiliensis* in south-central Texas, alone is estimated to provide up to \$1.725 million US in agricultural pest control services annually (Cleveland *et al.* 2006). In Australia,

for example, several species of insectivorous bats selectively prey on agricultural pest insects in dryland and irrigated cotton farms (Kolkert *et al.* 2019).

Many people in the wider community remain unaware, or are misinformed, about the diversity and importance of bat species (Tuttle 2015). Bats, particularly small insectivorous bats, are nocturnal, elusive and largely inaudible to human hearing, rendering many bat species ‘out of sight, out of mind’ of the public (Lunney and Moon 2011). Additionally, cultural prejudices and sensationalised media reporting can contribute to unnecessary fear and negative perceptions of bats, particularly in regard to disease risk (Lunney and Moon 2011; Tuttle 2015; Hoffmaster *et al.* 2016; MacFarlane and Rocha 2020). However, it is these so called ‘non-charismatic’ species that ‘may arguably be most in need of scientific and management research effort’ (Fleming and Bateman 2016, p.241). Concerningly, for over half of bat species assessed to date by the IUCN the population trend is declining or unknown, including 35% of bat species currently listed as Least Concern and therefore not considered a conservation priority (Frick *et al.* 2019).

Understanding and monitoring the population dynamics of species is important for detecting changes in population size and status, and the factors driving these changes (O’Donnell 2009). Key components of population dynamics include life-history traits such as rates of survival, births, and the timing and numbers of individuals moving in and out of the population (O’Donnell 2009). Bats typically have low reproductive rates, with females often giving birth to just one pup per year (Barclay and Harder 2003), and many species are exceptionally long-lived for their size. For example, some bat lineages live four times longer than other placental mammals of the same size (Wilkinson and Adams 2019). The current longevity record for a bat recaptured in the wild is 41 years (Podlutsky *et al.* 2005). Due to these traits, bat species are generally considered to have ‘slow’ life histories (Barclay and Harder 2003; Turbill *et al.* 2011).

Hibernation (i.e. use of prolonged periods of torpor) is common among temperate bats and is associated with high survival rates and slow-histories among mammals (Turbill *et al.* 2011). Some studies in bats have suggested a relationship between longevity and number of young, with species that birth two or more young per year having lower survival rates and shorter life expectancy (Wilkinson and South 2002; Barclay and

Harder 2003; Lentini *et al.* 2015). However, contrary to previous findings, Wilkinson and Adams (2019) found that reproductive rate did not predict longevity in bats, instead pointing to hibernation and cave use as influential factors increasing survival (both of which may protect from predation and adverse conditions). The authors attributed this revised perspective to further and more accurate survival estimates in recent years, coupled with little variation in reproductive rates among species (Wilkinson and Adams 2019). On a molecular level, long-lived bat species also have heightened DNA repair and autophagy activity compared to short-lived species (Huang *et al.* 2020).

The slow life-history traits of bats result in adult survival being a major driver of population dynamics (Schorcht *et al.* 2009). The population dynamics of bats is therefore strongly influenced by catastrophic events that impact adult survival, such as severe winters (Fleischer *et al.* 2017), droughts (O'Shea *et al.* 2011), human disturbance (López-Roig and Serra-Cobo 2014), roost collapse (Law *et al.* 2020) and novel diseases (Frick *et al.* 2015). Globally, over half of all reported multiple-mortality events in bats are anthropogenic in origin, and mortality events related to drought, storms, and other abiotic factors are likely to increase under climate change (O'Shea *et al.* 2016). Continued impact of such factors without opportunity for recovery will have a detrimental effect on population viability; driving species towards risk of extinction. For example, such trends have been observed in bat populations in North America, with local extinctions and 10-fold decrease in abundance resulting from the spread of white-nose syndrome, an infectious disease impacting hibernating bats (Frick *et al.* 2015). Another example is the continued mortality of hoary bats *Lasiurus cinereus* at windfarms, predicted to result in population declines as high as 90% over the next 50 years (Frick *et al.* 2017). The combination of increased mortality and chronic threats from widespread habitat loss (foraging and roosting) in the Anthropocene is particularly concerning for bat populations due to reliance on high survival rates in their population dynamics (O'Shea *et al.* 2016).

Nevertheless, there is some cause for hope; conservation action has thus far prevented numerous imperilled species from extinction (Garnett *et al.* 2018b; Bolam *et al.* 2020). Since 1993, global extinction rates in mammals and birds would have been 2.9–4.2 times higher without conservation action (Bolam *et al.* 2020). Such successful

conservation action relies heavily on an understanding of species ecology and population trends, the impact of identified threats and the options to control these threats (Garnett *et al.* 2018a).

Ranked among Australia's top 20 most imperilled mammals, the southern bent-winged bat *Miniopterus orianae bassanii* (Fig. 2) has been assessed as having an 18% likelihood of extinction in the next 20 years (Geyle *et al.* 2018). A national recovery plan for this species was recently adopted by the Australian Government (DELWP 2020) and in late 2019 a National Recovery Team was established (SWIFFT 2020). However, the cause of severe decline in the southern bent-winged bat is uncertain (DELWP 2020), current population trends are unknown, and whilst bent-winged bats are among Australia's most studied bat species (Chapter 2), numerous questions remain about its ecology. This thesis represents an effort (with assistance of numerous volunteers and scientists) to amend some of these knowledge gaps and help save the southern bent-winged bat from the same fate as the recently extinct Christmas Island pipistrelle.



Figure 2. A southern bent-winged bat *Miniopterus orianae bassanii*, held in gloved hands. Photo: Emmi van Harten.

The southern bent-winged bat *Miniopterus orianae bassanii*

Description, range and taxonomy

The southern bent-winged bat (average 15 g) is an insectivorous cave-dwelling bat with a restricted distribution in south-west Victoria and south-east South Australia (Fig. 3) (DELWP 2020). From spring to autumn, southern bent-winged bats congregate *en masse* at two main maternity caves located approximately 220 km apart: Bat Cave located in Naracoorte Caves National Park World Heritage Area in South Australia, and a cave on private property near Warrnambool in Victoria (Dwyer and Hamilton-Smith 1965; DELWP 2020). A third maternity site, with significantly smaller numbers of bats, has recently been found near Portland, Victoria (DELWP 2020). The maternity sites are of critical importance to the populations by facilitating the microclimate needed for raising their young. For example, the domed ceiling of the maternity chamber at Bat Cave has been demonstrated to trap heat (primarily

generated by the presence and activity of the bats themselves), thereby increasing the temperature in the dome of the chamber to more than 30° C over the breeding season (Baudinette *et al.* 1994). During the winter, bats disperse to non-breeding caves and rock crevices across the distribution. These sites primarily occur in limestone, however, some basalt caves are also used (DELWP 2020).

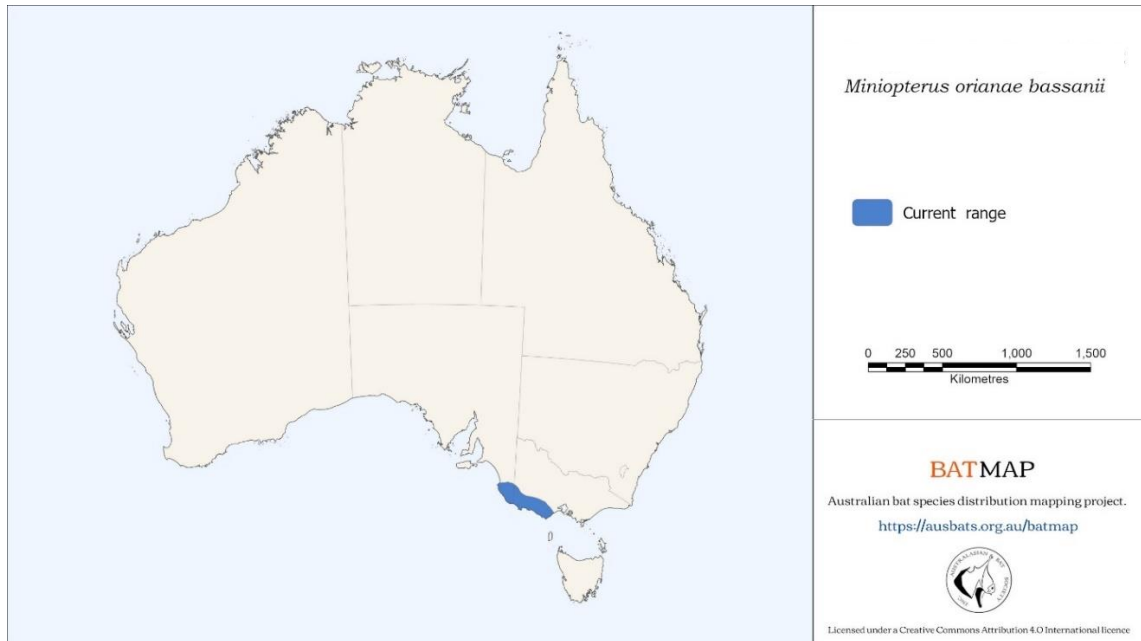


Figure 3. Distribution of the southern bent-winged bat.

The southern bent-winged bat was originally identified as belonging to the species *Miniopterus schreibersii* (subspecies *M. s. blepotis*) from specimens collected from the South Australian population (Leche 1884). *Miniopterus schreibersii* was once considered the most widespread bat species in the world, occurring over regions of Africa, Asia, Australasia and Europe (e.g. Dobson 1878). However, taxonomic revision has shown that the widespread distribution of *Miniopterus schreibersii* was due to ‘incorrect taxonomy and not exceptional dispersal ability’ (Appleton *et al.* 2004, p.437). It has since been recognised that *M. schreibersii* is, in fact, a taxonomic complex containing many species (Appleton *et al.* 2004; Miller-Butterworth *et al.* 2005), including the large bent-winged bat *Miniopterus orianae* on mainland Australia (Jackson and Groves 2015). The southern bent-winged bat is currently described as one of three distinct subspecies of *M. orianae* (Cardinal and Christidis

2000; Jackson and Groves 2015); however, investigations are currently underway to determine if the southern bent-winged bat warrants elevation to full species status (Wiantoro and Armstrong 2019). Differences between the southern bent-winged bat and other large bent-winged bat subspecies in Australia include genetics (Cardinal and Christidis 2000), morphometrics (Cardinal and Christidis 2000; Wilson 2008; Holz *et al.* 2020), echolocation frequency (Conole 2000), the presence of adult males at maternity sites (Dwyer and Hamilton-Smith 1965), and earlier typical birthing periods (Dwyer and Hamilton-Smith 1965; Richardson 1977). Morphometric differences also occur between southern bent-winged bats from the Naracoorte and Warrnambool populations (Wilson 2008; Holz *et al.* 2020), which may be explained by climatic variation between the two regions, despite close geographic proximity (Wilson 2008).

[NB: while the southern bent-winged bat is regarded as a subspecies, *Miniopterus orianae bassanii*, for the purpose of simplicity in this thesis I regularly use the term 'species' to refer to this taxon].

Historical overview and biology

Extensive guano deposits at roosting caves of the southern bent-winged bat, particularly maternity caves, attracted guano mining in the 19th century (Hamilton-Smith 1998). Records report private and commercial mining at Bat Cave from the 1870s to 1897, with guano being sold by the tonne for use as fertiliser (Hamilton-Smith 1998). Guano 'poaching' was also common practice. At the maternity cave near Warrnambool, guano was winched to the surface (Gill 1948), with observations of a windlass in place as early as 1857 (Bonwick 1858). Some caves were altered to facilitate such retrieval of the guano, resulting in a significant change in cave microclimate. Several caves were abandoned by the bats, including some that are thought to have previously been maternity caves (Baudinette *et al.* 1994). A shaft was sunk into the ceiling of Bat Cave's maternity chamber circa 1888; however, fortunately it was refilled after mining ceased (Hamilton-Smith 1998). The roof of a second suspected maternity cave near Naracoorte was not restored until over a century later in 1994 (Baudinette *et al.* 1994). Bats have resumed use of this cave after the restoration, but not as a maternity site. It is not known what occurred to the bats at Bat Cave during the guano mining era: if they deserted the maternity cave, then they apparently returned soon afterwards (Hamilton-Smith 1998).

The first research into the ecology of the southern bent-winged bat began in the 1960s, including banding, documentation of cave sites, and some population counts (Dwyer and Hamilton-Smith 1965; Dwyer 1969). The peak population at Bat Cave was estimated at 100,000–200,000 individuals and 10,000–20,000 at Warrnambool (Dwyer and Hamilton-Smith 1965). Analysis of banding data has suggested little migration occurs between these two maternity caves; however, movement from both these areas to non-maternity caves in the intermediate Portland and Byaduk areas were somewhat more common, comprising less than 5% of the total identified movements (Dwyer 1969). Interestingly, the remaining movements were concentrated in three main regions – South Australia, Portland-Byaduk, and Warrnambool – leading Dwyer (1969) to speculate that there may be a third unknown maternity cave in the Portland-Byaduk region. It is unknown how long the newly-located maternity cave near Portland has been used as a breeding site.

The reproductive biology of this species has been studied by using adult female and male specimens collected from caves at Naracoorte (Richardson 1977; Crichton *et al.* 1989; Krutzsch and Crichton 1990). Mating occurs in autumn, with spermatogenesis, insemination, ovulation and fertilisation being synchronised over April and May (Richardson 1977; Crichton *et al.* 1989; Krutzsch and Crichton 1990). A period of delayed implantation (Richardson 1977; Crichton *et al.* 1989) and delayed embryonic development (Crichton *et al.* 1989) occurs during winter torpor, with development of the foetus resuming in spring. Crichton *et al.* (1989) describe late-May to mid-August as a period of prolonged torpor or hibernation, and the remainder of May and mid-August to mid-September as intermittent torpor, based on the behaviour of bats in the caves during collection of study specimens. Mothers birth one pup per year (Richardson 1977). Observations in the 1960s and 1970s record birthing periods ranging between mid-late October to mid-December at Bat Cave (Dwyer and Hamilton-Smith 1965; Hamilton-Smith 1972; Richardson 1977) and late November to late December at Warrnambool (Dwyer and Hamilton-Smith 1965; Hamilton-Smith 1972).

In 1995, infra-red cameras were installed in Bat Cave to provide video footage to the nearby Bat Televue Centre for bat tours conducted at the national park (Reed and Bourne 2013). Observations from the cameras showed that bats were significantly more active in the maternity chamber compared to cooler parts of the cave, and

overall spent 62% of their roosting time at rest, 16% grooming and 22% active (Codd *et al.* 2003). Bats were also observed drinking water dripping or permeating through the limestone, as well as licking the limestone, which in addition to hydration may provide an important source of calcium (Codd *et al.* 1999).

Little is known about diet and foraging habitat of the southern bent-winged bat. Genetic analysis of guano deposits collected in autumn 2019 showed that prey were almost entirely Lepidoptera (moths) (Kuhne 2020). It remains unknown whether dietary preferences vary seasonally. Moth wings are sometimes observed at southern bent-winged bat roosts (McKean and Hall 1964; DELWP 2020) and moths have also been described as the main stomach contents of bent-winged bats in other parts of Australia (now recognised as other subspecies) (Vestjens and Hall 1977). Radio-tracking has been used to try to determine preferred foraging grounds of southern bent-winged bats; however, efforts were hampered due to the difficulty in following tagged bats (Bourne 2010). Southern bent-winged bats are fast flyers, typically flying high over the canopy in treed areas: therefore, an airplane with an attached receiver was used to follow a small number ($n = 6$) of tagged bats (Bourne 2010). Radio-tagged individuals tended to emerge from Bat Cave in the same order each night and fly in the same direction on successive nights. Two lactating females flew more than 25 km south in the first two hours of emergence, ending up in the same location. An adult male was tracked more than 35 km northeast from Bat Cave on successive nights. Unfortunately, the signal was consistently lost after approximately two hours. Radio-tagged bats were recorded flying over both forested and open areas as well as vineyards. Wetlands appear to provide important foraging habitat (Stratman 2005; DELWP 2020).

For conservation planning purposes, aspects of the behaviour and ecology of the southern bent-winged has been assumed to follow a similar pattern to the eastern bent-winged bat *Miniopterus orianae oceanensis* (DELWP 2020). Research on this taxon (predominantly by banding) in New South Wales has described the biology of the different sex and age cohorts in detail, including seasonal movement, activity patterns, changes in body mass and inferred survival rates (Dwyer 1963; Dwyer 1964; Dwyer 1966b; Hall 1982). Dwyer (1966a) also assessed mortality factors in the eastern bent-winged bat and suggested that starvation may be a significant cause of mortality, particularly if individuals are unable to lay down enough fat reserves before winter.

This could lead to bats needing to search for food in ‘unfavourable conditions’ (Dwyer 1966a). Understanding of these population dynamics in southern bent-winged bats, and the full seasonal cycle, would greatly assist in assessing the relative importance of known population threats and how these threats may be effectively managed.

Decline and threats

The southern bent-winged bat was listed as critically endangered under the Australia’s *Environment Protection and Biodiversity Act* in 2007, due to severe decline in numbers and dependence on just two main breeding sites (DELWP 2020).

A mark-recapture study undertaken in 2000 estimated a population of 65,000 in Bat Cave, a decline from 100,000–200,000 in the early 1960s; however, there was high uncertainty around this newer estimate (DELWP 2020). Further monitoring using video recording of bats as they emerged from the cave at dusk suggested continued decline from 35,000 in 2001 to as few as 20,000 in 2009 (Kerr and Bonifacio 2009). Regular counts were conducted using missile-tracking software and thermal imagery for 12 months from August 2011 to 2012. The breeding season counts during this period (undertaken two to three times per week) showed that numbers emerging fluctuated between approximately 25,000 and 37,000, peaking at approximately 40,000 after the juveniles commenced flying (Lear 2012b). The cause of this fluctuation was unclear. Possible explanations include bats temporarily roosting at other cave locations in the summer (despite previous assumptions that virtually all bats remained at Bat Cave) (Lear 2012b). A potential relationship between numbers counted and minimum temperature was also suggested by Lear (2012b) but not statistically tested.

Summer counts at the maternity cave in Warrnambool are in the order of 17,000 (Lumsden *et al.* 2019), and as such does not appear to have undergone significant decline compared to the estimates of 10,000–20,000 in the 1960s (Dwyer and Hamilton-Smith 1965). However, it is difficult to compare such estimates due to the developments in counting methods, which have significantly improved accuracy in recent years. Recent monitoring undertaken at key Victorian caves, with new software (Hield *et al.* 2018) and conducted on successive nights, are also revealing large fluctuations in bat numbers between nights (Lumsden *et al.* 2019). There is a

discrepancy between summer population numbers and winter cave counts, the latter of which account for less than half of individuals, including when counts were undertaken simultaneously across the South Australian and Victorian range (Lear 2012a). This may be due to some bats using rock crevices or unknown cave locations such as sea cliff caves over winter.

The cause of decline from the early 1960s to 2000s at Bat Cave is uncertain: pesticides were initially implicated as a potential cause (Allinson *et al.* 2006). Pesticides (including DDT) have been identified in the guano deposits, in adult bats (Allinson *et al.* 2006) and juvenile bats, likely through their mother's milk (Mispagel *et al.* 2004). The effect of sub-lethal levels of pesticides in southern bent-winged bats is not known. Authors that have investigated pesticide levels in this species have suggested that potential effects (based on literature on other species) could include increased metabolic rates, which could decrease winter survival if bats are unable to store sufficient fat reserves for hibernation (Allinson *et al.* 2006), and suppressed immune function (Holz 2018). However, Allison *et. al.* (2006) suggested that other factors such as landscape change, disturbance and a drying climate may be more influential.

Drought and climate change are identified as key threats to the southern bent-winged bat (DELWP 2020). Hundreds of dead bats, predominantly emaciated pups, were observed in Bat Cave in late 2006 (Bourne and Hamilton-Smith 2007) during the severe Millennium Drought in southeast Australia (Ummenhofer *et al.* 2009; Rashid and Beecham 2019). Notably, the dripping points accessed within Bat Cave by the bats for drinking dried up during this time. The drought, in conjunction with unusually low nightly temperatures occurring during the birthing period in 2006, is also thought to have reduced food availability leading to females abandoning their young (Bourne and Hamilton-Smith 2007). Foraging success is likely further affected by the significant reduction in former native habitat and wetlands across the range of the southern bent-winged bat.

Two disease outbreaks in southern bent-winged bats have also coincided with drought events. An unknown virus caused an epidemic in the Bat Cave population in 1967, with qualitative assessments reporting that numbers dropped to about 60,000 (DELWP 2020). However, accounts from the following decades suggest that by the

early 1980s, population numbers had recovered to prior levels (DELWP 2020). An outbreak of nodular skin lesions caused by nematodes (possibly transmitted by Nycteribiid flies, known as ‘bat flies’) occurred in September 2009; however, no significant adverse impact on individuals was noted, with bats otherwise in good body condition (McLelland *et al.* 2013). Health and disease were recently investigated by wildlife veterinarian Dr Peter Holz and compared to that in eastern bent-winged bats. Several herpes viruses (Holz *et al.* 2018a) and a diverse range of fungal skin flora (Holz *et al.* 2018c) were identified, as well a number of internal and external parasites (Holz *et al.* 2018b; Holz *et al.* 2019a); however, none were associated with any signs of illness in the bats and were considered unlikely to be a leading cause of mortality or decline. Holz (2018, pp.200–201) states that ‘while disease is not driving the southern bent-winged bat to extinction it may be acting as a red flag, indicative of a species that is currently struggling with a multitude of challenges which it faces into an uncertain future’.

As part of recent health assessments in southern bent-winged bats, a risk assessment was undertaken for the threat of white-nose syndrome in Australian bats (Holz *et al.* 2019b). White-nose syndrome is a fungal infection caused by *Pseudogymnoascus destructans* (Lorch *et al.* 2011) and has caused mass fatalities of hibernating bats in North America since 2006 (Turner *et al.* 2011) (see Chapter 2 for further background about white-nose syndrome). The Australian risk assessment found that it is ‘almost certain/highly likely’ that *P. destructans* will enter Australia and ‘likely’ to contact Australian bats in the coming decade (Holz *et al.* 2019b). The Australian species considered most at risk is the southern bent-wing bat, because of three main factors. First, southern bent-winged bats inhabit caves within the optimal growth temperatures for *P. destructans* (Holz *et al.* 2019b; Turbill and Welbergen 2020). Second, southern bent-winged bats cluster in large groups, which is a factor associated with high susceptibility to white-nose syndrome due to increased bat-to-bat contact (Holz *et al.* 2019b). Third, further population decline could be detrimental as the southern bent-winged bat is already critically endangered (Holz *et al.* 2019b).

Little is known about winter activity and hibernation behaviour of many Australian bat species, including the southern bent-winged bat. More information is urgently needed to better assess the vulnerability to white-nose syndrome (Turbill and Welbergen 2020) and to strengthen response strategies (Holz *et al.* 2019b). Further, if

winter is a time of high mortality, as suggested by Dywer (1966a) in eastern bent-winged bats, further information about winter ecology may provide important information to improve management and conservation.

Windfarm development in the range of the southern bent-winged bat is also an emerging and increasing threat, with both white-nose syndrome and collision with wind turbines being the current leading causes of mass mortality events in bats globally (O'Shea *et al.* 2016). Migrating bats are known to be at higher risk of windfarm mortality (Cryan and Barclay 2009). Dead southern bent-winged bats have been recovered through monitoring of Victorian windfarms, but there is a high degree of uncertainty around estimates of the level of bat mortality and the effect on population viability (Moloney *et al.* 2019). Information is also needed about population migration patterns, such as routes and timing of movements, to facilitate targeted monitoring and mitigation strategies (DELWP 2020). Despite the significant banding efforts of the 1960s (Dwyer 1969), little is known about southern bent-winged bat movements to and from maternity caves and other cave roosts. Hamilton-Smith (1972, p.69) stated that 'the greater part of the population departs the Bat Cave during February and early March' and that 'large numbers of animals commence to return to the cave in September'; whilst Codd *et al.* (2003, p.309) describe many bats still present at Bat Cave in March 1997 and that 'many bats had left for their overwintering caves' by May of the same year.

The *National recovery plan for the southern bent-winged bat* (DELWP 2020) was drafted in 2013 and has recently been adopted by the Australian Government. The recovery plan summarises known and potential threats to the subspecies and provides a list of recommended research and management actions. Highlighted in the plan is the 'urgent need to determine the factors contributing to decline, so that the most effective and targeted management actions can be implemented' (DELWP 2020, p.1). Of pivotal importance is identifying which bats in the populations are dying and when this occurs, so that the cause of mortality can be better understood. The recovery plan includes a recommendation for investigating the use of passive integrated transponder (PIT) technology to undertake passive monitoring at cave locations, and to conduct a survival analysis of sex and age cohorts (DELWP 2020). It was through this recommendation that the PhD research presented in this thesis was conceived.

Study aims and objectives

The overall aim of this research is to investigate the population dynamics of the southern bent-winged bat for the purpose of informing conservation and recovery. This aim has been addressed through setting the following objectives.

1. Investigate the use of passive integrated transponder (PIT) tag technology and develop methods for passively monitoring flying bats in large cave-passages, without interrupting the flight path of the bats.
2. Following PIT-tagging and application of surgical adhesive, determine any potential effects on recaptured southern bent-winged bats (including changes in body mass and healing of the PIT-tag injection site).
3. Investigate survival rates of PIT-tagged bats and predict population trends at the major maternity site, Bat Cave.
4. Describe the full seasonal cycle of the southern bent-winged bat, including identifying migration and congregation events undertaken by the population's sex and age classes.

Thesis outline

The aim and objectives of this study form the basis of six subsequent chapters in this thesis. In Chapter 2, I further review the context of the plight of the southern bent-winged bat by examining the ecology, research methods and conservation issues of cave-dwelling bats in Australia. In this chapter, I highlight the number of cave-dwelling bat species in Australia, the diversity of cave use and requirements, and the evolving research methods being used to better understand the ecology of these species. I outline the past, current and emerging threats to cave-dwelling bats which have led to this group of mammals being disproportionately threatened with extinction. [NB: Please note that this is an invited chapter in an edited book, written for a general audience with an interest in karst and caves in Australia].

Chapter 3 describes the key challenges in mark-recapture and tracking of small bat species and some of the limitations to date in using PIT-technology to overcome these challenges, including the size and read-range of antennas. The chapter details the methods used in this study, and the results obtained, to optimise performance of a large antenna system for successfully detecting southern bent-winged bats in flight.

Several recommendations are made for other researchers considering using these methods for other species.

Chapter 4 describes the procedure used in this study for PIT-tagging individuals and the recovery observed in recaptured bats, including body mass and physical appearance of the injection site. The work reported in this chapter significantly increases the number of individual insectivorous bats physically recaptured and reassessed in the wild after PIT-tagging (and the associated use of surgical adhesive on the injection site). It adds to the knowledge on marking effects and will assist researchers and wildlife managers to make informed ethical considerations in regards to their study species.

The fifth chapter presents a seasonal survival analysis of PIT-tagged, southern bent-winged bats over a three-year period. The final survival model is presented, including seasonal and annual variability in apparent survival of different sex, age and reproductive classes in the population. The survival rates are used to predict current population trends, and the likely drivers of past and present decline are discussed.

Chapter 6 describes the full seasonal cycle of the southern bent-winged bat, including the timing of congregation and migration events undertaken by population sex and age classes. The impact of observed movement patterns and extended congregation at the maternity cave is discussed with regard to identified population threats and implications for the emerging risks of windfarm development and white-nose syndrome in Australia.

The final chapter, Chapter 7, provides a general synthesis of the findings, management implications for the conservation and recovery of the southern bent-winged bat, and recommendations for further research in light of the results of this study.

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Chapter 2. Cave-dwelling bats in Australia: ecology and conservation

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Cave-dwelling bats in Australia: ecology and conservation

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Bats have inhabited cave and karst systems in Australia for millions of years. A cave-dwelling species dating to the early Miocene (23.3–16.3 Ma), and a close relative of the extant orange leaf-nosed bat *Rhinonictoris aurantia*, has been recovered from the Riversleigh fossil deposits in Queensland in their thousands (Hand 1998). The earliest known species of bat in Australia, dating from the Eocene (~54.6 Ma), was also recovered from fossil deposits in Queensland. These ancient mammals were already adapted for sustained flight and had the ability to echolocate, though their roosting habits remain unknown (Hand *et al.* 1994).

Bats are loosely categorised as ‘forest bats’ or ‘cave bats’ according to their day-time roosting habits. Of the 81 species of bats currently recognised in Australia (Armstrong *et al.* 2020), approximately one-third are known to use caves (Table 1, Churchill 2008) and half of these species are endemic (Tanalgo and Hughes 2019). Some species use both caves and forest roosts (such as tree-hollows). For example, the chocolate wattled bat *Chalinolobus morio* primarily roosts in tree-hollows, but is cave-dwelling in regions such as the Nullarbor Plain where the landscape is relatively treeless. Interestingly, despite there being numerous caves in Tasmania, none of the bat species found in Tasmania are known to commonly use caves (Cawthen 2015).

Evidence of the use of caves by bats can be noted through the presence of guano. Some sites that have long-term use as maternity sites have large guano deposits, forming huge mounds that were historically mined in Australia for fertiliser and gunpowder (Hamilton-Smith 1998; Hall and Richards 2003). Bats have high site fidelity to roosts, especially to maternity caves, and there is evidence that some have been used for hundreds of thousands of years. Cases occur where the accumulated guano mounds have effectively filled the cave and rendered it no longer useful for bat habitation (Hall and Richards 2003). Less frequently used roost sites in caves, or sites

used in smaller numbers such as for wintering sites, may have small guano deposits, observed as small piles or littered across the floor of the cave.

Guano and fossil deposits provide evidence of the historical range contraction of the ghost bat *Macroderma gigas* (Fig. 1) to its current restricted range in northern Australia. High numbers of mummified carcasses of ghost bats are found in guano from the Flinders Ranges, South Australia (Hamilton-Smith 1998). Ghost bat guano deposits are found in central Australia, including in the caves of Uluru, where ghost bats were recorded until 1970 (Churchill 2008).



Figure 1. Ghost bat *Macroderma gigas* emerging from a limestone cave in Far North Queensland. Photo: Jannico Kelk.

Table 1. Conservation status of cave-dwelling bats in Australia. Species and subspecies listed are those known to commonly use cave roosts (as per Van Dyck *et al.* 2013). An addition is the chocolate wattled bat, usually tree-roosting but which commonly uses cave roosts in some regions (Churchill 2008). Species thought to use caves only occasionally (e.g. little pied bat *Chalinolobus picatus*, greater northern free-tailed bat *Chaerephon jobensis*) are excluded; and roosting preferences for some species, such as the intermediate horseshoe bat *Rhinolophus* sp. (intermediate form) remain unknown (although this species is likely cave-roosting). Taxonomy follows Armstrong *et al.* (2020). National conservation status is according to listing on the *Environment Protection and Biodiversity Conservation Act 1999* and state/territory listings refer to the respective environmental state legislation (NSW=New South Wales, NT=Northern Territory, SA=South Australia, VIC=Victoria, WA=Western Australia) in October 2020.

Family	Binomial name	Common name	Roost	Conservation status
Pteropodidae	<i>Dobsonia magna</i>	bare-backed fruit bat	caves, boulder piles, mines, abandoned houses, dense vegetation	
Megadermatidae	<i>Macroderma gigas</i>	ghost bat	caves, boulder piles, mines	Vulnerable (National, WA), Endangered (QLD), Near Threatened (NT)
Rhinonycteridae	<i>Rhinonictis aurantia</i>	orange leaf-nosed bat	caves, mines in dry season; probably trees in wet season	Vulnerable (QLD)
	<i>R. aurantia</i> (Pilbara form)*	Pilbara leaf-nosed bat	caves, mines	Vulnerable (National, WA)
Hipposideridae	<i>Hipposideros ater</i> * <i>H. a. aruensis</i> <i>H. a. gilberti</i>	dusky leaf-nosed bat	caves, mines, tree-hollows	

	<i>Hipposideros cervinus</i>	fawn leaf-nosed bat	caves, mines	Vulnerable (QLD)
	<i>H. c. cervinus</i>			
	<i>Hipposideros diadema</i>	diadem leaf-nosed bat	caves, mines, old sheds, large culverts	Near Threatened (QLD)
	<i>H. d. reginae</i>			
	<i>Hipposideros inornatus</i>	Arnhem leaf-nosed bat	caves, mines	Endangered (National), Vulnerable (NT)
	<i>Hipposideros semoni</i>	Semon's leaf-nosed bat	caves, mines, overhangs, cracks	Vulnerable (National), Endangered (QLD)
	<i>Hipposideros stenotis</i>	northern leaf-nosed bat	cracks, caves, boulder piles, mines	Vulnerable (NT, QLD)
Rhinolophidae	<i>Rhinolophus megaphyllus</i> *	eastern horseshoe bat	caves, mines, culverts, bunkers, boulder piles, houses	Vulnerable (VIC)
	<i>R. m. megaphyllus</i>			
	<i>R. m. ignifer</i>			
	<i>Rhinolophus robertsi</i> *	large-eared horseshoe bat	caves and mines	Vulnerable (National), Endangered (QLD)
Emballonuridae	<i>Taphozous australis</i>	coastal sheath-tailed bat	sea caves, fissures, boulder piles	Near Threatened (QLD)
	<i>Taphozous georgianus</i> *	common sheath-tailed bat	vertical cracks in caves or mines	
	<i>Taphozous hilli</i>	Hill's sheath-tailed bat	vertical cracks in caves or mines	Rare (SA)
	<i>Taphozous troughtoni</i> *	Troughton's sheath-tailed bat	caves, mines, cracks, solution pipes	
Miniopteridae	<i>Miniopterus australis</i> *	little bent-winged bat	caves, tunnels, mines, stormwater drains	Vulnerable (NSW)
	<i>M. a. australis</i>			
	<i>Miniopterus orianae</i> *	large bent-winged bat		
	<i>M. o. orianae</i>	northern bent-winged bat	caves, bunkers, drains, silos	
	<i>M. o. oceanensis</i>	eastern bent-winged bat	caves, mines, bunkers, lava tubes	Vulnerable (NSW, VIC)
	<i>M. o. bassanii</i>	southern bent-winged bat	caves, lava tubes	Critically Endangered (National, VIC), Endangered (SA)

Vespertilionidae	<i>Chalinolobus dwyeri</i>	large-eared pied bat	rock overhangs, caves, mines, fairy martin nests	Vulnerable (National, NSW, QLD)
	<i>Chalinolobus morio</i>	chocolate wattled bat	usually tree-hollows; cave- dwelling in south-west and Nullarbor regions	
	<i>Myotis macropus</i>	large-footed myotis	caves, mines, tree-hollows, bridges	Vulnerable (NSW), Endangered (SA), Near Threatened (VIC)
	<i>Vespadelus caurinus</i>	northern cave bat	caves, mines, culverts	
	<i>Vespadelus douglasorum</i>	yellow-lipped cave bat	caves	Vulnerable (NSW)
	<i>Vespadelus finlaysoni</i>	Finlayson's cave bat	caves, fissures, mines	
	<i>Vespadelus troughtoni</i>	eastern cave bat	caves, overhangs, mines, culverts, fairy martin nests, buildings	

*Taxonomic revision in progress

Almost all cave bats in Australia are insectivorous, and insect remains can often be identified in the crumbly guano on which numerous cave guano invertebrates feed (Moulds 2004). Discarded moth wings are observed at roosts, especially under the roosts of bent-winged bats which favour Lepidopteran prey (Vestjens and Hall 1977). The ghost bat takes both vertebrate and invertebrate prey, with prey remains such as bones, feathers and even the wings of smaller bats often being observed on the ground at caves that are used as night roosts (Vestjens and Hall 1977; Tidemann *et al.* 1985). The cave-dwelling diadem leaf-nosed bat *Hipposideros diadema* is also occasionally carnivorous (Pavey and Burwell 1997). However, two species of fruit bats have also been observed using caves in Australia. The bare-backed fruit bat *Dobsonia magna* uses caves, granite boulder piles and mine sites in Cape York (Hall and Richards 2003), whilst the black flying fox *Pteropus alecto* has been observed using the ‘better lit portions of large open caves’ at Chillagoe, Queensland and Tunnel Creek, Western Australia (Churchill 2008, p.70). Camps of this latter species normally roost in forests and mangroves.

Why do bats use caves? With cave passages extending up to hundreds of metres underground, there is protection from predators and little competition for space (unlike tree hollows, for example), particularly with echolocation allowing most bat species to navigate well beyond the twilight zone. Additionally, many caves provide a relatively stable temperature and humidity year round (Sanderson and Bourne 2002). Indeed, as two of Australia’s pioneering bat researchers stated, ‘bats have not adapted to caves, they have exploited them’ (Hall and Richards 2003, p.112).

The aim of this chapter is to give an overview of changes in understanding of the ecology of cave-dwelling bats in Australia (focusing on cave use), the evolving ecological research methods used to study these bats, and issues in the conservation of these species in Australia.

Early understanding of Australian cave bats

Indigenous peoples were the first people to encounter cave bats on the Australian continent over 60,000 years ago; for example, a cave used by the large-eared pied bat *Chalinolobus dwyeri* in Ukerbarley Aboriginal Area, New South Wales, also contains tools and signs of extended occupation by the Kamilaroi people (M. Pennay, pers.

comm). Bats were named in hundreds of Aboriginal languages before European colonisation, in some cases to species-level (e.g. Burbidge *et al.* 1988), and they remain an important part of First Nations cultures and knowledge of Country.

The first studies of Australian cave bats by Europeans were largely focused on taxonomic description of species (e.g. Leche 1884; Troughton 1937); a difficult and ongoing task. Taxonomy of bats is continually evolving and some species, such as the bent-winged bats of Australasia (and indeed across the globe), have been particularly problematic and confusing due to their similar appearance, overlapping morphological measurements and the piecemeal approach to their taxonomic descriptions (Appleton *et al.* 2004; Wiantoro and Armstrong 2019). Beyond taxonomy, other early studies of bats in Australia included the distribution, ecology, and economic impact of flying foxes by Francis Ratcliffe from 1929–1931, who travelled thousands of kilometres of the Australian east coast on motorbike (Ratcliffe 1931; Richards and Hall 2012). Ratcliffe reported that these species did not pose an economic problem to fruit orchards and that numbers of some flying fox populations were in decline. By 1938, the widespread demise of Australian terrestrial mammals and the resulting economic impact was recognised, including the importance of insectivorous bats as providers of insect control (Troughton 1938). However, the ecology of insectivorous bats was still relatively poorly understood until the ‘banding boom’ during the mid-twentieth century.

The first cave bats to be banded in Australia occurred in 1957 in Canberra as a ‘weekend hobby’ by members of the Canberra Speleological Society (Purchase and Hiscox 1960). Colonies of the large bent-winged bat *Miniopterus orianae*, eastern horseshoe bat *Rhinolophus megaphyllus* and large-footed myotis *Myotis macropus* were the first to be banded. By 1959, the first patterns were emerging from the data and the first report on bat-banding in Australia was published (Purchase and Hiscox 1960). Probable seasonal migration was reported for the large bent-winged bat, with a female being recovered 180 miles (~280 kilometres) from the original banding site. Fewer individuals of the large-footed myotis had been banded, but they appeared to be comparatively stationary with a high proportion recovered in the same cave, including some individuals that were handled on five out of seven trips.

A bat banding scheme was developed under the Australian Bird Banding Scheme in 1960. By the sixth, seventh and eighth annual reports of the Scheme, bats were reportedly being banded in all states and territories of Australia (Purchase 1969). Eleven bat species had been banded with either bird bands or flanged bat bands, though 15,602 of the 17,227 individuals banded (91%) were large bent-winged bats. Initially bird bands were applied to the forearm of the bats, however, flanged bat bands were introduced in 1962 and produced fewer injuries (Simpson and Hamilton-Smith 1965).

Cave-dwelling bats were the first to be targeted for study because they could be reliably caught in large numbers using simple methods such as plucking bats off cave walls, using hand-held nets and a 'cluster-basket' (a rigid, funnel-type instrument that was placed over clusters to capture the bats) (Purchase and Hiscox 1960). At Bat Cave (U2), Naracoorte, South Australia, bats were hauled up to the entrance in large numbers to be banded (I. Lewis, pers. comm). In contrast, only a small number of forest bats were banded in these early research efforts due to difficulty catching them; however, the emergence of the harp trap (Constantine 1958a), first used in Australia in the late 1960s (Fig. 2), facilitated more research into forest bats in subsequent decades.



Figure 2. A harp trap pictured in the narrowest restriction of Bat Cave (U2), Naracoorte, used to successfully catch bats for research in the 1960s. It is believed to have been Australia's first harp trap and was constructed by Jan Nevill and Andy Spate at the request of Elery Hamilton-Smith. The photographer is unknown but probably Elery Hamilton-Smith. Photo and description provided by Andy Spate.

Maternity caves and roosting requirements

It was soon established that maternity caves were of critical importance to Australian bat populations. The early banding efforts with the large bent-winged bat revealed just eight maternity sites across south-east Australia (Dwyer and Hamilton-Smith 1965; Dwyer 1969). These sites were often large, with a domed chamber providing warm and humid conditions to facilitate growth of the young (like a humidi-crib) (Dwyer and Hamilton-Smith 1965). The raised temperatures in these chambers are primarily generated by the activity of the bats themselves, which congregate in the thousands, raising the temperature of the cave; much higher than the heat that is created by the guano or seasonal temperature increase alone (Baudinette *et al.* 1994). Birthing is typically observed *en masse* and the pups are left in clusters ('creche') on the cave

ceiling at night when the mothers leave the cave to forage (Fig. 3). The little bent-winged bat, *Miniopterus australis*, is also known from just a small number of maternity caves. The largest maternity colony, located at Mount Etna in central Queensland, serves as a maternity site for approximately 100,000 bats (Churchill 2008). This colony has been estimated to consume 400 kg of beetles, moths and mosquitoes per night (Richards and Hall 2012). At the southern tip of its range, in northern New South Wales, this species shares caves with the eastern bent-winged bat *Miniopterus orianae oceanensis* and probably relies on this population to meet the required microclimate conditions (Dwyer 1968; Churchill 2008).



Figure 3. Pups and an adult female of the southern bent-winged bat *Miniopterus orianae bassanii*, clustered on the ceiling of Bat Cave (U2), Naracoorte. Photo: Steve Bourne.

Other species of cave-dwelling bats in Australia also form maternity colonies, though the characteristics of the sites of such colonies differ between species and generally serve smaller populations than those observed in bent-winged bats. The largest maternity roost for the ghost bat is in a disused mine, which provides a large chamber

for raising young, has warm and humid conditions, and a complex tunnel arrangement with many exits for bats to retreat if the site is disturbed (Hall and Richards 2003; Hanrahan 2019). A number of leaf-nosed (*Hipposideros* spp.) and horseshoe (*Rhinolophus* spp.) species tend to favour much smaller maternity roosts, often located over pools of water, with chambers closer to the entrance and very high temperature and humidity (Hall and Richards 2003; Churchill 2008). For some species, knowledge of maternity roosts has remained elusive; for example, the first maternity roost described for the threatened large-eared pied bat was a granitic mine tunnel in northern New South Wales (Dwyer 1966a) and another maternity site was not confirmed for a further 35 years. The second site differed markedly in physical characteristics, a comparably smaller sandstone cave in central New South Wales with a low ceiling providing stable temperatures at approximately 15° C (Pennay 2008). At both sites, clusters were observed roosting in ceiling indentations or cracks.

Cave-dwelling sheath-tailed bats (*Taphozous* spp.) and evening bats (*Vespadelus* spp.) are more variable in their choice of roost sites (including maternity sites), which can include boulder piles, fissures, mines, shallow caves and the twilight zone of larger caves; though some maternity sites are further into cave systems where the temperature and humidity are less variable (Hall and Richards 2003; Churchill 2008). In New South Wales, a maternity population of the eastern cave bat *Vespadelus troughtoni* regularly switches between several sites, most of which are sandstone cave overhangs, with a dome at the rear providing stable temperatures (Law *et al.* 2005). Lactating females of this species also regularly roost under the tin roof of a shed where highly varying temperatures are experienced (cold at night and increasingly hot during the day) (Law and Chidel 2007). This temperature variation appears to be energetically favourable for the bats, saving 60–69% of a lactating female's daily energy requirements compared to a natural cave roost. These bats apparently are trading-off the costs of increased temperature variation and leaving young in a cold night roost, with the potential benefit of high diurnal temperatures to reduce daily thermoregulatory costs.

Energy and water balance requirements differ greatly among cave bat species and can influence roost selection (Baudinette *et al.* 2000). Some species, such as the orange leaf-nosed bat *Rhynictotis aurantia*, have precise requirements for maintaining energy and water balance, roosting in caves and mines with temperature between 28–

32° C and 96–100% humidity (Churchill 1991; Churchill 2008). Interestingly, no maternity roosts of the orange leaf-nosed bat have been found, with pregnant females vanishing during late pregnancy and returning to caves after the young are independent (Churchill 2008). It is thought that these bats may become tree-dwellers during this time. The orange colour of this species is presumed to be caused by ammonia in humid caves (Constantine 1958b) and can vary in hue (Fig. 4). Orange forms of other cave-dwelling species are sometimes also observed in northern Australia, including the eastern horseshoe bat, dusky leaf-nosed bat *Hipposideros ater* (Churchill 2008) and ghost bat (N. Hanrahan, pers. comm).



Figure 4. Three orange leaf-nosed bats *Rhinonicteris aurantia* showing varying hues of orange colouration. Gulf of Carpentaria, Northern Territory. Photo: D Fergusson/Australian Wildlife Conservancy.

Roosting requirements of the large-footed myotis are less stringent for temperature and humidity, but roosts above water are favoured and all roosts occur in close

proximity to water (Campbell 2009; Campbell *et al.* 2010). As initial banding efforts suggested, colonies of the large-footed myotis have smaller ranges and high fidelity to roosts; these are centred on waterways where this species specialises in trawling the water surface for insects and small fish (Campbell *et al.* 2009; Gonsalves and Law 2017; Law *et al.* 2020). In addition to caves, this threatened species also roosts in tree hollows, under bridges, in tunnels, jetties and culverts (Campbell 2009; Gonsalves and Law 2017; Gorecki *et al.* 2020).

Availability of water near roosts is also important to many other cave-dwelling species, which typically drink on the wing while foraging (Williams and Dickman 2004; Straka *et al.* 2016). These water bodies also provide ‘hot spots’ for insectivorous prey and become increasingly important in dry areas and seasons (Richards and Hall 2012). However, even in arid areas, some Australian bats persist without close proximity to permanent water (Williams and Dickman 2004). The southern bent-winged bat *Miniopterus orianae bassanii* has been observed licking water from dripping stalactites within Bat Cave (U2), in Naracoorte, South Australia, which may additionally serve to increase their calcium intake (Codd *et al.* 1999). The ghost bat has never been observed drinking and it has been suggested that individuals may meet their fluid requirements through ingesting the blood of their vertebrate prey (Toop 1985). Internationally, some insectivorous bats (including species occurring in arid areas) have been observed to be able to withstand long periods without drinking, instead obtaining water requirements through food intake and metabolic processes (Geluso 1978); however, many other bat species living in arid areas require continued access to water (Geluso 1978; Adams and Hayes 2008).

Winter behaviour of cave-dwelling bats in Australia

Little is known of the winter activity of cave-dwelling bats in Australia (Holz *et al.* 2019; Turbill and Welbergen 2020). For bent-winged bats in south-eastern Australia, banding and cave visits in the 1960s revealed patterns of dispersal and migration away from the maternity cave to non-breeding caves for the winter months (Dwyer 1966b). These non-breeding caves represent a wider range of sites than maternity caves, with a number of roosting sites typically being associated with each maternity cave; forming discrete, or partially discrete, populations (Dwyer 1969). Eastern bent-

winged bats were observed to accumulate fat reserves and then during winter select caves with colder microclimates, or move to colder cave sections, and lower their metabolic rate and temperature into a state of torpor (Dwyer 1964; Hall 1982).

Torpor is a physiological behaviour commonly described amongst temperate bats. The traditional view has been that this energy-conserving adaption facilitates survival of individuals during seasonal extremes and food shortages during the winter months (e.g. Kunz 1982). However, more-recent research is showing that expression of torpor in bats is much more complex, with diversity in its use among species and at different times of the year, including use during summer and among tropical and subtropical species (Geiser 2020). Torpor occurs in a variety of forms, from short-term, daily torpor bouts (e.g. until evening emergence) through to longer-term hibernation with multi-day torpor bouts, sometimes over an extended period of time (McNab and O'Donnell 2018). International research has suggested there are differences in the pattern of torpor between sexes. For example, length of torpor bouts in the cave-dwelling little brown bat *Myotis lucifugus* do not differ between the sexes, but adult males arouse from torpor for longer periods (possibly to increase mating opportunities) than females (probably to save energy for spring pregnancy) (Czenze *et al.* 2017). Such sex-based differences in winter behaviour have been described as the 'thrifty females, frisky males, hypothesis'.

Much is still to be learned about the use of torpor by cave-dwelling bats in Australia (Holz *et al.* 2019; Turbill and Welbergen 2020). In an experiment in June 1973 (Hall 1982), the location of five torpid eastern bent-winged bats was marked on a cave wall and then inspected again the following day, and after 12 days and 21 days. The following day, two bats were no longer present. After 12 days, just one of the original five individuals remained, and it too had left its position by 21 days (Hall 1982). The little bent-winged bat appears to remain active throughout the year in tropical Queensland, but has been observed to utilise torpor in the cooler parts of its range; though individuals of this species remain more active than eastern bent-winged bats in the same cave systems (Dwyer 1968; Churchill 2008). Similar apparent latitudinal variation in wintering behaviour has also been described in the eastern horseshoe bat, whose range extends from tropical Cape York to temperate eastern Victoria (Dwyer 1966c; Churchill 2008).

Research methods for studying cave-dwelling bats

Banding of bats and cave visitation evidently played a key role in the formation of knowledge about Australian cave-dwelling bats. However, low recapture rates, concern about disturbance at cave roosts, and banding injuries in some species, contributed to banding being used less frequently; and now it is used only for selected species known to have low rate of injury from application of bands (Baker *et al.* 2001). Radio-telemetry has also been an important tool in obtaining new knowledge on the ecology of cave bats, enabling additional key cave roosts to be located and protected: for example, radio-tracking provided essential baseline data for the threatened Pilbara leaf-nosed bat *Rhinonictoris aurantia* (Pilbara form) (Armstrong 2001) and the diadem leaf-nosed bat (Pavey 1998), each of which has a restricted range in northern Australia. Despite the challenges with using radio-tracking (e.g. relocating and/or following fast-flying nocturnal animals from the ground or an aircraft can be exceptionally difficult), radio-telemetry remains a valuable tool for studying the roosting and foraging ecology of cave bats, including threatened species (Gonsalves and Law 2017; Williams and Thomson 2019). Unfortunately, the small size of insectivorous bats (e.g. often as little as 4–20 g) and the weight requirements for transmitters or loggers has meant that options for using some new technologies, such as GPS loggers (particularly with remote data download), are still relatively limited.

Identification of insectivorous bats by the analysis of their echolocation calls was an exciting development in the 1980s (Fenton and Bell 1981). Using a combination of acoustic identification and harp trapping methods has allowed for greater detection of species, including in open and urban environments where bats may be more difficult to capture (Duffy *et al.* 2000; Hourigan *et al.* 2008). The development of acoustic detectors and analytical methods using ‘zero crossing’ (essentially recording and/or analysing only the loudest points of the calls) is computationally efficient (Parsons and Szewczak 2009) and has been popular in Australia due to the decreased size of the files being recorded, stored and analysed. This has enabled longer-term deployment of detectors in the field and increased affordability of acoustic methods. Further advances in technology have now alleviated many of the data challenges once faced by researchers, allowing for routine collection of information-rich data recording the full-breadth of information about echolocation and social calls. Some

devices can now plug directly into a smart phone and are available at relatively small cost.

However, the analysis of acoustic data from bats remains complex. There is a large number of bat species in Australia, many with similar and overlapping call characteristics that can differ between geographic regions (Duffy *et al.* 2000). Additional complexity arises from factors such as the environmental conditions (e.g. weather, open vs cluttered environments) and behaviour of the bat when the data were recorded (Barclay 1999; Parsons and Szewczak 2009; Goerlitz 2018). Researchers need to be appropriately trained to analyse such data and auto-ID (used in Europe and North America, for example) is unlikely to be possible, or accurate, in Australia for the foreseeable future.

Current research is continuing to move towards further utilisation of passive research methods that minimise the need for cave disturbance and trapping and are revealing high complexities of bat behaviour and ecology. For example, using acoustic analysis with ghost bats has revealed the use of at least 12 distinct social vocalisations that vary seasonally due to associated changes in behaviour and ‘dialects’ evident across the geographic range, including potential use of song (Hanrahan 2019). Thermal imagery and tracking software is showing high fluctuations in nightly fly-out numbers in the southern bent-winged bat (Lumsden *et al.* 2019). Further, the use of passive integrated transponder tags and large antennas at cave roosts has shown that this critically endangered bat is more dynamic than previously thought, with individuals flying between two cave sites approximately 72 km apart, in just a few hours (van Harten *et al.* 2018; van Harten *et al.* 2019). Weather radar has been used in Texas, USA, to retrospectively analyse changes in timing of seasonal migration in the Mexican free-tailed bat *Tadarida brasiliensis* at Bracken Cave, showing that spring migration has advanced by two weeks over a 20-year period (Stepanian and Wainwright 2018). Similar studies using weather radar may be valuable to conduct long-term monitoring of Australian cave-dwelling bat species.

Further use of novel, and increasingly passive, research methods will be critical for informing conservation of Australia’s cave-dwelling bat fauna. For example, the use of marine radar and acoustic devices mounted to weather-balloon kites (at 100 m altitude) have been used to assess activity and flight height of eastern bent-winged

bats near a maternity cave and a proposed windfarm site (Pennay and Mills 2018; Mills and Pennay 2018). Results of this pilot study found that bats fly at heights that put them at risk of collision with wind turbines and that acoustic surveys underestimated true bat activity at these locations, both of which are important for informing windfarm development.

Conservation of cave-dwelling bats

Despite their long history on the Australian continent, cave-dwelling bats are extremely vulnerable to a range of factors that affect cave systems and the wider landscape. This is particularly true for species that are obligate cave-dwellers, with a large proportion of these bats being threatened with extinction in Australia (Table 1). Caves that meet the species-specific requirements of cave-users are limited. Such species are particularly vulnerable to loss or disturbance of caves, as well as factors that affect the availability of resources (food, water) in the regions around these locations, such as drought, bushfires or land clearance and modification. Some cave-dwelling species congregate in very large numbers at specific sites, so catastrophic loss of a site, such as cave collapse, may mean the loss of a significant portion of the population. Bat species also generally have a ‘slow’ life history, with females of most species giving birth to just a single young per year (Barclay and Harder 2003). As a result, factors affecting adult survival rates can have a profound impact on the long-term viability of populations (Schorcht *et al.* 2009; Frick *et al.* 2017).

Speleologists were some of the earliest supporters for bat conservation in Australia and have been key advocates for protecting caves and their fauna. In 1966, speleologist and bat researcher Elery Hamilton-Smith wrote, ‘We cannot be complacent about the conservation of our bats. Planning for effective conservation needs to be done now, rather than when populations are seriously on the wane’ (Hamilton-Smith 1966). It was around this time that several caves came under the threat of limestone quarrying (for cement manufacturing) at Mount Etna, Queensland. This included an important maternity cave of the little bent-winged bat, as well as caves used by the ghost bat and eastern horseshoe bat.

The Mount Etna campaign became one of the longest environmental conflicts in Australia, spanning from 1966–2004 (Berrill and Vavryn 2008). Cavers sought to

gain support for protecting the caves by producing photographs, supporting research, guiding tours to watch bat emergence fly-outs from the caves, writing letters and lobbying government (Gistitin 2010). The imminent destruction of two key caves sparked direct action, including refilling the miner's drill holes with concrete and organising a cave sit-in (Gistitin 2010). In November 1988, the mining company ended the blockade by using high pitch sirens to force out protestors, and then subsequently blasting the two caves (Berrill and Vavryn 2008). The Central Queensland Speleological Society (CQSS) brought the case to the High Court of Australia where they were awarded 'leave to appeal', but had to abandon the case due to insufficient funds (Berrill and Vavryn 2008). On the day the case was due to be heard, the mining company again blasted the two caves, completing their destruction (BCI 1989). Both caves were used by the ghost bat, a species in decline and listed as vulnerable to extinction on the IUCN Red List 1988. Speaking Tube Cave (E7), in particular, was a critical winter cave for pregnant ghost bats before it was destroyed (Augusteyn *et al.* 2018). A reconciliation in 1999 saw the mining company drop legal action and costs against CQSS and donate funds to the purchase and protection of another important cave system at Mount Etna (Berrill and Vavryn 2008). Mining eventually ceased in 2004 and the quarry site was formally added to the Mount Etna National Park in 2008; however, since the late 1990s the ghost bat population at Mount Etna has declined by a further 79% (Augusteyn *et al.* 2018).

In addition to quarrying, Australian bats and bat caves were exposed to several other threats in the twentieth century including: guano mining, the use of caves as rubbish dumps or otherwise filling or blocking caves, the use of problematic pesticides including DDT, direct killing of bats, disturbance of wintering sites, and in some cases, excessive or inappropriate collection of specimens for research (Hamilton-Smith 1968; Hamilton-Smith 1998; Augusteyn *et al.* 2018). Many of these issues no longer pose major threats in Australia, though persecution of bats remains a major threat in other parts of the world (Frick *et al.* 2020). Some bat caves previously used as rubbish dumps have been cleaned, and bats have returned to some sites following restoration (Bourne 2015).

Loss of nearby foraging resources is a continuing threat to some populations of cave-dwelling species. Since European settlement, the Australian continent has experienced broadscale deforestation and habitat clearance, which in some areas such as regions of

Queensland and Western Australia, accelerated following World War II (Bradshaw 2012). In south-east South Australia, significant areas of wetlands were drained and converted to agricultural land (PIRSA 2017). Loss of such foraging habitat is a particularly important conservation issue in the areas around significant maternity caves, where the surrounding landscape needs to support foraging by large colonies for extended periods of time.

Direct disturbance to cave-dwelling bats also remains a threat to many species due to the risk that it may result in site abandonment; or that the unexpected activity may waste valuable fat reserves in winter months, which may lead to lowered survival. The Australian Speleological Federation Inc (ASF), the umbrella organisation for most Australian caving groups, updated their Code of Ethics in 1992 to state that no disturbance should be caused to maternity or over-wintering roosts of bats. ASF's Minimal Impact Caving Code 2010 also mentions avoiding shining light on cave biota, including bats. The effect of both tactile and non-tactile disturbance, and arousal of cave bats from torpor, has been recognised for some time (Thomas 1995); however, understanding the effect of light disturbance on bats remains an emerging area of research. Acoustic data for the southern bent-winged bat has shown that cave populations had elevated activity for up to several weeks following brief cave visits involving the use of white flash photography. The cessation of flash photography at cave visits decreased these spikes in activity (Bush *et al.* 2017).

Other studies have begun to investigate aspects of the way bats are affected by changes to lighting. Experimentally introducing lights at wetlands in Sydney showed that bat assemblages changed significantly following the introduction of white light, but not red light (Haddock 2019). Some bats also showed decreased activity after switching streetlighting to LEDs (Haddock *et al.* 2019). Light pollution and disturbance should be considered a threat to bats and managed to minimise and avoid effects on populations. Red light is generally less disturbing to bats (Straka *et al.* 2020); therefore, if necessary to visit caves where bats may be present, it is recommended that red light be used rather than white (e.g. by covering headlamps with red cellophane). At Naracoorte Caves National Park, World Heritage Area, in South Australia, infra-red cameras were installed in 1995 in the major maternity cave of the southern bent-winged bat to allow visitors to observe bats in their natural cave habitat without disturbing this critically endangered species (Reed and Bourne 2013).

Gating at caves and mines can protect sites from human access and disturbance; however, the effect of gating itself can cause site abandonment, collisions, and behavioural changes (such as increased circling before emergence) depending on the bat species and the gating design implemented (Slade and Law 2008; Tobin and Chambers 2017). Generally, gates with horizontal bars at 14.6 cm spacing are more readily accepted by bats (Tobin and Chambers 2017). However, some Australian species, such as bent-winged bats, have great difficulty navigating cave gates and alternative management strategies are recommended (Thomson 2002). Other infrastructure around caves, such as fencing, can also pose risk to bats, especially at maternity caves where juveniles/subadults appear to be at increased risk of injury and fatality from collisions as they begin to fly (Ingeme *et al.* 2019; Holz *et al.* 2020). All gating, fencing, lighting and other infrastructure in and around caves should be carefully designed and implemented to consider bat populations, and include post-installation monitoring to check for any effects on bat populations.

There are a number of broadscale, global issues which are emerging threats to bats, which will require stakeholders to work together to ensure the viability of bat populations (Frick *et al.* 2020). Analysis of IUCN listings for threatened species of bats show that two leading threats worldwide are deforestation and agriculture, including logging, the loss of foraging habitat to agricultural production, and the use of pesticides which further decrease availability of insectivorous prey (Frick *et al.* 2020). Climate change will certainly affect bat populations; however, it is difficult to predict the likely effects, particularly with so many species remaining ‘data deficient’ due to lack of ecological knowledge. Species at risk related to climate change are predicted to include those bat species ‘inhabiting regions more likely to become water-stressed and those that are reliant on temporally and spatially variable food resources’ (Sherwin *et al.* 2013, p.173), hence encompassing most Australian cave bats.

Globally, windfarms and white-nose syndrome are currently the leading causes of mass mortality events in bats (O’Shea *et al.* 2016). Windfarms pose an unfortunate ‘green-green dilemma’ between reusable energy and biodiversity loss (Voigt *et al.* 2019). For example, recent research predicts that windfarms may lead to the decline of up to 90% of hoary bats *Lasiurus cinereus* in North America (Frick *et al.* 2017). With numerous windfarm developments in progress or in planning stages in south-

east Australia, this poses a potentially serious emerging threat to bat populations. There is still a high degree of uncertainty around estimates of bat mortality associated with windfarms in Australia (Moloney *et al.* 2019). Robust pre- and post-construction monitoring accounting for the full seasonal activity of bats will be vital, as well the use of mitigation strategies to minimise effects on biodiversity (such as curtailment (Hayes *et al.* 2019)), to ensure that energy production is truly sustainable.

White-nose syndrome is a fungal infection caused by *Pseudogymnoascus destructans* (Lorch *et al.* 2011) and has caused mass fatalities of millions of hibernating bats in North America since 2006 (Turner *et al.* 2011). The pathogen has also been identified in bats in Europe, Russia, and China, but without the associated mass mortality that has occurred in North America (Hoyt *et al.* 2016; Zukan *et al.* 2016). Genetic analysis of *P. destructans* suggests that the pathogen was most likely inadvertently spread by humans (probably cave visitors) from Europe to North America into naive bat populations (Drees *et al.* 2017). Bats infected with white-nose syndrome experience a cascade of physiological effects (Verant *et al.* 2014), subsequently leading to more frequent arousals from torpor and depletion of valuable fat reserves (Reeder *et al.* 2012).

A risk assessment for Australia found that it is ‘almost certain/highly likely’ that *P. destructans* will enter Australia and ‘likely’ that it will come into contact with cave-roosting bats in the coming decade (Holz *et al.* 2019). Eight cave-dwelling species in south-eastern Australia are most likely to be affected, including seven already listed as threatened with extinction (Turbill and Welbergen 2020). White-nose Syndrome Response Guidelines have been developed by Wildlife Health Australia. Such guidelines would be strengthened by further research into the biology of hibernating bats in Australia, including the timing and length of bouts of torpor and movement patterns of individuals over winter (Holz *et al.* 2019). All cave visitors, including cavers and scientists, can help prevent the spread of white-nose syndrome by following decontamination protocols, especially after visiting caves outside of Australia (see www.caves.org.au/conservation).

Finally, the parlous state of knowledge for most of Australia’s cave-dwelling bat species is concerning. Whilst a few species described here have been reasonably well studied, very little is known about key conservation factors of cave-dwelling species,

especially with regard to population trends. Indeed, cavers have reported bats in some Australian cave systems where the bat populations are yet to be studied at all. For example, an estimated congregation of 200,000–300,000 bats was reported in central-north Queensland lava tunnels in the 1970s (Hamilton-Smith 1978), but no known studies have been undertaken to verify this report.

Clearly, many challenges lie ahead in conserving Australia's cave-dwelling bats. Seven species/subspecies are currently listed as threatened nationally and 18 (62%) are listed as threatened or near threatened on a state and territory level (Table 1). Population trends of cave-dependent bat species that are currently not listed are largely unknown.

A new wave of research underway will play a pivotal role in informing the conservation of Australia's diverse bat fauna and developing further understanding of their ecology, population trends, and contribution to provision of ecosystem services (e.g. control of agricultural pests (Kolkert *et al.* 2019)). However, among the simplest ways for people to help bats include simply leaving them undisturbed and spreading the word about these fascinating creatures that are often misunderstood and feared by the public (Lunney and Moon 2011).

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Chapter 3. High detectability with low impact: optimizing large PIT tracking systems for cave-dwelling bats

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High detectability with low impact: optimising large PIT tracking systems for cave-dwelling bats

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Abstract

Passive integrated transponder (PIT) tag technology permits the ‘resighting’ of animals tagged for ecological research without the need for physical re-trapping. While this is effective if animals pass within centimetres of tag readers, short-distance detection capabilities have prevented the use of this technology with many species. To address this problem, we optimised a large (15 m-long) flexible antenna system to provide a *c.* 8 m² vertical detection plane for detecting animals in flight. We installed antennas at two roosting caves, including the primary maternity cave, of the critically endangered southern bent-winged bat (*Miniopterus orianae bassanii*) in south-eastern Australia. Testing of these systems indicated PIT-tags could be detected up to 105 cm either side of the antenna plane. Over the course of a three-year study, we subcutaneously PIT-tagged 2966 bats and logged over 1.4 million unique detections, with 97% of tagged bats detected at least once. The probability of encountering a tagged bat decreased with increasing environmental ‘noise’ (unwanted signal) perceived by the system. During the study we mitigated initial high noise levels by

earthing both systems, which contributed to an increase in daily detection probability (based on the proportion of individuals known to be alive that were detected each day) from <0.2 (noise level $\geq 30\%$) to $0.7\text{--}0.8$ (noise level $5\text{--}15\%$). Conditional on a low (5%) noise level, model-based estimates of daily encounter probability were highest (>0.8) during peak breeding season when both female and male southern bent-winged bats congregate at the maternity cave. In this paper we detail the methods employed and make methodological recommendations for future wildlife research using large antennas, including earthing systems as standard protocol and quantifying noise metrics as a covariate influencing the probability of detection in subsequent analyses. Our results demonstrate that large PIT antennas can be used successfully to detect small volant species, extending the scope of PIT technology and enabling a much broader range of wildlife species to be studied using this approach.

Keywords: PIT-tag, microchip, mark-recapture, wildlife tracking, RFID, bats

Introduction

Ecological research often requires wild-living individuals to be marked and then recaptured, tracked or re-sighted over time. Applying these techniques can be challenging due to low recapture rates, technological constraints, welfare considerations, and the need to minimise disturbance to threatened populations (Cooke *et al.* 2013; Schorr *et al.* 2014). A wide range of marking and tagging techniques are available to monitor wildlife, including mutilation (e.g. toe clipping or ear notching), banding, radio-transmitters, acoustic tags and bio-loggers (Murray and Fuller 2000; Perry *et al.* 2011; Walker *et al.* 2012; O'Mara *et al.* 2014; Wilmers *et al.* 2015; Bino *et al.* 2018). Marking can, however, have potential negative effects on wildlife, including injury, reduced survival and reproduction rates and changes to behaviour and movement (Murray and Fuller 2000; Baker *et al.* 2001; Griesser *et al.* 2012; Bodey *et al.* 2018; Rosen *et al.* 2018). Many methods also necessitate repeated trapping and handling, which is labour intensive and, despite continued effort being made to minimise impacts on wildlife, each trapping typically induces stress in trapped individuals (Reeder *et al.* 2004; Lynn and Porter 2008; Gelling *et al.* 2009), and has inherent (but low) mortality rates (Lemckert *et al.* 2006; Blomberg *et al.* 2018).

Exemplifying these challenges is the study of bats, of which a large proportion are small insectivorous species, that are cryptic, highly mobile and difficult to recapture (Schorr *et al.* 2014). These ecological and behavioural traits pose practical challenges and ethical considerations for marking and tracking individuals. Almost 40% of all assessed bat species worldwide are considered threatened, near threatened or data deficient under IUCN criteria (IUCN 2018). Therefore, it is critical to improve these techniques to enable effective research approaches without significantly impacting the bats' viability.

Banding has been used to mark bats since the 1910s (Allen 1921), but can cause significant injury and lower survival in some species (Baker *et al.* 2001). Another alternative is radio-tracking, however, a comprehensive review has found that most radio-tracking devices used to study bats are too heavy, are being used with minimal ethical justification, and remain attached for an average of just 9 days (O'Mara *et al.* 2014). A more recent innovation for the use on small bats has been miniaturised GPS-tags, however, currently this has only been successfully attempted with the use of anaesthesia and sutures to attach the loggers – and battery life, tag weight and recapture rates remain ongoing issues (Castle *et al.* 2015; Weller *et al.* 2016).

An alternative to these marking and tracking methods are Passive Integrated Transponder (PIT) tags, which weigh as little as 0.1 g, which is well under the 5% of body mass 'rule' recommended for bats under 70 g (Aldridge and Brigham 1988; Neubaum *et al.* 2005). To date, PIT-tags have shown no apparent effect on body condition or reproductive success of small bats (Rigby *et al.* 2012).

PIT-tags are glass encapsulated microchips that are injected into an animal and lay dormant until they are activated by a hand-scanner or antenna system, which reads the tag's globally unique identification number using radio-frequency identification (RFID). By positioning antenna systems at key locations, individuals can be passively tracked for a lifetime with just a single trapping event. PIT-tag technology has been used extensively in fish research since the 1980s, and has also been used to study birds, reptiles, amphibians, invertebrates and mammals (Gibbons and Andrews 2004; Unger *et al.* 2012; Soanes *et al.* 2015; Schlicht and Kempnaers 2018). PIT-tag

technology has advanced the study of movement patterns and survival of wildlife, however, a major limitation of this technology has been low detection distance, with tagged individuals normally needing to pass within 30 cm or less of an antenna to be detected (Gibbons and Andrews 2004; Norquay and Willis 2014; Adams and Ammerman 2015).

To date, microbat studies using PIT-tags and passive detection have been limited to close-range applications, typically using loop antennas at small roost entrances, such as tree hollows (Garroway and Broders 2007; O'Donnell *et al.* 2011; Toth *et al.* 2015), bat boxes (Kerth and König 1996; Kerth and Reckardt 2003; Godinho *et al.* 2015) or small building entrances (Safi *et al.* 2007; Ellison *et al.* 2007a; O'Shea *et al.* 2010). Bats have also successfully been detected at an artificial water source when tagged individuals came within 15 cm of a submerged plate antenna (Adams and Hayes 2008). Large roost entrances, such as with caves, provide additional challenges for using PIT antennas due to the detection ranges required. PIT antennas have been installed on timber frames partly covered with mesh to modify the cave-exit and funnel the bats through small 'windows' (Britzke *et al.* 2014), or by using a serpentine antenna configuration that zig-zags across the cave entrance (Adams and Ammerman 2015). A drawback of these approaches is that they altered the flight path of the bats and led to short-term responses and effects such as circling, landing on the infrastructure, avoidance behaviour and wing-strikes. Furthermore, some bats have limited tolerance to structural changes at their roost entrances. For example, gates at caves and mines have caused some bats to modify their behaviour and have been linked to declines in numbers and, in some cases, total site abandonment (Tuttle 1979; Pugh and Altringham 2005; Slade and Law 2008). Increased predation risk can also result, with predators using infrastructure to catch bats exiting the roost (White and Seginak 1987).

The critically endangered southern bent-winged bat (*Miniopterus orianae bassanii*) is an obligate cave-dwelling bat with a restricted distribution in south-eastern Australia. The national recovery plan for the southern bent-winged bat recommends investigating and developing techniques that would enable PIT technology to be used for quantifying age- and sex-structured survival rates, to help identify the cause of population decline (Lumsden and Jemison 2015), whilst minimising trapping

occasions and disturbance. Bent-winged bats in south-eastern Australia generally favour large caves with relatively large entrances (Dwyer 1963), and do not readily accept cave gates (Thomson 2002; Slade and Law 2008). Therefore, modifying cave-entrances to detect PIT-tagged southern bent-winged bats was deemed to pose an unacceptable risk to the species. As a result, there was a need to develop a system that could detect bats as they flew through large passages, without impacting their behaviour.

Here we describe the challenges and successes of using large PIT antenna configurations for monitoring a small, volant and fast-moving organism, the southern bent-winged bat, over a three-year period. We PIT-tagged and monitored 2966 individuals, optimised an RFID system to successfully meet our aims of high detectability and low impact, and provide recommendations for other researchers considering using this technology for other wildlife species.

Methods

Study sites

Our study was based at two limestone caves used by the southern bent-winged bat in south-east South Australia. From spring to autumn, southern bent-winged bats form a large colony at their primary maternity cave, Bat Cave, in the Naracoorte Caves National Park, World Heritage Area. This was our primary study site. It is a horizontal cave system with a roof window entrance measuring approximately 7 m by 4 m. Mains (240 V AC) electricity is connected to the cave to power permanent infra-red and thermal cameras located inside the cave. These cameras transmit live images of the bats to the nearby Bat Observation Centre for visitor tours, which form part of the tourist attractions for the national park. The secondary study site was a non-breeding cave located on private property near Glencoe, South Australia, about 72 km from Bat Cave. The entrance of this cave measures approximately 6 m wide by 2 m high and is fenced from livestock. The southern bent-winged bat is the only bat species that is known to roost in these caves.

RFID systems and installation

The radio frequency identification (RFID) system used in this study was the Biomark IS1001 – a low frequency (134.2 kHz) system with dynamic, automatic tuning. The system consists of a reader, data logger and 15 m flexible cord antenna that collectively powers, detects and records PIT-tags. The antenna is intended to be configured as a loop that detects tagged individuals as they pass through the loop. All data are recorded as log files to the internal memory or a USB flash drive connected to the data logger. We coupled this system with Biomark high performance 12.5 mm FDX-B tags (HPT 12) which are reported by the manufacturer to provide a greater read-range than other PIT-tags of the same size.

The entrance of Bat Cave was too large for the 15 m antenna. The narrowest section of the cave (hereafter, referred to as ‘the restriction’) is located approximately 100 m from the entrance, measures approximately 5 m wide and up to 2.8 m high, and was identified as the most suitable position for the RFID system. Despite the distance from the cave entrance, we assumed that bats would fly through the restriction when present at Bat Cave because the restriction is a high traffic area for bat movement. Individuals fly through this passage to access the three main roosting chambers, including the maternity chamber where the bats raise their young (Dwyer and Hamilton-Smith 1965). Individuals also move through the restriction during the day to drink from dripping stalactites in the ‘drinking chamber’, located in an alcove off the main passage between the entrance and the maternity chamber (Codd *et al.* 1999).

The placement of the antenna at the restriction in Bat Cave needed to satisfy two conditions: firstly, that bats would not collide with the antenna nor have their flight paths altered, and secondly, that the antenna configuration gave the best coverage and sensitivity for reading the tags. Despite the length and flexibility of the antenna, the Biomark IS1001 cord system will not successfully create a detection field in all configurations. Large rectangular antenna configurations (with a width exceeding 2.5 m) are likely to obtain the greatest antenna sensitivity by minimising the height of the rectangle as much as possible (ideally to 1 m) and by laying the excess antenna cable close together (K. Pomorin, Karl Tek, pers. comm.). As such, the dimensions of the restriction at Bat Cave were substantially larger than those advised for successful PIT-

tag detection. To determine the optimal antenna placement and configuration, we first observed the flight path of the bats through the restriction for several hours (including during a dusk fly-out) in August 2015, using a thermal camera (FLIR Photon 320). Analysis of the footage demonstrated that the bats flew in the upper-half of the restriction. It was therefore determined that the cord antenna could be safely configured with the bottom of the antenna set up to 1 m above the cave floor, thereby creating a more desirable height for the rectangular antenna configuration. As metal can interfere with antenna performance (Freeland and Fry 1995; Biomark Inc 2015), the cord antenna was attached to the wall and ceiling of the cave using plastic saddle clips drilled into the limestone. The bottom of the antenna was supported off the ground with flexible fibreglass poles which were drilled into the cave floor and fastened using plastic cable ties. The final dimensions of the antenna were a maximum of 4.8 m wide and 1.8 m high (Fig. 1). The excess cord of the antenna was laid together in parallel (touching, or close to touching) and kept in place with cable ties.



Figure 1. Southern bent-winged bats flying through the 15 m loop antenna which was installed at the restriction in Bat Cave. The bottom of the antenna-loop was raised above the cave-floor. Only a small area of the restriction (to the right of the

stalagmites) was not included in the detection space. Note that the ‘tail’ of excess antenna cord was laid together and leads to the RFID reader on the right hand-side of the image. Boxes containing the batteries, charger and battery-switching unit are located to the right of the camera’s field-of-view. The structure in the middle of the photo is a decommissioned infra-red camera which provided real-time footage to the Bat Observation Centre prior to our study – other cameras are still in operation in other parts of the cave.

The system was connected in January 2016 and powered using two battery banks because the Biomark IS1001 RFID system is not compatible with Australian 240 V AC mains power. Each battery bank was comprised of two deep-cycle 12 V DC batteries run in series to create an output of 24 V DC. The batteries were charged by a battery charger (CTEK MXT 14) connected to the mains power supply in the cave. The charger and batteries were separated from the RFID system by a battery-switcher unit (Biomark standard battery-switcher) that switches between charging and drawing power from each of the battery banks on a three-hour rotation. This system is designed to sustain the life of the batteries by ensuring the batteries are not drawn too low, and to keep the RFID system electrically isolated from mains power so that it did not interfere with the system’s performance. The batteries, charger and battery-switcher were placed in plastic tubs with ventilation holes.

After the antenna was installed, the restriction was monitored with a video camera (Sony HDR-CX900E used with an infra-red illuminator) over three nights in January 2016. No avoidance behaviour was observed, with bats flying through the loop unhindered. No bats were seen evading detection by going under or to the side of the antenna.

A second RFID system was installed at the cave near Glencoe in April 2017 (Fig. 2). The antenna was installed at the mouth of the cave using plastic saddle clips drilled into the limestone and raised off the ground using small rectangular strawbales and plastic cable ties. The RFID system was powered by a single battery bank, comprised of two AGM 100 AH deep-cycle 12 V batteries (RITAR RA12-100) run in series. The batteries were charged by a 265-watt polycrystalline solar panel (Hanover HS265-30) and a 12/24 V 20 A solar charge controller (Projecta SC320). The solar

panel and controller were installed 6 m from the cave entrance. To protect it from weather, the battery bank was placed within a heavy-duty plastic tub underneath the tilted solar panel. The 6 m of cabling between the RFID system and the solar controller was protected with PVC conduit. The final dimensions of the antenna were a maximum of 4.5 m wide by 1.7 m high.



Figure 2. The Glencoe study site, with the RFID system and associated solar set up installed at the cave entrance. (a) shows the overall layout and shape of the entrance, and proximity of the solar installation (on the left of the image). (b) is a close up of the left side of the cave entrance, showing: the Biomark IS1001 (covered with a foam matt for added protection) under a rock ledge on the left of the image; the flexible cord antenna in place around the mouth of the cave; the strawbales used to raise the antenna; disused metal irrigation infrastructure just within the lip of the cave; and the red tip of the copper earthing rod in the bottom left corner.

Trapping and tagging

We trapped and PIT-tagged bats at Bat Cave in January and February over three consecutive years, 2016–2018. Bats were trapped with Austbat harp traps (Faunatech, Mount Taylor) set exterior to the fence that surrounds the cave entrance. Each bat was PIT-tagged using a sterilised 12-gauge needle (Biomark MK10 implanter and N125 needles in 2016, and Biomark MK 25 Implant Guns and HPT12 Pre-load Trays in 2017 and 2018). The 12 mm tag (Biomark HPT 12) was injected subcutaneously so that the tag rested between the scapulae, and the injection site was sealed with a drop of surgical glue (3M™ VetBond™) to minimise tag loss (Lebl and Ruf 2010). A total

of 2966 southern bent-winged bats were tagged over the course of the study (approximately 1000 per year). During the handling and tagging, the bats typically remained calm and were released minutes after the procedure. All trapping, handling, tagging and data collection procedures were approved by the La Trobe Animal Ethics Committee (AEC15-67) and the South Australian Department of Environment and Water (U26453).

Data collection

The Biomark IS1001 data logger recorded two types of data chronologically into daily log files: tag data and system data. Each tag detection is recorded with the exact time and date of detection and the PIT-tag's unique identification number. The system data records status and noise reports which include system settings and noise levels (i.e. unwanted signal). As a range of system settings can be chosen, the settings used in this study are provided in Appendix 1. Full status reports were generated by the system hourly and noise reports were recorded every five minutes. Data files were recorded directly to USB flash drives plugged into the data logger board. Data were collected from the study sites regularly (approximately monthly) by manually retrieving the flash drives. Other system maintenance included initiating a full tune of the antenna using the BioTerm program (Biomark, Boise) on a laptop connected to the RFID system via the mini USB port (undertaken approximately every two months) and the installation of a software update to both of the Biomark IS1001 units (undertaken once).

Quantifying and minimising noise

Noise is the summation of unwanted in-band frequency signals being received by the RFID system, including electromagnetic interference and natural environmental factors, which degrade system performance by competing with the tag signal. The Biomark IS1001 measures noise as 'FDX-B signal' in millivolts (0–900 mV range) and then converts this measurement into a percentage for ease of reference. At Bat Cave, initial noise levels were high (>25%). Potential sources for electromagnetic interference included the five pre-existing thermal and infra-red cameras situated in various chambers of the cave that were linked to the Bat Observation Centre. Associated with the cameras was a network of 240 V AC cabling. To find and

eliminate the source/s of the noise, we turned off power to the cave, measured noise levels (by initiating a noise report with the BioTerm program) and then systematically turned back on each of the cameras and cabling networks. After each change, the read-range and noise levels were recorded.

To decrease noise levels and increase system performance, we electronically earthed the RFID system at Bat Cave on 4 May 2016. The floor of the cave near the antenna is bed rock, with little to no available earth or soil. Dry limestone is a poor electrical conductor, so instead of drilling and inserting an earth rod into the floor of the cave, we buried a two-metre copper earth rod horizontally under a thin bed of bat guano. The earth was connected to the exposed negative post terminal of the Biomark IS1001 with a saddle, 6 mm earthing cable and ring terminal. Two additional rods were attached in series with additional saddles and earthing cable in February 2017 in an attempt to strengthen the earth. An earth was also added to the system at Glencoe on 7 May 2018, by hammering a 1 m long earthing rod vertically into the soil near the entrance of the cave, and then connecting the rod to the negative terminal of the Biomark IS1001.

Read-range and the impact of noise

A standard measure of RFID system performance is read-range, which we defined as the maximum horizontal distance from the loop antenna's vertical plane that a tag was detected. The greater the read-range, the greater the total detection field and the less influence that angle and speed of the passing PIT-tag has on the probability of a successful detection. Maximum read-range was assessed by holding a test PIT-tag and slowly moving it through the antenna loop at various points of the configuration. The read-range was measured with a non-metal measuring tape from the vertical plane of the antenna loop to the maximum perpendicular point that the tag was detected. Read-range was measured after installation and after changes to the system set up or external conditions (e.g. potential noise sources).

As read-range could only be measured in person at the study sites, we had limited capacity to measure the response of read-range to the full variation in noise levels affecting the two systems. However, the Biomark IS1001 detects and records tag data

at a rate of 30 ‘pings’ per second, and so each flight of a tagged bat through the antenna loop is typically logged numerous times. We reasoned that, on average, larger read-ranges (and hence larger detections fields) would result in more logged detections per detection event. To test our hypothesis that a negative relationship existed between noise and read-range, we calculated the number of consecutive detections recorded for each bat pass and modelled this response variable as a linear function of noise using a zero-truncated poisson regression, implemented with package VGAM with the R software for statistical computing, version 3.5.1 (R Core Team 2018). All incidents of >50 consecutively logged detections of the same tag number were removed from this analysis, because occasionally very large numbers of consecutive detections were logged (e.g. thousands of detections) likely due to tagged bats roosting near the antenna.

Detection and encounter probability

We investigated detection probability *in situ* at Bat Cave with free-flying bats tagged in early February 2017. After tagging, 209 bats were released at night in small batches within the cave, beyond the antenna, between the restriction and the maternity chamber. Each bat therefore needed to fly through the antenna at least once to exit the cave. Under the assumption that all 209 bats exited the cave after release, detection probability was estimated as the proportion of released individuals detected on the RFID system by midnight following their release, i.e., bats were released after midnight, in the early hours of the morning, and needed to be detected by midnight on the same date to be included in the proportion detected. This estimate is conditional on noise levels at the time of the experiment and can only serve as a coarse estimate of detection probability (the true detection probability for each animal pass is impossible to quantify directly).

We also used detection histories for each individual to consider how the daily probability of encounter varied with system noise and time of year, using data from the Bat Cave antenna system. To achieve this, we first derived capture-resight histories for each of the 2966 PIT-tagged bats, to produce a binary response variable (undetected/detected) for each individual across each day of the study period, with a ‘day’ being defined as the 24 hours between successive middays. Using this variable,

we identified the first and last detection event for each individual, and derived a second binary variable indicating whether each individual was known to be alive. We calculated the daily encounter rate as the proportion of individuals known to be alive that were detected each day. We also used a binomial generalised additive model (R package ‘mgcv’) to estimate the per-individual daily probability of encounter (i.e., the probability of being present at Bat Cave and being detected) as a function of noise (averaged for each day) and day of year. For the latter effect, we fitted a cyclic cubic regression spline to ensure continuity of the modelled response between the first and last day of the year.

Results

System optimisation and noise minimisation

Noise levels were a major factor in the RFID system performance. Earthing the system at Bat Cave decreased noise levels, increased read-range (see section below, *Read-range and the impact of noise*) and resulted in an immediate increase in the number of bats detected per day (Fig. 3). Attaching a further two rods in series, on a later date, did not decrease noise levels further. A major source of noise (daily noise ~30–40%) was inadvertently introduced in September 2016, when park management made changes to a thermal camera in the maternity chamber, approximately 50 m away from the RFID system. The interference caused major disruption to system performance with few bats being detected (Fig. 3). The issue was resolved by disconnecting the camera; thereafter, average daily noise typically ranged between 5% and 18%.

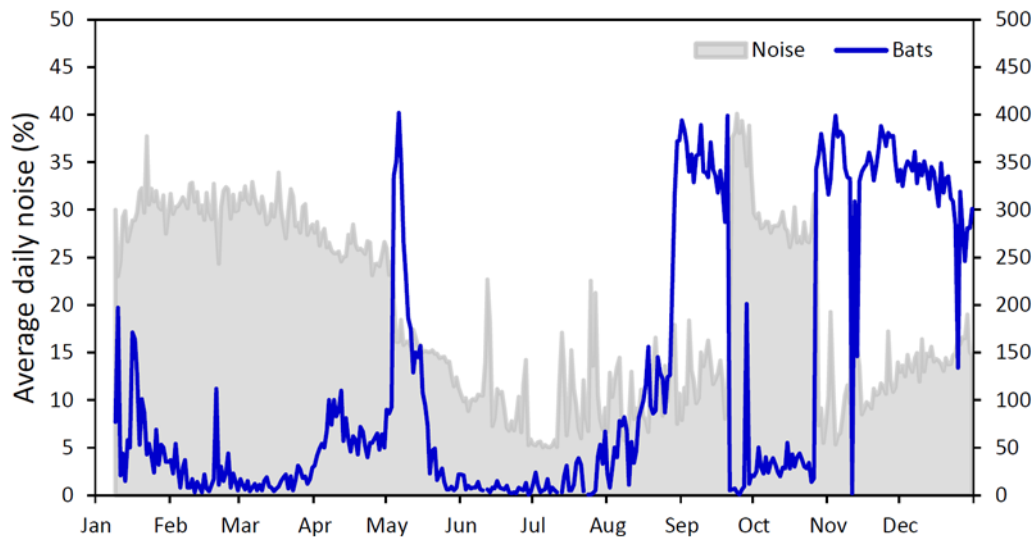


Figure 3. Average daily noise levels (%) and number of individuals detected (out of possible 962 bats tagged) at Bat Cave in 2016. When an earth was installed on the RFID system at the beginning of May, there was a significant increase in the number of bats detected due to lower noise levels. Bats naturally dispersed from Bat Cave soon after earthing and began returning in August. High noise was inadvertently introduced when changes were made to a nearby thermal camera in late September. This dramatically decreased system performance and the number of bats detected. Minor improvements were made when the issue was discovered a week later, including tuning the antenna. The source of the interference was discovered after extensive trouble shooting in late October. The high noise ceased when the camera was unplugged, and the number of bats detected immediately returned to prior levels. A high noise event of unknown origin also occurred on a single date in mid-November.

Noise levels recorded by the system installed at Glencoe were lower and less variable than at Bat Cave. The RFID system at Glencoe was initially powered directly from batteries and noise levels averaged 4%. After the solar panel and controller were installed to power the system for long-term use, noise levels became more variable. There was a daily cycle, whereby average noise only exceeded 5% between dawn and dusk, with a peak at 1 pm (Fig. 4). The likely source of this noise was the solar controller (which charged the batteries during daylight hours), but this was unlikely to

have affected detection success since bat activity at Glencoe is typically recorded between dusk and dawn. Nevertheless, as a precaution, the system was earthed in May 2018 which stabilised the noise levels throughout the day (Fig. 4).

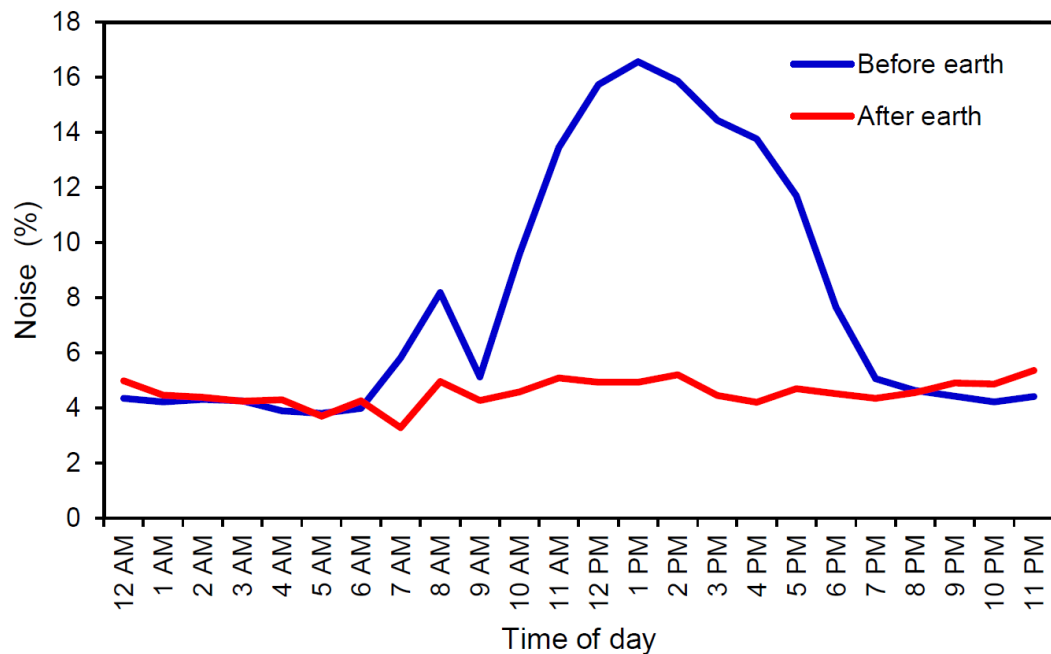


Figure 4. Mean hourly noise levels (%) at the cave at Glencoe before and after earthing, using all available data (2017–2018).

Read-range and the impact of noise

The maximum read-ranges measured at Bat Cave varied under different conditions over the study period and was negatively related to noise (Fig. 5). The highest read-range for this site (89 cm) was measured under testing conditions, when all mains circuits in Bat Cave were turned off, equating to a total detection field of more than 15 cubic meters. During the initial installation, maximum read-range was just 30 cm near the antenna cable and the read-range decreased towards the centre of the antenna loop where there were large detection dead-spots. Temporarily unplugging the battery-charger from mains power for testing purposes increased maximum read-range by an additional 20 cm. We therefore unplugged the battery charger during trapping trips in 2016 to detect as many bats as possible after their initial tagging. As a result, small peaks in the number of individuals detected during these trapping trips can be seen in

Fig. 3 (two in January, and one in late February). This was not required in subsequent years when performance issues had been resolved. After earthing the RFID system, read-range increased to 58 cm across the antenna configuration with no dead-spots. This further increased to 75 cm later in the study (from mid-2017) when the cabling and protective conduit between the cameras in the maternity chamber and Bat Observation Centre were replaced and upgraded by cave management. At Glencoe, maximum read-range was measured at 89 cm and increased to 105 cm after earthing, with no dead spots.

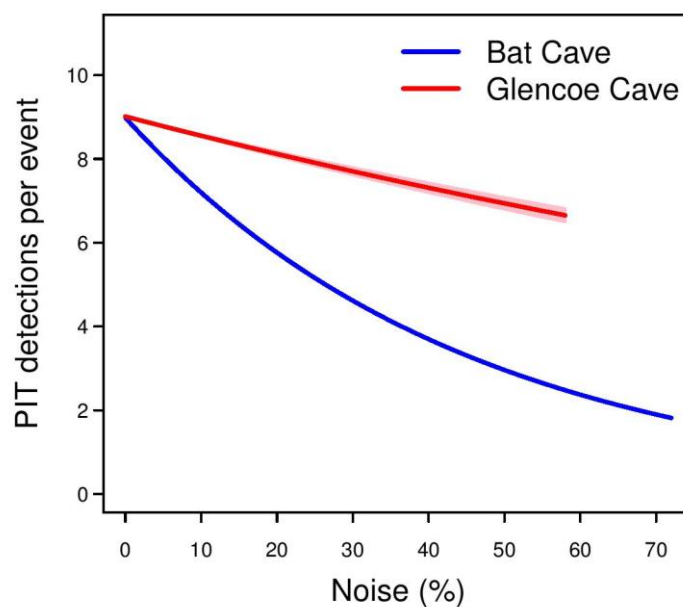


Figure 5. The negative relationship between average daily noise levels and the number of consecutive PIT detections per detection event at both study sites. The error margins are indicated in pink for Glencoe and are not visible for Bat Cave due to their very small size.

Detection and encounter probability

The number of individuals tagged in the study and subsequently detected on the system at Bat Cave was lowest in the first year at 92.3%, when noise levels were higher, and improved in the following years when noise levels were lower. In 2017 and 2018 these rates were 99.1% and 98.7%, respectively, of the bats tagged in that

year – with 95.7% and 94.6% still detected >10 days after tagging. In total, 2875 of the 2966 (96.9%) tagged individuals were detected at least once.

The trial in 2017 where tagged bats were released within Bat Cave past the RFID system, revealed that not all bats that were assumed to have flown through the antenna were detected. A total of 154 of the 209 bats were detected by midnight on the date of their release. This indicated an apparent probability of a tagged bat being detected at least once while present at Bat Cave (on a given date with average daily noise at 15%) at 0.74. Of the bats not detected ($n = 55$), 94.5% were detected on a later date (hence removing the possibility of death and tag loss for non-detection of these individuals), and just three individuals were never detected at Bat Cave or Glencoe.

At Bat Cave, the daily encounter probability per individual (i.e. the probability that a tagged bat was both present and detected) reflected both the effect of varying noise levels and seasonality of bat congregation at the maternity cave (Fig. 6). Encounter rate and probability peaked at >0.8 over the breeding season when larger numbers of bats congregated at the maternity site and decreased over winter coinciding with natural dispersal to non-breeding roost sites. Infra-red video monitoring (using the existing cameras in Bat Cave) confirmed that the decline in bat numbers over winter was real, and not due to detection problems, with few bats being observed until August, when clusters of thousands of bats began reforming at the maternity cave. Higher noise levels decreased encounter probability overall, however, there was particularly pronounced drop in encounter probability once daily average noise levels exceeded 15% (Fig. 6c), e.g. model-based estimates (when day of year = 1) were 0.59 (95% CI [0.590, 0.597]), 0.39 (95% CI [0.385, 0.393]) and 0.19 (95% CI [0.184, .0191]) when noise was 20%, 25% and 30% respectively, compared to 0.72 (95% CI [0.721, 0.726]) at 15%. Encounter probability on the date of the release-experiment outlined above (when day of year = 35 and noise levels were 15%), was 0.66 (95% CI [0.655, 0.660]).

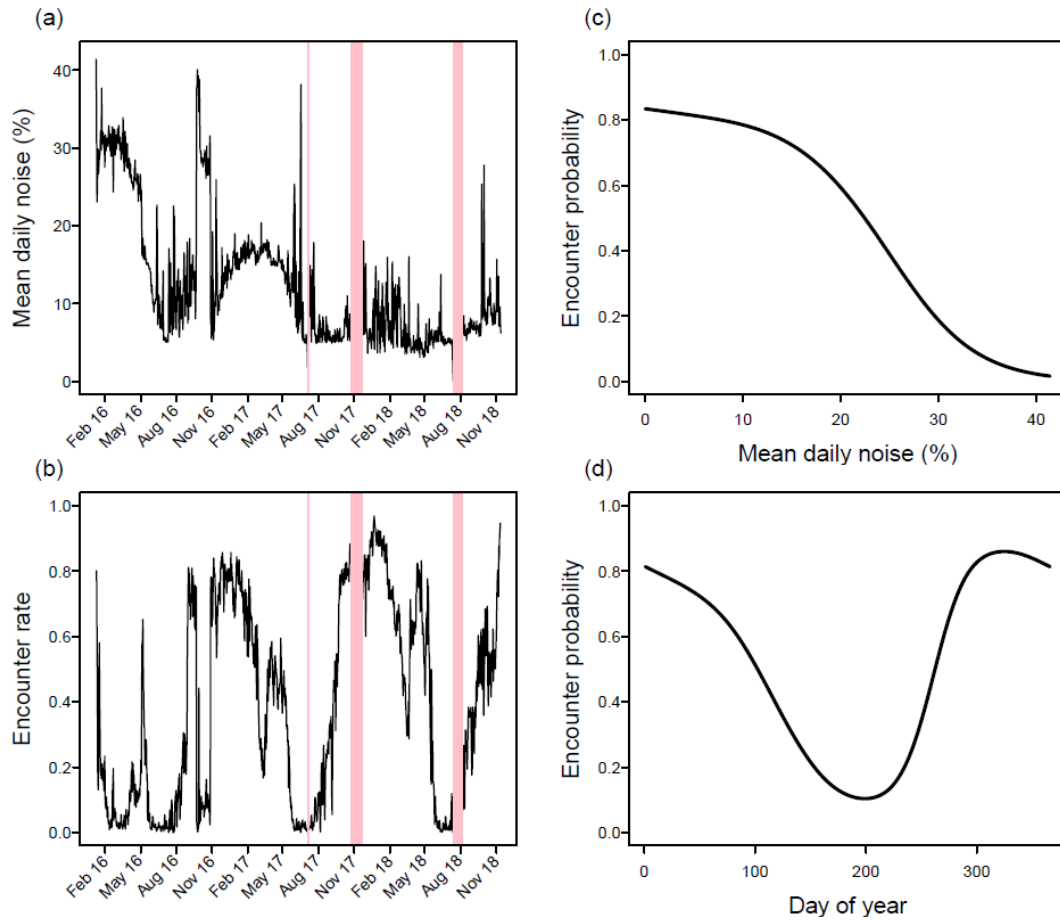


Figure 6. Encounter probability models of tagged individuals at Bat Cave in relation to noise levels and day of year. (a) and (b) show the fluctuating noise levels and encounter rates (i.e. proportion of bats detected that are known to be alive) by day of year, with pink bars indicating power outages when no data was recorded on the RFID system. c) Encounter probability in relation to noise levels (when day of year =1); d) Encounter probability throughout the year (using noise levels at 5%). Earthing occurred in early May 2016.

High encounter rates and high RFID system sensitivity meant that data accumulated quickly. More than 17.8 million PIT-tag detections were logged over the course of the study. Collapsing consecutive tag detections of the same tag number (representing a single pass through the antenna), resulted in 1,304,784 unique detection events at Bat Cave and 129,284 at Glencoe. The number of unique individuals detected per day at Bat Cave ranged between 0 and 1743, and up to 534 for Glencoe. Tagged individuals

were detected over multiple seasons and years, with a high rate of return to Bat Cave after seasonal dispersal periods (Fig. 7).

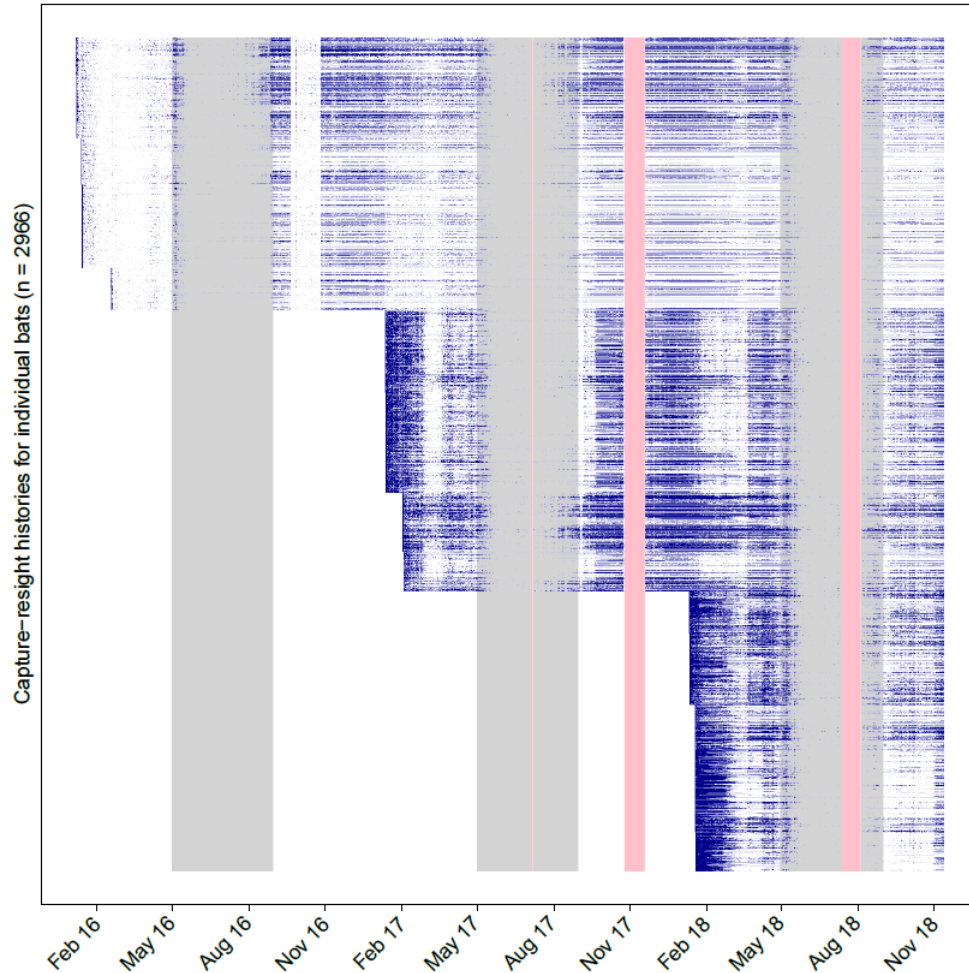


Figure 7. Capture-resight histories of all PIT-tagged individuals at Bat Cave over the three-year study. Each of the 2966 tagged bats is represented as an individual row on the y-axis, with initial capture and subsequent daily detections/presence at Bat Cave marked in blue. The data occurs in blocks because individuals were tagged over three years and seven trapping events. Absence (white) could be due to death, tag loss, migration to other cave locations, or lack of detection (especially due to noise problems such as those encountered before earthing in early May 2016 and during the high noise event in Oct–Nov 2016). The pink shading indicates missing data due to power outages and grey shading indicates May to August, when bats typically disperse away from Bat Cave.

Discussion

A limitation of PIT-tag technology for wildlife research has been the short read-range capabilities of PIT antennas (Gibbons and Andrews 2004). With the installation of large RFID antenna systems at southern bent-winged bat roosting caves, we have demonstrated that antenna dimensions and read-range distances can reach greater magnitudes than previously described. Earlier studies using PIT technology at bat roosts or water sources described read-ranges as small as 5 to 15 cm (e.g. Neubaum *et al.* 2005; Adams and Hayes 2008), including with the same antenna as used in our study but in a different configuration and set-up (Adams and Ammerman 2015). The greatest read-range we found in the literature for a PIT antenna was 35 cm using a plate antenna (Norquay and Willis 2014). We have shown that large loop-style antenna configurations can achieve read-ranges up to 105 cm on both sides of the detection plane. These results demonstrate greater flexibility of applications for PIT technology to study a wider range of organisms, many of which could not be studied with this technology previously, including many cave-dwelling bat species.

We had high overall detection success, particularly in the second and third years when performance of our RFID system was optimised. Across the full study period, 97% percent of bats were detected at least once. This compares with 76% (Adams 2015), 67% (Adams and Hayes 2008) and 62% (Horn 1998) of bats PIT-tagged in shorter-term bat studies, and 65% of tagged juveniles and 77% of adult females successfully detected in a longer-term study over four years and multiple roost sites (Ellison *et al.* 2007b). Factors that may have contributed to the higher overall detection success in our study likely include the advancement in technology used, concerted efforts made to monitor and increase RFID system performance, and the behaviour of southern bent-winged bats that show high fidelity to the Bat Cave site and reliably congregate at this maternity cave in large numbers.

Compared with traditional microbat marking and trapping methods, the use of small PIT antennas at roost sites has been demonstrated to significantly increase ‘recapture’ probability and the accuracy of survival estimates, without incurring the cost of increased disturbance from re-trapping (Ellison *et al.* 2007b). Our data obtained with large antennas likewise demonstrates high rates of passive detection success over

time. The magnitude of the data demonstrates exciting possibilities for future research, which could answer important ecological questions to inform threatened species recovery, such as survival rates, as well as behaviour, movement and migration patterns. Whilst our testing with hand-released bats demonstrated imperfect daily detection rates, mark-recapture methods assume detection/recapture probabilities <1 , consequently, this is not usually a problem unless recapture rates are very low (e.g. Waller and Svensson 2016).

A key finding from this study is that large PIT antennas are highly sensitive to noise (unwanted signal) levels. Bat Cave system was notably affected by noise introduced by the power supply. Before earthing the RFID system, unplugging the system's battery charger from mains power increased read-range by an additional 20 cm. This was despite the RFID system running on batteries and the battery-switcher unit separating the RFID system from the battery charger and associated mains power. Earthing mitigated this issue; however, total collapse in detection capacity resulting from a thermal camera installed 50 m from the RFID system demonstrates the sensitivity of the system to unexpected noise sources, even after earthing. Noise levels are under constant flux and can be affected by a wide-range of man-made and natural environmental factors (e.g. atmospheric noise) (ITU 2016), as such, not all noise sources could be identified or removed and over the course of the study, noise levels fluctuated over minutes, hours, days, and seasons.

Our encounter probability model demonstrated that noise levels and seasonal activity patterns of the bats (time of year) were major factors influencing detection (Fig. 6). Encounter probability (the likelihood that a bat was both present at Bat Cave and successfully detected) was just 0.08 lower than the proportion of bats detected in the release experiment (under known presence). The relatively narrow difference between these two measures may have been due to the timing of the release experiment, which occurred at peak season at Bat Cave, when most bats are thought to be present at the maternity cave (Dwyer and Hamilton-Smith 1965). Whilst the release experiment was undertaken only on one occasion, the similar results during high levels of presence at Bat Cave suggest that noise level and time of year may be suitable proxies in our model for other factors affecting detection of our tagged population, such as

behaviour of the bats, and speed and angle of the tags as they pass through the antenna.

Early in the project, we conducted preliminary testing to attempt to quantify and predict the effect of speed and angle on detection success, however, this proved difficult and was inconclusive. A major issue was that factors affecting detection were interdependent; for example, slightly different antenna configurations, environment, or noise levels altered the level to which speed and angle affected detection. Furthermore, replicating natural bat flight was difficult, and recording equipment (such as cameras) used to record the experiments introduced electromagnetic interference, which altered detection outcomes. Using noise metrics as a covariate in analysis may be a way around these issues, because noise is a major determinant of read-range (Fig. 5). Given that PIT-readers detect tags at a fixed rate per second, the larger the detection field, the faster a tag should be able to pass through the antenna and still be detected. Additionally, greatest read-ranges are achieved with the RFID system when tags pass perpendicular to the detection plane (K. Pomorin, pers. comm.). Ad hoc experimentation upon setting up the antenna, confirmed that passing a test tag through the antenna at increasing angles from perpendicular to the antenna plane dramatically decreased the maximum read-range (E.v.H, pers. obs.). In fact, holding a test tag parallel to the antenna plane resulted in the tag not being detected at all. Therefore, lowered read-range due to elevated noise would likely compound angle issues, whilst greater read-ranges should allow for a greater range of angles for passing tags. In our study, read-range is likely important for accommodating the natural flight behaviour of southern bent-winged bats, and may explain the notable differences in encounter probability with small (e.g. 5%) increases in noise levels (Fig. 6c). We have found little literature examining these or other factors affecting PIT-tag detection success (but see Freeland and Fry 1995 for close-range detection, using hand-held PIT-tag scanners) and we therefore suggest that further investigation into this area is warranted.

Our secondary system at Glencoe was less prone to noise issues than Bat Cave and recorded higher read-ranges throughout the study. However, even under low noise levels (e.g. 5%) at both sites, read-range (and detections per event) were higher at Glencoe (Fig. 5). The higher read-ranges at this study site were therefore not due to

average daily noise levels alone. Other factors that may have contributed to the greater read-ranges at Glencoe may be the slightly smaller antenna configuration and that higher noise levels only occurred during the day, when bats were not passing through the antenna to enter or exit the cave (Fig. 4). We were initially concerned that metal infra-structure located at the entrance to the cave at Glencoe, including old irrigation pipes and pumping equipment (Fig. 2), might interfere with system performance and successful tag detection. The effect of metal disturbing RFID has been experimentally demonstrated using hand-held PIT-tag readers (Freeland and Fry 1995) and is highlighted as a potential noise source in the Biomark IS1001 user manual (Biomark Inc 2015). However, the presence of this metal did not appear to cause any notable issues in our study. Unlike Bat Cave, Glencoe was free from nearby electronic equipment and cabling within 100 m of the set-up, except for electric fencing and our RFID and solar systems themselves. In most instances RFID systems can be charged with solar power rather than requiring access to mains power. Our Glencoe study site may therefore provide a more typical example of the potential performance of large PIT antennas for other studies. Unfortunately, at Bat Cave we were unable to bypass mains power by using solar due to the RFID system needing to be placed within the cave, approximately 100 m from the entrance and sunlight. However, our results offer the opportunity to contrast the performance of large PIT antennas in two different environments and set-ups, which can assist other researchers make informed decisions to optimise their methods.

Based on our study, we make seven recommendations for the use of large PIT antennas:

- (1) Monitor animal behaviour before and after installation to ensure that antennas do not cause adverse effects on wildlife (such as avoidance behaviour or collisions);
- (2) Minimise the presence of electronic equipment, devices and cabling within 100 m of the antenna;
- (3) Where possible, choose necessary devices and power supply (such as solar controllers) that emit low noise levels;
- (4) Earth large antenna systems as a standard protocol to optimise system performance;

- (5) Experiment with antenna configuration (including the placement of excess antenna length) to achieve maximum read-range, as small configuration changes can have significant effects;
- (6) Continually monitor noise levels, because noise levels fluctuate naturally, and can be influenced by unexpected sources; and
- (7) Quantified noise metrics should be included as covariates influencing the probability of detection in subsequent statistical analysis of marked populations.

Overall, compared to alternative methods, PIT-tagging appears to be a safe marking method with favourable benefits to the study population, such as reduced disturbance by minimising trapping events and low tag weight. Importantly, this technique boasts high re-detection rates and therefore can yield large volumes of continuous data over multiple seasons and years. While the initial cost of equipment may appear as a limitation, this is off-set by the comparatively low cost of subsequent re-detections of individuals over the course of a study, especially for larger studies such as ours. One limitation to current PIT-tag studies is the maximum length and potential configurations of commercially available cord antennas. The results of our study, using a 15 m antenna, suggest that even longer antennas may be successfully configured to cover larger entrances. At the time of writing, we have had some preliminary success detecting tagged bats at Bat Cave entrance using a third (specially ordered) 22 m antenna, and as technology progresses options are likely to continue to diversify. Our study demonstrates that large PIT antennas can successfully be used for long-term studies to monitor small, volant, fast-flying animals that move across large distances. The availability of large antennas with larger detection fields increase the potential applications of this technology and consequently, we believe that the full potential of PIT-tag technology as an ecological research tool is yet to be realised.

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Conflicts of interest

The authors have no conflicts of interest to declare.

Authors Contributions

E.v.H., R.L., L.F.L., N.M. and T.R. conceived and designed the study; E.v.H. led the trapping and tagging field work with assistance of L.F.L. and T.R.; E.v.H. and T.R. installed the RFID systems, troubleshooted system problems and downloaded data; E.v.H., T.A.A.P., T.R. and J.W. manipulated, explored and analysed the data; all authors contributed to data interpretation; E.v.H. drafted the paper; and all co-authors contributed to revising the manuscript.

Data accessibility

Data used in these analyses are available at Dryad DOI: 10.5061/dryad.vh8t993.

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Appendix 1

An example of a Full Status Report from the Biomark IS1001 installed at Bat Cave including the system settings chosen for this study.

INF: Start Of Full Status Report

Reader:

ID:	01
Model:	IS1001
S/N:	1442.0909
Date:	11/12/2018
Time:	00:28:35
Application Firmware Version:	1.6.2
Operation Mode:	Scan
Network Mode:	IS1001 Standalone
Exciter Sync. Mode:	Sec. Master
Date/Time Sync.:	Disabled
Beeper:	Disabled
Tag Display Format:	DEC
Initiation Delay:	Disabled
Reader Auto Standby Voltages:	16 V, 18 V
Idling Time:	Disabled
Alarms:	
Antenna Current Low Alarm:	1.0 A
Noise High Alarm:	40%
Tuning Capacit. High Alarm:	970
Tuning Capacit. Low Alarm:	50
Alarms Unique Delay:	60 sec
Antenna/Tuning:	
Exciter Voltage Level:	5
Dynamic Tuning:	Enabled
Tuning Target Phase:	393
Tuning Target Phase Deviation Threshold:	9
Measurements:	
Antenna Current Gain:	120
Antenna Current Offset:	110
Communication:	
Local Port Speed:	115200
Tags To Local Port:	Enabled
Alarms To Local Port:	Enabled
Messages To Local Port:	Enabled
Remote Port Protocol:	ASCII
Detection:	
HDX Tag Detection:	Disabled
Fastag Detection:	Disabled
Detection Counter Enabled:	Yes
Unique Mode:	Disabled

Unique Delay:	60 sec
FDXB Detection Scan Time:	120 ms
VTT Level:	128
Auto VTT Delay:	60 min
Memory:	
Tags Memory Size:	100015
Status Reports Memory Size:	1023
Save Tags To Memory:	Disabled
Save VTT To Memory:	Enabled
Save Stat. Reports To Memory:	Enabled
Reports:	
Auto Noise Report Delay:	5 min
Auto Status Report Delay:	60 min
Diagnostics:	
Detection Counter:	369491
Tags In Memory:	36529 (36%)
Status Reports In Memory:	1020 (99%)
Input Voltage:	24.0 V
Exciter Voltage:	19.8 V
Antenna Tuning:	Tuned
Antenna Current:	5.2 A
Tuning Capacitors:	76
Tuning Phase:	399
Tuning Relative Phase:	-6
FDXB Signal Level:	48 mV (5%)
Temperature:	23.2 C
Sync. Input Present:	No
Sec. Master Active:	Yes
Active Alarms:	
SRP:	01 11/12/2018 00:28:35.100 16,0,1,0,5,- 6,76,36,99,240,198,52,5,399,232,21,0,0,0,0
INF:	End Of Full Status Report

Chapter 4. Recovery of southern bent-winged bats (*Miniopterus orianae bassanii*) after PIT-tagging and the use of surgical adhesive

van Harten, E., Reardon, T., Holz, P. H., Lawrence, R., Prowse, T. A. A., and Lumsden, L. F. (2020). Recovery of southern bent-winged bats (*Miniopterus orianae bassanii*) after PIT-tagging and the use of surgical adhesive. *Australian Mammalogy* **42**, 216–219. doi:10.1071/AM19024

Recovery of southern bent-winged bats (*Miniopterus orianae bassanii*) after PIT-tagging and the use of surgical adhesive

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Abstract

Surgical adhesive is widely used to prevent shedding of injected PIT-tags, but the effect of this adhesive on individuals has not been documented. We recaptured 52 southern bent-winged bats up to 741 days after PIT-tagging. All recaptured individuals were in good body condition, with no signs of infection or skin irritation, however, temporary fur loss occurred at the injection site. We advocate that researchers consider the impact this may have on study species, particularly when PIT-tagging small mammals during cooler months.

Introduction

A key requirement for studying many aspects of wildlife ecology is the use of mark-recapture methods, such as using passive integrated transponder (PIT) tags. PIT-tags are glass encapsulated microchips that are injected subcutaneously to provide individuals with unique identification markers that can be read with hand-held readers

or passively through the use of antennas at key locations (Gibbons and Andrews 2004). A variety of small mammal populations have successfully been studied using PIT-tags including rodents, marsupials and bats (Schooley *et al.* 1993; O'Shea *et al.* 2004; Soanes *et al.* 2015), but a limitation is tag loss which can negatively bias recapture rates and subsequent survival estimates (McDonald *et al.* 2003).

PIT-tag loss predominantly occurs soon after tagging due to tags working their way out of the insertion hole (Schooley *et al.* 1993; Kerth and König 1996; Fokidis *et al.* 2006). Applying surgical adhesive to injection sites has been demonstrated to minimise tag loss (Lebl and Ruf 2010). This approach has been widely used in small mammal studies (Seebeck and Booth 1996; Horn 1998; Morley 2002; Wimsatt *et al.* 2005; Johnson *et al.* 2012) and is part of the recommended procedure for PIT-tagging bats (Kunz and Weise 2009). In bats, PIT-tag loss can be as high as 39% when surgical adhesive is not used (Rigby *et al.* 2012), and as low as 1.6% where it is applied (O'Shea *et al.* 2004).

PIT-tagging has generally not been associated with negative effects on body condition, survival or reproductive success in small mammals (Rao and Edmondson 1990; Rigby *et al.* 2012; but see Siegal-Willott *et al.* 2007); however, health and recovery following the use of surgical adhesive on PIT-tagged individuals has not been adequately documented. One unpublished study using surgical adhesive on little brown bats (*Myotis lucifugus*) reported no signs of infection 'or physical distress', however, observations were made on just five recaptured individuals (Horn 1998). Rigby *et al.* (2012), abandoned the use of surgical glue after observing matting of the fur on the first individuals they tagged, but with high rates of subsequent PIT-tag loss. Concern was also expressed for potential thermoregulative effects on individuals after tagging due to the use of hair-trimming and antiseptic preparation commonly used in conjunction with PIT-tagging and surgical adhesive (Rigby *et al.* 2012).

Research on the effects and ethical considerations of marking methods on wildlife, including capture, handling and marking procedures, is paramount (Murray and Fuller 2000). Here we report on the short- and long-term physical condition of recaptured southern bent-winged bats (*Miniopterus orianae bassanii*) following PIT-tagging with the application of surgical adhesive, to investigate the potential effects of this technique on small mammals.

Method

The southern bent-winged bat is a critically endangered, insectivorous, cave-dwelling bat weighing an average of 15 g (Churchill 2008). The species has a restricted range in south-eastern Australia, with Bat Cave at Naracoorte Caves National Park serving as a maternity and summer congregation site. As part of a larger study on the survival and population dynamics of this species, 2966 bats were trapped and PIT-tagged at Bat Cave in January and February, 2016–18. To minimise disturbance, only two consecutive trapping nights were undertaken at a time; a total of six nights in 2016, and four nights in each of 2017 and 2018.

Bats were trapped with Austbat harp traps (Faunatech, Mount Taylor) surrounding the cave entrance. Trapping continued from dusk until the early hours of the morning, catching bats as they left or re-entered the cave.

Bats were scanned for a pre-existing PIT-tag, using a hand-held PIT-tag scanner (Trovan LID560 and Biomark 601). If no PIT-tag was present, standard measurements were taken, including body mass, and the bat was PIT-tagged. The PIT-tagging process was undertaken by two people. The handler gently restrained the bat by covering its head with a cloth bag, loosely holding this to the bench with two fingers and, if required, holding the tail membrane with the other hand. The tagger cleaned the injection site with a 70% ethanol-soaked cotton tip, splaying hair outwards in a circle to reveal a patch of skin (rather than trimming the fur). Using a sterilised 12-gauge needle and applicator (Biomark MK10 implanter and N125 needles in 2016, Biomark MK 25 Implant Guns and HPT12 Pre-load Trays in 2017–18), the tag was injected subcutaneously from the distal edge of the shoulder scruff to rest between the scapulae. The site was sealed with a drop of surgical adhesive (3M™ VetBond™) and allowed to dry prior to release. During handling and tagging, bats typically remained calm and were able to fly within minutes of the procedure.

Any tagged bats that were re-captured during trapping were weighed to assess body condition (McGuire *et al.* 2018) and checked for any signs of irritation or inflammation (e.g. redness, swelling, ulceration) at the injection sites. Notes were taken on whether the surgical adhesive had been shed and fur characteristics at the injection site. Some re-trapped individuals were also examined gently with a gloved fingertip to check for any tag migration.

We assessed changes in body mass using the R software for statistical computing, version 3.5.1 (R Core Team 2018). For each recaptured individual, we calculated the difference between pre-tagging and recapture body mass and the number of whole ‘days’ elapsed since tagging (with zero indicating recapture on the same night as tagging). To test whether time-since-tagging affected the changes observed, we first discretised time-since-tagging into four levels (based on recapture opportunities): three short-term (0–1d, 7–21d, 34–42d) and one long-term (343–741d). The effect of time-since-tagging on body mass change was investigated using a linear model in R (i.e., a cell-means model with no intercept, body mass change \sim time since tagging – 1).

Results

A total of 52 bats were recaptured, 0–741 days after tagging. All appeared to be in good condition, based on body mass, and showed no signs of irritation, inflammation or infection at the injection site.

There was a significant effect of time-since-tagging on the body mass change of bats ($F_{4,48} = 9.1$, $p = <0.0001$). However, only bats recaptured 34–42 days after tagging exhibited a significant change in mass, being lighter (estimated change = -2.2 g) than when tagged (Table 1). All six individuals recaptured 34–42 days post-tagging were caught on the same trapping weekend in February 2016 and had a mean body mass of 14.2 g (range 13.2–14.8 g). The mean capture body mass of untagged bats was also lower on this trapping weekend (mean 13.2 g, 95% CI [13.07, 13.38], $n = 151$) compared to those bats captured at other times (16.5 g, 95% CI [16.51, 16.59], $n = 2815$).

Table 1: Number and estimated body mass (BM) change of recaptured southern bent-winged bats over the study period.

Days since tagging	Number of individuals recaptured (<i>n</i>)				BM change (g)	s.e.	<i>p</i>
	2016	2017	2018	Total			
0–1	4	8	12	24	-0.2	0.20	0.55
7–21	2	6	1	9	-0.3	0.32	0.31
34–42	6	-	-	6	-2.2	0.39	<0.0001
343–741	-	4	9	13	0.5	0.27	0.08

Adhesive applied to injection sites dried into a hard patch ranging from 3.6 to 12 mm in size. Observations from re-trapped individuals from the same trapping-year demonstrated that as sites healed, the patches of glue and attached fur were shed, leaving a bald patch (Fig. 1). In one individual, observed 17 days after tagging, the patch of glue and incorporated fur was still attached but lifting from one side, with the healed injection site (surrounded by normal skin) visible underneath. Fur re-growth was observed in recaptured bats three to six weeks after tagging.

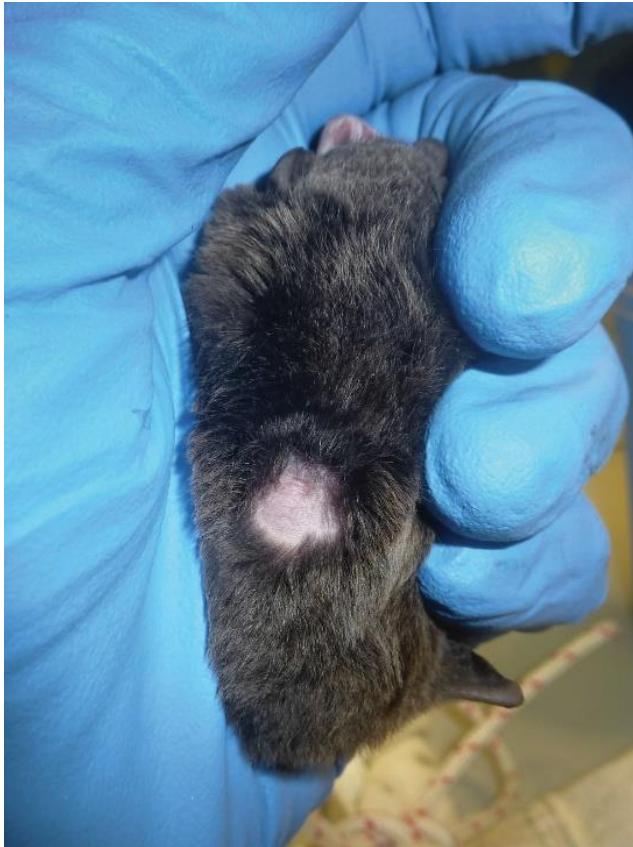


Figure 1. A southern bent-winged bat, recaptured three weeks after PIT-tagging, with a bald patch at the injection site after the surgical adhesive and attached fur were shed. Photo: Lindy Lumsden.

Most bats ($n = 10$) recaptured one to two years after tagging showed no external signs of tagging. Fur at injection sites of two individuals had re-grown white instead of brown. Another individual had markedly thinner hair at the injection site compared to the surrounding area, with skin observable through the fur.

No tag migrations were detected. Tags remained in line with the spine, cradled between the scapulae, except in one individual where the tag was located 5 mm posterior to the scapulae.

One deceased tagged bat was found next to a nearby fenced cave-entrance, nine days after tagging. Necropsy revealed brain trauma, likely due to collision with the fence. The tagging and use of surgical glue had no apparent adverse effects on this individual (tag was in the correct position with no inflammation or trauma around the

injection site). The bat had successfully foraged following tagging, evidenced by excellent body condition (17 g) and a stomach full of invertebrates.

Discussion

Surgical adhesive is commonly used to minimise tag loss in PIT-tagging studies (Morley 2002; Wimsatt *et al.* 2005; Johnson *et al.* 2012). However, to our knowledge, this is the first study to document body condition and recovery of the injection site following its application.

Change in body mass after PIT-tagging and the use of surgical adhesive was not significant for most recaptured individuals in our study. This is consistent with results of PIT-tagging studies that compared body condition in tagged and untagged big brown bats (*Eptesicus fuscus*) and laboratory mice without use of adhesive (Rao and Edmondson 1990; Rigby *et al.* 2012). The exception in our study was six bats that followed the same pattern of lowered body mass as untagged bats from the same capture period. This may have been influenced by seasonal factors as this trapping period was later in the breeding season than all other trapping trips, and seasonal variation in body mass is common in bats (Dwyer 1964; Rughetti and Toffoli 2014; Kohyt *et al.* 2016).

The effects of surgical adhesive in our study were predominantly short-term. Rigby *et al.* (2012) abandoned using surgical adhesive after observing matted fur in tagged individuals. We made similar observations due to the adhesive drying into hard patches incorporated with fur in the mid-dorsal region. Rigby *et al.* (2012) also cautioned that hair-trimming and aseptic preparation of injection sites – common in PIT-tagging procedures – could affect bat body temperatures during recovery. After careful welfare consideration amongst our team, including a wildlife veterinarian (PHH), we decided not to use hair-trimming for preparation of injection sites. Instead, we splayed hair away from the area during sterilisation to reveal a patch of skin for injection. Not trimming fur reduced handling times and potential stress levels in the bats. Due to large numbers being tagged in this study, we considered processing efficiency important to reduce population disturbance by minimising the number of tagging nights. Fur loss still occurred with this method, when dried adhesive and attached fur was shed from injection sites. Localised fur loss has also been observed

when using adhesives to attach radio transmitters in small mammals, including bats (O'Mara *et al.* 2014) and bandicoots (Coetsee *et al.* 2016). It is unknown whether the sloughing caused any discomfort to the bats in our study, nor whether the extent of fur loss was caused by repeated scratching or grooming of the site, however, we did not observe any signs of scratching, wounds, scabs, redness, or swelling on the skin to indicate that the process was causing irritation or trauma. The fur loss is unlikely to have caused problematic thermoregulation effects due to our tagging taking place in mid-summer when temperatures in the region and within Bat Cave were warm (Baudinette *et al.* 1994).

Some minor long-term effects of surgical adhesive were also observed in our study, with two individuals re-growing white fur at the injection site. Localised fur loss and white re-growth are comparable to the effect of freeze branding, which is considered a safe marking method for bats (Sherwin *et al.* 2002). As recommended for freeze-branding (Sherwin *et al.* 2002), we suggest avoiding PIT-tagging bats (and use of surgical adhesive) during and before hibernation or cold seasons due to the partial fur loss associated with the method. In addition, the smallest drop of glue possible should be applied to reduce the size of the resultant bald patch. Further studies are needed to assess whether trimming the fur before applying surgical adhesive, or whether using other (non-cyanoacrylate) glue types (e.g. latex based), result in less fur loss than we report. An additional method for closing PIT-tag insertion sites is the use of sutures under anaesthesia (Currie *et al.* 2015); however, this presents further welfare considerations that would need to be assessed, including the inherent risks of anaesthesia, infection, as well as the experience and training of the practitioners.

Overall, our observations suggest that use of surgical adhesive in PIT-tagging was a safe method in our study, with no signs of irritation, infection, trauma or significant changes in body condition being observed. However, researchers should be aware that using adhesive may result in fur loss at the application site and assess the welfare impact this may have on their study species when choosing their methods.

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Conflicts of interest

The authors declare there are no conflicts of interest

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Chapter 5. Low apparent breeding-season survival in a critically endangered bat: survival analysis using large-scale passive detection

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Low apparent breeding-season survival in a critically endangered bat: survival analysis using large-scale passive detection

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Abstract

1. Capture-mark-recapture/resight (CMR) methods are used for survival-rate studies and to inform conservation action planning for threatened species. Advances in PIT technology have allowed passive detection or ‘resight’ of marked individuals using strategic positioning of large area antennas with greater read-ranges than previously possible. This technique may help address the need for information on insectivorous bats globally, of which a large proportion of species are either declining or data deficient.

2. We used passive CMR methods to study survival rates of the southern bent-winged bat, a critically endangered, cave-dwelling bat which has undergone serious decline in previous decades. We aimed to estimate apparent seasonal survival probability structured by age, sex and reproductive status over consecutive seasons, which has

hitherto been impossible using traditional CMR methods due to low recapture rates and the unacceptable risk of negatively affecting this vulnerable population.

3. Over three years, we used PIT-tagging to passively monitor almost 3,000 individuals at the site of the bat's primary breeding aggregation, and used daily detection data to estimate apparent seasonal survival rates and parameterise population projection matrices for the species under different demographic assumptions.

4. Bats exhibited lowest apparent survival over summer and autumn, with survival rates particularly low for reproductive adult females in summer (when lactating) and juveniles in autumn (after weaning). Survival rates were particularly low in the summer and autumn of 2016, which corresponded with severe regional drought, suggesting that dry conditions affect the viability of this critically endangered population. Winter survival rates were high for all age and sex classes. Under all assumptions, analyses of population projection matrices suggested the population is in deterministic decline.

5. This study is one of the first to assess differences in survival between reproductive and non-reproductive adult females of insectivorous bats. Lactating females experienced higher apparent mortality rates than non-reproductive females, suggesting an energetic cost of lactation and/or increased foraging activity, particularly during drought conditions. With climate-change models predicting more frequent and severe droughts throughout the species' range, survival rates of the southern bent-winged bat, especially lactating females, may worsen in the future. Passive CMR methods can now provide robust and detailed information to inform population ecological studies for insectivorous bats.

Introduction

Survival analyses are a key tool for understanding wildlife population variation and can provide valuable information for the effective recovery of threatened species (O'Donnell 2009). Survival-rate studies for terrestrial vertebrates have relied on labour intensive mark-recapture studies; however, technology advances are providing new opportunities. One technique that can be employed for estimating survival rates

in animals is the use of passive integrated transponder (PIT) tag technology, which can be used to passively re-detect tagged individuals at key locations without the need for physical recapture (Gibbons and Andrews 2004). This method has been demonstrated to significantly increase resight probability and more precisely estimate survival compared to traditional methods (Ellison *et al.* 2007). A limitation of PIT technology for undertaking long-term passive mark-resight studies has been the size and read-range capabilities of PIT antennas, with animals needing to pass close (usually *c.* 15 cm) to the readers to be detected, thereby restricting the potential application of this technology for many species. However, PIT-tracking systems have recently become available that can be successfully optimised to detect small bats flying in cave passages up to 2 x 5 m (van Harten *et al.* 2019).

The use of PIT-tag technology has been recommended for studying microbats due to challenges such as low recaptures rates (Schorr *et al.* 2014) and adverse impacts associated with traditional banding in many species (Baker *et al.* 2001). O'Shea *et al.* (2004) published the first estimates of survival-rates for bats based on PIT technology and remote detection. To date, survival estimates using passive mark-resight approaches have been published only for a few cool-temperate species, including big brown bats *Eptesicus fuscus* roosting in buildings (O'Shea *et al.* 2004; O'Shea *et al.* 2010; O'Shea *et al.* 2011), lesser short-tailed bats *Mystacina tuberculata* using tree hollows (O'Donnell *et al.* 2011; Edmonds *et al.* 2017), and Daubenton's bats *Myotis daubentonii* and Natterer's bats *Myotis nattereri* hibernating in an old well shaft (Reusch *et al.* 2019). Undertaking passive survival analyses of further species in different environments and seasons could provide critical information to inform conservation and recovery of bat populations, which are declining worldwide (IUCN 2020).

Survival studies of bats have been published for almost a century, but most early studies had methodological issues including reliance on potentially injurious banding and repeated sampling at hibernacula (creating disturbance which may lower bat survival due to burning valuable winter fat stores) (O'Shea *et al.* 2004). A global synthesis of survival estimates found that bat survival rates were strongly associated with age, sex and the number of young produced per year, as well as additional factors including season, species guild and data collection methods (Lentini *et al.* 2015).

Survival was highest for adult females in summer and those that produce fewer young per year (Lentini *et al.* 2015). First-year survival is commonly lower than annual adult survival (O'Shea *et al.* 2004; Lentini *et al.* 2015; Culina *et al.* 2017; Bailey *et al.* 2017). Several studies have reported higher survival rates in females than males (Pryde *et al.* 2005; Schorcht *et al.* 2009; Lentini *et al.* 2015; Culina *et al.* 2017), while others found no significant difference between the sexes (Sendor and Simon 2003; Sripathi *et al.* 2004; Papadatou *et al.* 2009). Similarly, a number of studies found no effect of seasonal or climatic effects on bat survival (Sendor and Simon 2003; López-Roig and Serra-Cobo 2014; Monadjem *et al.* 2015; Law *et al.* 2018), whilst others identified higher survival in summer (Lentini *et al.* 2015) or winter (O'Shea *et al.* 2011; Reusch *et al.* 2019). CMR studies using traditional mark-recapture methods require intermittent capture periods that often suffer from low recapture rates (Schorr *et al.* 2014), so the power to detect such sex- and season-specific differences in survival can be small. Whilst much is yet to be learned about survival, bats typically have significantly higher survival rates and slower life-histories than expected for their small size (Brunet-Rossinni and Austad 2004), with the oldest bat recorded in the wild being 41 years old. (Podlutsky *et al.* 2005).

The subject of this PIT-based survival study is the critically endangered southern bent-winged bat *Miniopterus orianae bassanii*, an insectivorous cave-dwelling bat with a restricted range in south-eastern Australia. The southern bent-winged bat has undergone serious decline since the 1960s; however, the cause of this historic decline remains uncertain (DELWP 2020). The current population trajectory is also unclear. The maximum longevity of the species is at least 20.5 years (Lumsden and Gray 2001) and current population mortality does not appear to be due to parasitic or pathogenic factors (Holz *et al.* 2018a; Holz *et al.* 2018b; Holz *et al.* 2018c; Holz *et al.* 2019). Survival estimates by age, sex and season are urgently needed to assist managers to identify the most likely population threats, determine the current population trend and whether any cohort or time of year is contributing disproportionately to mortality (DELWP 2020). Historical literature on other Australian bent-winged bats suggest that winter may be associated with highest mortality, particularly if individuals are unable to accumulate sufficient fat stores prior to the winter (Dwyer 1966a; Dwyer 1966b). We therefore predicted that

apparent survival rates would be lowest in winter, particularly for juveniles that may enter the season with low fat stores (Dwyer 1964).

Here we investigate age-, sex- and season specific survival rates of the southern bent-winged bat over three years, by PIT-tagging and monitoring almost 3,000 individuals at their largest breeding aggregation. We analyse seasonal variation in estimates of apparent survival for the respective age, sex and reproductive classes, consider potential explanations of mortality, calculate population growth rates to assess whether population decline is ongoing, and discuss the benefits and limitations of the PIT methods employed. The results provide urgently needed data for implementing targeted recovery actions for the southern bent-winged bat, and highlights areas that would benefit from further research for analysing rich capture-mark-resight (CMR) datasets in other wildlife species.

Materials and methods

PIT-tagging and data collection

Southern bent-winged bats were trapped and PIT-tagged at Bat Cave within the Naracoorte Caves National Park, South Australia, which serves as a maternity and congregation site from spring to autumn. Trapping occurred over six nights in 2016, and four nights in each of 2017 and 2018, at the end of the breeding season (January and February) by which time juveniles born in November were emerging from the cave to forage at night. To minimise disturbance, only two consecutive trapping nights were undertaken at a time. Bats were trapped with Austbat harp traps (Faunatech, Mount Taylor) surrounding the cave entrance. Trapping continued from dusk until the early hours of the morning, catching bats as they left or re-entered the cave. Both female and male southern bent-winged bats congregate at Bat Cave, so both sexes could be tagged. The total number of tagged juveniles and adults was monitored as tagging progressed throughout each night to ensure a large sample of each age cohort per year. Juveniles or adult bats were at times targeted by noting emergence times, which varied for the different cohorts at different stages of the study; for example, newly volant juveniles typically emerged late in the evening, after the main adult fly-out, whereas a few weeks later in the season, juveniles were caught

in the main fly-out at dusk. There was no targeting of one sex over the other, and hence the tagged samples reflect the ratio of the genders trapped. A potential male bias (from the expected 1:1) in juvenile sex ratios in 2017 was tested for statistical significance using a Chi-squared test.

For each PIT-tagged bat, individual covariates were recorded including sex, body mass and age. Age was described as juvenile (first year) or adult based on the respective absence or presence of a cartilaginous core at the metacarpal-phalangeal joints (Brunet-Rossinni and Wilkinson 2009). The reproductive condition of adult females was classified as pre-parous, lactating or post-lactating through examination of the individual's nipples (Churchill 2008). PIT-tags were subcutaneously injected dorsally using a sterilised 12-gauge needle and applicator (Biomark MK10 implanter and N125 needles in 2016, Biomark MK 25 Implant Guns and HPT12 Pre-load Trays in 2017–18). The injection site was sealed with a drop of surgical adhesive (3M™ VetBond™) to minimise tag loss, and allowed to dry prior to release. All PIT-tags (Biomark HPT 12) were checked for correct function using a hand-held PIT-tag scanner (Trovan LID560 and Biomark 601) both before and after insertion. During handling and tagging, bats typically remained calm and were able to fly within minutes of the procedure. Recaptured individuals were in good physical condition, with no sign of infection or other detrimental effects (van Harten *et al.* 2020).

Tagged bats were monitored by using a large PIT-tracking system (Biomark IS1001) which employed a 2 x 5 m loop antenna as described in van Harten *et al.* (2019), installed within Bat Cave, which detected tagged individuals in real time as they flew through the cave passage. When the system was working optimally, there was a large read-range before and after the antenna plane and high detection success (van Harten *et al.* 2019). Data files were recorded directly to USB flash drives plugged into the data logger board of the Biomark IS1001. Data were collected from the cave regularly (approximately monthly) over a 36-month period by manually retrieving the flash drives.

Survival analyses

To prepare the data for analysis, we derived capture-resight histories for each of the 2966 PIT-tagged bats to produce a binary response variable (undetected/detected) for each individual across each day of the 1120-day study period, with a ‘day’ being defined as the 24 hours between successive middays. Accumulative age functions were incorporated to allow juvenile bats to age appropriately (i.e., juveniles were classified as adults at 1 year of age). As reproductive status in adult females could be determined only by physical examination during PIT-tagging, these individuals were defined as ‘reproductive’ (i.e. lactating) or ‘non-reproductive’ for the summer and autumn following tagging, and then pooled into an ‘unknown’ reproductive category for all subsequent times. We then modelled daily survival using Cormack-Jolly-Seber (CJS) models which were fitted using the R package ‘RMark’ (Laake 2013). CJS models allow estimation of apparent survival probabilities (ϕ) whilst also accounting for (potentially variable) encounter probabilities (p).

Given the impact of environmental noise on antenna performance (van Harten *et al.* 2019), and the regular migratory nature of the southern bent-winged bat, we modelled encounter probability with flexible spline functions such that

$$p \sim s(yday, k = 5) + s(noise, k = 2)$$

where *yday* is the day of year, *noise* is the average environmental noise (summation of unwanted signal being received by the PIT tracking system, %) over the course of that day, and *k* is the dimension of the spline. The basis functions for the splines were calculated with the R package ‘mgcv’, and a cubic regression spline was assumed for the day-of-year effect to ensure continuity in the response between the first and last day of year.

We then developed a candidate set of models for daily survival probability (ϕ) that included different covariates including age, sex, season, year and reproductive condition (for adult females only), as well as possible interaction terms. When modelling the effect of both season and year, we coded December as a component of summer in the following year (e.g. December 2016 data were coded as summer 2017). We also tested a variable *first6months* which fitted separate survival estimates for the first six months after an individual’s tagging and for the remainder of the re-sight

history. Model selection was undertaken by comparing Akaike information criterion (AIC) for each alternative model. The AIC includes a penalty for increasing complexity (i.e. number of parameters) in the model. The ‘best’ or top-ranked model is the one with the lowest AIC value (provided that the difference between the compared models is ≥ 2).

Estimation of population growth rates

In this study, we use ‘population’ to refer to the colony of southern bent-winged bats that occupy the Bat Cave maternity site during the warm season. Current population trends for the study population are unknown. To estimate the exponential rate of population growth (r), we constructed pre-breeding Leslie matrices (Caswell 2006) under different demographic assumptions. To achieve this, we initially used annual survival-rate estimates for each age, sex and reproductive class (based on the top AIC-ranked model), assumed a female age of reproductive maturity of two years (as described for eastern bent-winged bats *Miniopterus orianae oceanensis* (Dwyer 1963) and observed in this study as reported below) and fertility estimates of one offspring per adult female per year (Richardson 1977) as baseline parameterisation. We then calculated the effect on population growth rates of differing juvenile sex ratios (from observation in this study), potential emigration rates, breeding probabilities and tag loss. Two potential rates of tag loss were included: 1.6% which was calculated for the big brown bat in a double-tagging experiment in which surgical adhesive was applied to the injection site, as per this study (O’Shea *et al.* 2004); and 5%, the approximate proportion of bats not detected more than 10 days after tagging during this study in 2017 and 2018 (van Harten *et al.* 2019) which provides an estimate of the maximum tag loss over this period.

Results

Capture demographics

A total of 2966 southern bent-winged bats were PIT-tagged, with approximately 1000 bats tagged per year (Table 1). The juvenile sex ratio approached the expected 1:1 in 2016 and 2018 but had statistically significant ($P < 0.01$) male bias in 2017 (Table 1). As expected at a maternity site, adult captures had female bias across all study years.

The proportion of adult females classed as lactating ranged between 63 and 100% of adult females captured between 8 and 19 January (across study years). Just 29% of captured adult females were classed as lactating on a trapping trip on 3 February 2017, with a further 54% classed as post-lactating, suggesting that juveniles were being weaned at this time.

Table 1: The number of southern bent-winged bats captured and tagged from each age/sex class (Juv=juvenile, Ad=adult) at Bat Cave, Naracoorte, 2016–2018.

Year	Capture summary (n)					Sex ratio (♂:♀)	
	Juv♂	Juv♀	Ad♂	Ad♀	Total	Juv	Ad
2016	271	282	176	243	972	49:51	42:58
2017	358	292	161	188	999	55:45	46:54
2018	249	269	222	255	995	48:52	46:54

A small number of tagged females recaptured in subsequent years provided some observations of reproductive maturity. Two females tagged as juveniles were recaptured one year after tagging and classed as pre-parous (i.e. non-reproductive). A further two females tagged as juveniles were recaptured two years after tagging and classed as lactating. Whilst the sample size was small, these observations suggest that females first breed at two years of age.

Body mass

Body mass was recorded for all tagged individuals. Sexual dimorphism was evident, with males consistently weighing more than females of the same age cohort (Table 2). In January, juveniles were newly volant, yet already approximated adult proportions and juvenile males typically exceeded the weight of adult females. Each of the respective sex and age cohorts appeared to maintain relatively consistent measures of mean body mass for January capture periods, regardless of year. A later capture period in mid-February 2016 saw a notable decline in body mass for juveniles of both sexes compared to during the previous month. No adults were tagged (and hence weighed) during this later trip so it is unknown whether adults also experienced decline in body mass at this time.

Table 2: Body mass (g) of southern bent-winged bats at each capture period (with date of the first capture night).

Capture period		Juvenile females			Juvenile males			Adult females			Adult males		
year	date	mean	s.e.	range	mean	s.e.	range	mean	s.e.	range	mean	s.e.	range
2016	8 Jan	16.2	0.19	15.4-17.3	17.0	0.31	15.8-17.5	16.2	0.06	13.3-19.0	16.7	0.07	12.6-18.9
2016	15 Jan	16.1	0.06	14.2-18.4	16.7	0.06	14.0-18.8	16.1	0.11	14.5-18.9	16.3	0.19	14.4-17.6
2016	19 Feb	13.1	0.11	10.8-15.8	13.4	0.11	11.0-15.7	-	-	-	-	-	-
2017	13 Jan	16.1	0.05	13.6-18.2	16.7	0.04	14.7-18.6	16.2	0.08	14.6-17.5	17.1	0.16	15.9-19.0
2017	3 Feb	15.8	0.12	14.5-18.1	16.3	0.13	14.4-19.0	17.3	0.18	13.8-22.5	17.5	0.11	14.4-24.8
2018	12 Jan	16.5	0.14	14.3-18.2	17.1	0.15	14.5-19.0	16.7	0.06	12.7-18.7	17.3	0.07	15.2-20.0
2018	19 Jan	16.1	0.05	14.1-18.5	16.6	0.06	14.1-19.2	15.9	0.08	14.0-17.9	16.7	0.10	13.5-19.4

Survival analysis

The top AIC-ranked survival model included the variables age, sex, the interaction between season and year, and female reproductive condition (Table 3). All population cohorts had lowest apparent survival in summer and autumn, particularly in 2016 (Fig. 1), which coincided with record-breaking drought conditions in the study region (a 43-month severe rainfall deficiency with rainfall totals at the lowest on record) (Bureau of Meteorology 2019). By contrast, monthly regional rainfall for the remainder of the study period was classed as ‘very much above average’ from mid-late 2016, ‘above average’ in 2017, ranging between ‘below average’ to ‘above average’ in 2018, and ‘average’ in early 2019 (Bureau of Meteorology 2019).

Winter survival was high for all population cohorts (Fig. 1). Apparent survival estimated for juveniles was generally lower than for adult classes, particularly in autumn and spring – the exception was summer estimates which were even lower in reproductive females. Adult females that were assessed as reproductive (lactating) had lower survival estimates than those individuals classed as non-reproductive or for which reproductive condition was unknown (i.e. individuals tagged in previous years).

Table 3. Model selection table for assessing best fit for apparent survival of the southern bent-winged bat. Shown are the deviance, AIC value, Δ AIC (difference from the ‘best’ or top-ranked model) and Akaike weight for each model. All candidate models also incorporated encounter probability (p) (Supplementary data, Fig. S1).

Model	Deviance	AIC	Δ AIC	Akaike weight
~ age + year:season + sex + reproductive	1181390	1206565	0	0.9995
~ age + year:season	1181413	1206581	16	0.0003
~ age + year:season + sex	1181412	1206583	18	0.0001
~ age + season + sex + age:season + age:sex + season:sex + age:first6months	1181549	1206718	153	<0.0001
~ age + season + year	1181572	1206728	163	<0.0001
~ age + season + sex + age:first6months	1181605	1206762	197	<0.0001
~ age + season + sex + reproductive	1181720	1206877	312	<0.0001

~ age + season	1181775	1206925	360	<0.0001
~ age + season + sex	1181774	1206927	362	<0.0001
~ age	1182694	1207839	1274	<0.0001
~ age + sex	1182693	1207840	1275	<0.0001
~ 1	1183065	1208208	1643	<0.0001

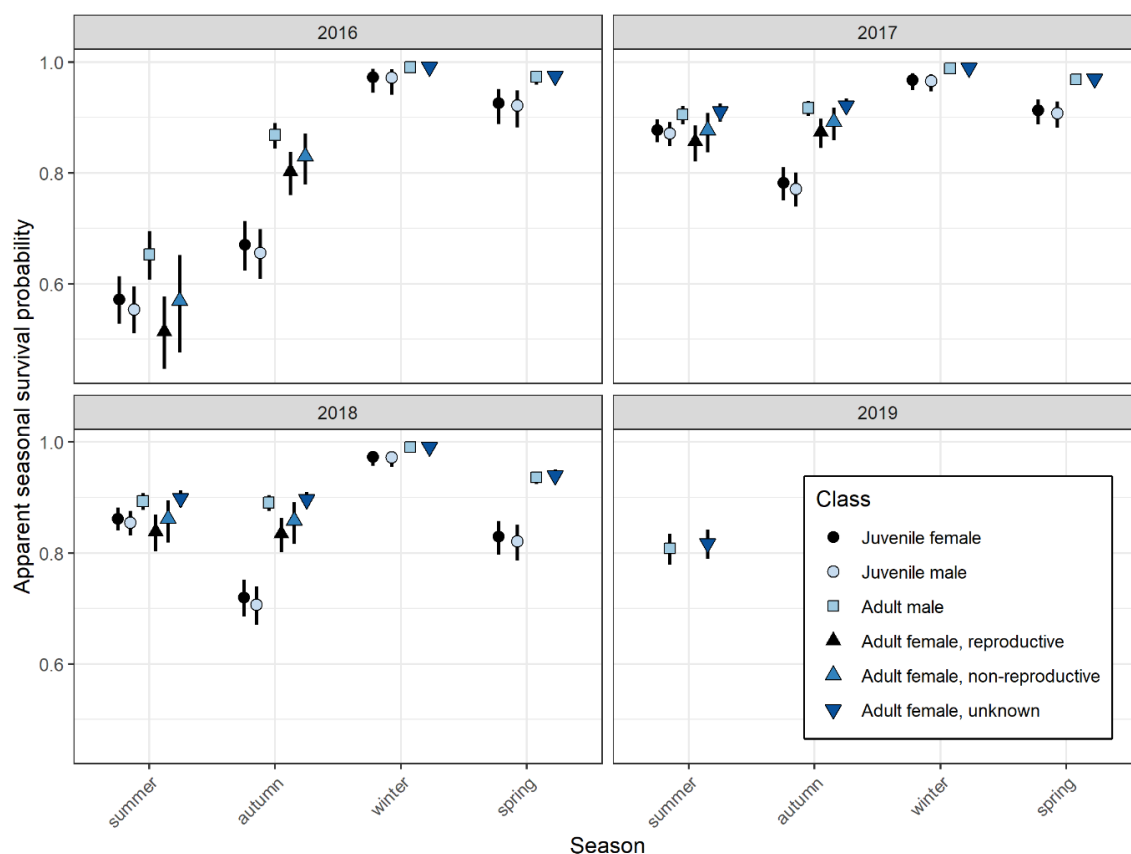


Figure 1. Estimates of apparent seasonal survival (by year) for each of the defined age, sex and reproductive classes of the southern bent-winged bat.

Estimated population growth rates

The exponential rate of population growth (r) was calculated for each study year using a variety of different parameter assumptions (Table 4). All calculations of r predicted population decline under the apparent survival rates experienced in 2016 (i.e., all r values were negative), with the baseline value as low as -0.603. Predicted rates of decline were markedly smaller for 2017 and 2018, though all r values were

negative (Table 4) unless including a permanent migration rate of at least 0.1. Emigration rates in southern bent-winged bats are unknown, however, historical banding records suggest a rate less than 0.05 (Dwyer 1969). Varying other parameters, including juvenile sex ratio, pre-volant survival and potential tag loss, made comparatively small differences to the population growth rate.

Table 4. Estimated exponential rates of population growth (r) of the southern bent-winged bat at Bat Cave. Estimates of r are calculated from a pre-breeding Leslie matrix parameterised using apparent survival rates for each study year (using top-ranked model presented in Table 3) and assuming reproductive maturity of adult females at two years of age and additional parameters as specified. If parameters are not listed, they remain at the baseline parameterisation.

r parameters	exponential population growth (r)		
	2016	2017	2018
baseline parameterisation	-0.603	-0.054	-0.168
sex ratio = 1:1			
permanent emigration = 0			
breeding probability = 1			
pre-volant survival = 1			
tag loss = 0			
sex ratio ($\text{♂}:\text{♀}$) = 55:45	-0.603	-0.074	-0.187
permanent emigration = 0.05	-0.552	-0.002	-0.117
permanent emigration = 0.1	-0.498	0.052	-0.063
breeding probability = 0.6	-0.603	-0.131	-0.238
pre-volant survival = 0.8	-0.603	-0.095	-0.207
tag loss = 0.016	-0.587	-0.037	-0.152
tag loss = 0.05	-0.552	-0.002	-0.117
example of combined parameters #1	-0.497	-0.116	-0.198
permanent emigration = 0.05			
breeding probability = 0.6			

pre-volant survival = 0.8			
tag loss = 0.05			
example of combined parameters #2	-0.441	0.002	-0.103
permanent emigration = 0.1			
breeding probability = 0.6			
pre-volant survival = 0.8			
tag loss = 0.05			

Discussion

Passive monitoring of PIT-tagged wildlife populations can provide rich data on survival rates compared with traditional recapture-based methods (Ellison *et al.* 2007), due to high encounter rates and reduced effort and disturbance. Our study using PIT technology to study the critically endangered southern bent-winged bat has revealed that all sex and age classes have high winter survival, with lower survival in summer and autumn. This is contrary to our expectation that survival would be lowest in winter, based on historical research in Australian eastern bent-winged bats (Dwyer 1966a; Dwyer 1966b). Our study adds to an increasing body of literature showing no evidence of increased mortality risk in insectivorous bats during winter (Sendor and Simon 2003; López-Roig and Serra-Cobo 2014; Giavi *et al.* 2014; Fleischer *et al.* 2017), except during severe or exceptional winters (Fleischer *et al.* 2017; Reusch *et al.* 2019), or with additional factors, such as human disturbance (Thomas 1995) or white-nose syndrome (Reeder *et al.* 2012).

Factors affecting survival and population decline of insectivorous bats

Apparent survival rates in this study varied across years, with markedly lower survival in the summer and autumn of 2016. This period (January–May 2016) coincided with a severe 43-month rainfall deficiency (with rainfall totals at the lowest on record) in the south-east South Australian region, ending in mid-2016 (Bureau of Meteorology 2019). Our general finding of lower summer survival aligns with the results of other studies using passive PIT-tag monitoring to estimate survival in temperate insectivorous bats (O'Shea *et al.* 2010; O'Shea *et al.* 2011; Reusch *et al.*

2019), including the finding of lower survival in drought years in big brown bats (O'Shea *et al.* 2010; O'Shea *et al.* 2011). In contrast, a review of global survival studies in microbats has suggested higher survival rates in summer, particularly for adult females (Lentini *et al.* 2015); however, this finding may be confounded by sampling issues in early survival studies (O'Shea *et al.* 2004). In temperate regions, many bats have high survival associated with winter hibernation (Turbill *et al.* 2011; Wilkinson and Adams 2019), whereas summer survival is more likely to be affected by factors such as adequate availability of food resources to meet population demands. For example, high summer rainfall is associated with increased survival estimates in adult females of the little brown myotis *Myotis lucifugus* (Frick *et al.* 2010).

In this study on the southern bent-winged bat, summer and autumn are key times of mortality in the population. The probable impact of drought and human activity on prey and water availability may explain the apparent seasonal-survival patterns observed. The life-history of the southern bent-winged bat relies on much of the population congregating *en masse* over the breeding period (Dwyer and Hamilton-Smith 1965; Dwyer 1969; Baudinette *et al.* 1994), thereby placing concentrated demand for resources around maternity caves. The impact of dry conditions on resource availability may be exacerbated by diminished foraging availability due to habitat loss. Forested areas and wetlands are thought to be favoured foraging habitats of the southern bent-winged bat (DELWP 2020). In the geographic range of the southern bent-winged bat, over 90% of natural vegetation has been cleared (DELWP 2020). Most wetlands in the region (which previously regularly inundated approximately 40% of south-east South Australia) have been drained for agriculture (PIRSA 2017) and significant loss of wetlands has also been attributed to groundwater decline, as a result of both groundwater extraction and reduced rainfall (Harding *et al.* 2018). Additionally, whilst many Australian mammals are larger-bodied in southern distributions (Prowse *et al.* 2015; Correll *et al.* 2016), southern bent-winged bats are heavier than the more common eastern bent-winged bat, despite no significant difference in forearm length (Holz *et al.* 2020). This suggests that southern bent-winged bats may have higher energy demands and may be more susceptible to adverse conditions such as drought (Holz *et al.* 2020). A changing climate is bringing drier conditions to this region in south-eastern Australia, including droughts predicted

to become longer and more severe (Rashid and Beecham 2019). As a result, warm/dry season survival rates for this critically endangered bat may worsen in the future.

Adult survival is a major driver of population dynamics in long-lived species (Schorcht *et al.* 2009). Here, apparent survival in adults was lowest in lactating females during the summer, particularly during the drought period when reproductive females had 11.1% lower apparent seasonal survival (0.51, 95% CI (0.45, 0.58)) compared to non-reproductive females (0.57, 95% CI (0.48, 0.65)). This is one of the first studies to show increased survival costs in lactating females, compared to non-reproductive females – though Culina *et al.* (2019) recently reported reduced winter survival in breeding females of Daubenton’s bat but not Natterer’s bat. This included a 33% lower winter survival in successful first-time breeders compared to failed first-time breeders (Culina *et al.* 2019). Lactation places high energy and water demands on nursing females (Kunz 1974; Anthony and Kunz 1977; Kurta *et al.* 1989; Kunz *et al.* 1995; Mclean and Speakman 1999; Adams and Hayes 2008). Home-ranges and foraging distance are significantly decreased during lactation (Henry *et al.* 2002; Lučan and Radil 2010), there is increased dependence on water sources (Adams and Hayes 2008; Amorim *et al.* 2018), and bats probably rely on lactation coinciding with peaks in insect levels to meet the energetic and timing demands of nursing (O’Donnell 2002). As such, it is expected that resource limitation arising from drought disproportionately affects lactating females compared to other adult classes. Indeed, the large size of juvenile southern bent-winged bats (not yet weaned) upon emergence of the maternity cave shows an enormous energetic investment from adult females, presumably to increase survivability of their young. Additionally, lactation observations in this study suggest that juveniles continued to be nursed by their mothers for a number of weeks after juvenile emergence.

Apparent survival rates of juveniles were lowest in summer and autumn 2016, and juveniles generally had lower survival than adults (except for lactating females in summer) (Fig. 1). Whilst apparent survival often underestimates true survival, our summer survival rates do not include pre-volant juvenile survival (as bats were tagged after they began emerging from Bat Cave), so true summer survival of juveniles may be even lower than our results suggest. Bats commonly have lower first-year survival rates than adults (Hoyle *et al.* 2001; Sendor and Simon 2003; Pryde *et al.* 2005;

Schorcht *et al.* 2009; O'Shea *et al.* 2010; Lentini *et al.* 2015; Monadjem *et al.* 2015; Bailey *et al.* 2017; Culina *et al.* 2017). Juvenile mortality is likely related to inexperience. In summer, juveniles newly emerging from the cave with little flying experience appear to have higher chance of injurious collisions, as observed in newly-flying juvenile southern bent-winged bats (Ingeme *et al.* 2019; van Harten *et al.* 2020). Inexperience may also place juveniles at increased risk of predation due to being less able to evade predators. During the study, owls were observed hunting at the entrance of Bat Cave during emergence and, on one occasion, an owl was observed roosting inside the cave (E.vH, pers. obs.). Furthermore, if young lose their mother due to mortality, as indicated by lower apparent survival in lactating females, their chance of subsequent survival is presumably low.

After weaning, juvenile mortality may be influenced by a lack of foraging experience. There was a conspicuous loss of body mass in capture periods during and following the period of weaning (Table 3). Lower or declining body mass is commonly observed in juvenile bats following the onset of flight (Hughes *et al.* 1995; Hamilton and Barclay 1998) and experience of juvenile bats appears to influence foraging success (Wund 2005). Body mass is a strong predictor of fat stores in insectivorous bats (McGuire *et al.* 2018) and is associated with higher survival (O'Donnell 2002; O'Shea *et al.* 2010). For example, in big brown bats, female juveniles that did not return to monitored roosts as one-year-olds had lower body condition in late summer of their natal year than those known to survive (O'Shea *et al.* 2010). In this study, juveniles had markedly lower spring survival than adults, which could suggest that whilst winter is not a time of high mortality as initially thought, juveniles may enter spring with lower fat stores affecting subsequent spring survival. Juvenile survival estimates can be negatively biased by permanent migration from the natal site (Moussy *et al.* 2013; Lentini *et al.* 2015). However, migration between the two major maternity populations of the southern bent-winged bat is thought to be low, as suggested by historical banding records (Dwyer 1969), relative pesticide loads (Mispagel *et al.* 2004; Allinson *et al.* 2006) and viral diversity (Holz *et al.* 2018a).

The apparent survival estimates and derived rates of population growth in this study indicate further decline of the southern bent-winged bat population, particularly in dry years. The highest population growth rates are estimated if permanent juvenile

emigration is higher than previously assumed, although all estimates predict population decline under the apparent survival rates identified in 2016 (Table 4). Whilst the current population trend of this key population has been uncertain, there has been a severe historical decline at this maternity site since the 1960s (DELWP 2020). Additionally, at least two mass mortality events have been observed during droughts in 1967 and late 2006 (DELWP 2020). Widespread clearing of natural forest and woodland vegetation did not occur in this region until after World War II. Whilst most wetland drainage in the lower southeast of South Australia occurred prior to 1970s, in the upper southeast (where Bat Cave is located) widespread drainage mostly occurred later – undertaken privately in the 1980s and then through a government program in the 1990s (PIRSA 2017). Therefore, habitat loss approximately coincides with reported population declines (DELWP 2020) and should be the focus of further study. Additional pressure on foraging may include decreased prey availability due to the use of pesticides (DELWP 2020). Taken together, our results suggest that challenging conditions during the breeding season are affecting population viability of the southern bent-winged bat. Given the timing of mortality, and in the absence of further research, an emphasis of recovery strategies should be on boosting foraging habitat and prey availability in the vicinity of maternity caves.

The southern bent-winged bat is just one of more than a third of bat species listed as threatened or data-deficient globally (IUCN 2020). Many bats provide important ecosystem services such as agricultural pest control (Puig-Montserrat *et al.* 2015; Kolkert *et al.* 2019). Drought, and other climatic extremes, can negatively impact bat survival (O'Shea *et al.* 2010; O'Shea *et al.* 2011; Fleischer *et al.* 2017; Reusch *et al.* 2019) and recruitment (Law *et al.* 2020), and climate change will likely have a profound impact on population dynamics into the future (Sherwin *et al.* 2013; O'Shea *et al.* 2016). An increasingly drier and hotter climate has also been linked to increasing male bias in juvenile sex ratios of several bat species (Adams and Hayes 2018). In our study, the male bias of juveniles in 2017 differed significantly from the expected 1:1 sex ratio. Male-biased sex-allocation as a result of drought is a plausible explanation because conception occurs immediately after mating in late autumn (Crichton *et al.* 1989) and drought-breaking rainfall did not occur until the winter of 2016 (Bureau of Meteorology 2019). Without further sampling years, little can be implicated statistically between climate and sex ratios in southern bent-winged bats,

however, such questions are clearly of critical importance for predicting long-term population dynamics.

Use of PIT technology and CMR analyses for survival-rate estimation

Low physical recapture rates in bats provides challenges for the use of traditional mark-recapture approaches. Here, the use of passive monitoring at roosts provided an abundance of re-sight data, resulting in high encounter probabilities with reduced disturbance (van Harten *et al.* 2019). However, challenges also occur in using PIT-data for survival analyses. Continuous data violates the assumption of instantaneous sampling in CJS models and can bias resulting survival estimates, particularly if sampling periods are long (Olsen 2006). The Barker joint model has been demonstrated to outperform CJS models in estimating survival from continuous data when using monthly and ten-day sample bins (Barbour *et al.* 2013). Increasing sample size of n (number of individuals) in these comparisons did not overcome bias in CJS models, because increasing n resulted in overly narrow confidence intervals. A drawback is that the Barker joint model is prohibitively complex for use in many real-life applications (Barbour *et al.* 2013). Additionally, the Barker model requires primary capture periods dispersed between the continuous mark-resight data, and this may not always be possible or appropriate for reasons such as disturbance to vulnerable populations, or very low recapture rates for elusive species that are hard to capture, such as bats. During trapping we recaptured just 52 of our 2966 tagged individuals (van Harten *et al.* 2020).

Our approach to the problem of instantaneous sampling was to choose daily time intervals for binning detection data, to ensure the data was as close to instantaneous as possible (whilst still ecologically and practically reasonable). However, in three years of monitoring, we accumulated in excess of 17.8 million PIT-tag detections (van Harten *et al.* 2019). Fitting models for this quantity of data is time consuming, requires the use of high-performance computing (HPC) clusters and converging more complex models (for example with higher numbers of interacting variables) becomes increasingly difficult. An alternative approach by Reusch *et al.* (2019) used simpler mixed-effects logistic regression (with an individual-specific random intercept) to examine bat survival from continuous PIT-tag data, but limited justification or

explanation was provided on how this approach compares to traditional CMR models. We highlight a need for research and review into the development of robust methods for the analysis of increasingly large, continuous mark-resight datasets emerging from the use of new technologies. These solutions will need to balance the challenges that can arise from larger datasets, such as analysis time, computing power and false confidence, with usability in applied ecology for informing species management.

Another assumption of CJS models is that tags are not lost: therefore, tag loss can negatively bias estimates (McDonald *et al.* 2003). PIT-tag loss predominantly occurs soon after tagging due to tags working their way out of the insertion hole (Schooley *et al.* 1993; Kerth and König 1996; Fokidis *et al.* 2006) and can be minimised by the use of surgical adhesive on the injection site (Lebl and Ruf 2010), as in this study.

Double-tagging (with a second alternative marking method) can allow for estimating tag loss rates for interpreting subsequent survival results, but requires continued physical trapping to confirm tag loss. We decided that ongoing trapping to confirm tag loss rates posed too much disturbance risk for this critically endangered bat.

Although the ‘first6months’ variable (which fitted separate survival estimates for the first six months after an individual’s tagging and for its remaining resight history) did not provide the best fit for the data (Table 2), survival results from after six months of tagging showed similar seasonal results of lower summer and autumn survival. Thus, the seasonal survival pattern identified could not be explained solely by tag loss or other marking effects (Supplementary data, Fig. S2). Higher apparent summer and autumn survival in adult females for which reproductive condition was unknown (Fig. 1) may be in part due to tag loss, which is likely negligible in subsequent years (when reproduction condition is unknown) compared to the first year of tagging (when reproductive condition was assessed). Results in other studies suggest that PIT-tagging is a safe marking method for bats, with no evidence of effects on body condition, reproductive success, infection or other detrimental effects (Rigby *et al.* 2012; Locatelli *et al.* 2019; van Harten *et al.* 2020). It is unlikely that apparent survival differences are due to PIT-tagging affecting survivability, but we cannot preclude this possibility. Ongoing research and transparent documentation of tag loss rates and marking effects in a range of species is critical to inform data interpretation and to ensure the marking procedures continue to be informed by the best available knowledge to minimise disturbance to wildlife.

Conclusion

A passive CMR approach using PIT technology has provided rich data on apparent survival rates, including sex, age and reproductive classes across all seasons in consecutive years. This is one of the first studies of insectivorous bats to demonstrate that lactating females experience lower survival rates than non-reproductive females. We highlight lower overall survival rates during the warmer and drier summer and autumn seasons for all population cohorts and predict continued decline in this critically endangered population. Ongoing research to inform recovery of the southern bent-winged bat and other threatened or data deficient species is critical, and PIT technology evidently provides a valuable tool for passively obtaining rich data sets for this purpose (Ellison *et al.* 2007; van Harten *et al.* 2019). We contend that conservation actions for the southern bent-winged bat are a high priority, particularly greater provision of foraging resources in the vicinity of maternity caves. Recent animal extinctions have demonstrated that we need to act fast to avoid extinction and implement recovery actions while there is an opportunity to act (Martin *et al.* 2012; Woinarski *et al.* 2017).

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Supplementary material

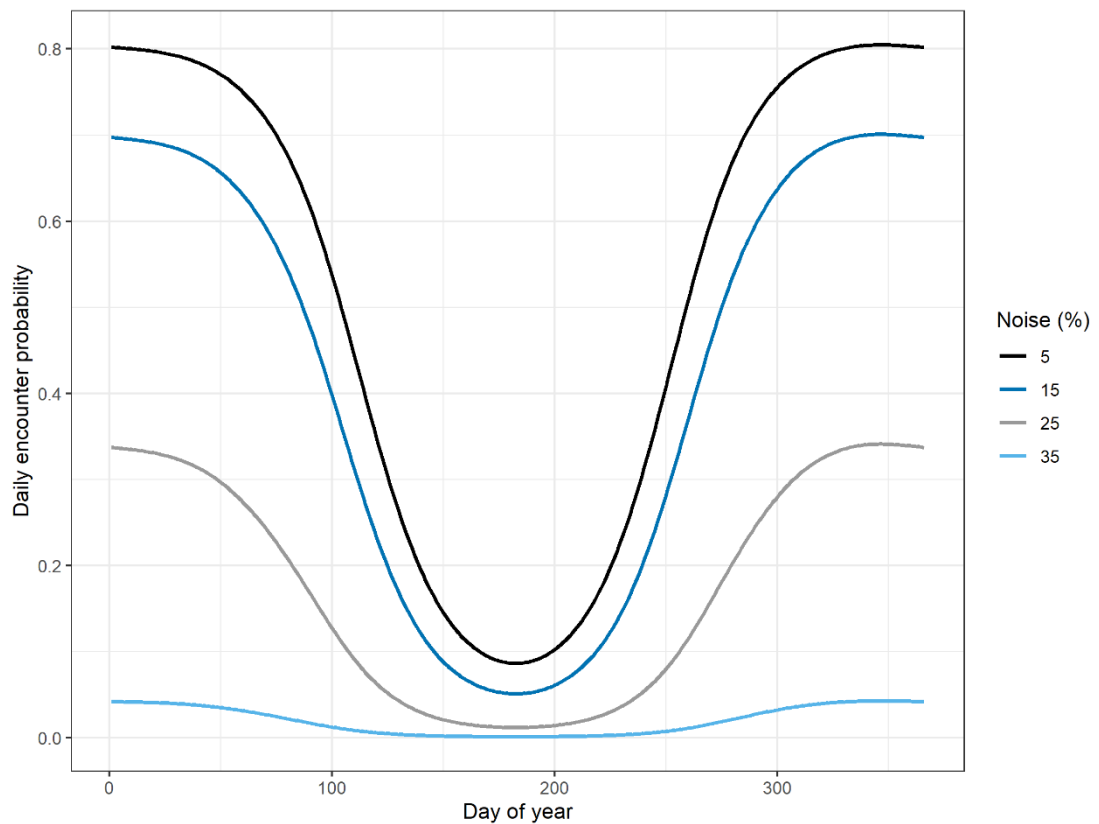


Figure S1. Daily encounter probability of southern bent-winged bats, showing the modelled effects of day of year (*yday*) when *noise* = 5%, 15%, 25% and 35%. Encounter probability was included in the survival models in this study to account for variation in seasonal behaviour of the bats and environmental ‘noise’ perceived by the antenna system. Daily average noise levels typically ranged between 5–15% (van Harten *et al.* 2019).

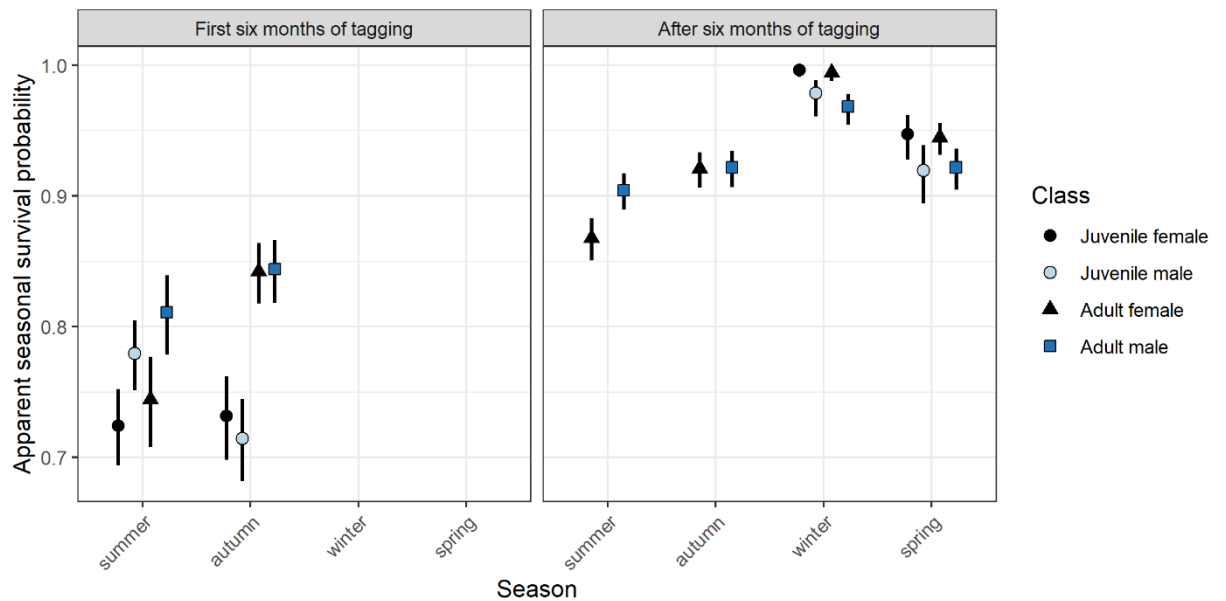


Figure S2. Apparent seasonal survival estimates for the first six months of PIT-tagging and subsequent survival of southern bent-winged bats. Although models using the ‘first-six-months’ variable did not provide best fit compared to the final model (Table 2), the results from after six months of tagging (when any tag loss is presumed to have negligible effect on survival estimates), show that subsequent survival is still lowest in summer and autumn and therefore this seasonal pattern could not be explained solely by tag loss or potential marking effects. It is important to note that estimates for the first six months of tagging include the summer and autumn of 2016, which was evidently a challenging season with higher mortality rates coinciding with drought (Bureau of Meteorology 2019). Therefore, the apparent survival rates in the first six months should not be taken as an indicator of marking effects on the population.

Chapter 6. Seasonal population dynamics and movement patterns of a critically endangered, cave-dwelling bat

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Seasonal population dynamics and movement patterns of a critically endangered, cave-dwelling bat

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Abstract

Context. Seasonal migration and movements of bats are poorly known, yet likely to have important implications for conservation and management. The southern bent-winged bat *Miniopterus orianae bassanii*, a critically endangered, cave-dwelling taxon in Australia, has been described as undertaking regional-scale migration between maternity and non-breeding caves.

Aims. To describe the seasonal cycle of movements by the southern bent-winged bat, including migration and congregation events of different sex and age classes in the population.

Methods. A total of 2966 southern bent-winged bats were tagged with passive integrated transponder (PIT) tags. Antennas were used to detect bats in flight at a major maternity cave and a key non-breeding cave in south-east South Australia, from

January 2016 to August 2019. Capture-resight histories were used to visualise population patterns and model daily encounter probability for each sex and age-class at the respective roost sites.

Key results. Bats congregated at the maternity cave for most of the year, with different seasonal patterns among sex and age classes. Seasonal movements were associated with behaviour over winter months: most of the population dispersed from the maternity cave from May and a staged return occurred among population classes from July through September. A previously undescribed movement event also occurred in adult females and juveniles each year: these classes departed from the maternity cave in late summer as juveniles became independent and returned in early to mid-autumn. Complex underlying movements of individuals occurred throughout the year, with individuals able to fly 72 km between the two study sites in just a few hours.

Conclusions. Seasonal movements are a key aspect of the life-history of this taxon. In addition to seasonal movements, some individuals moved 72 km between caves on successive nights. The newly reported movement by adult females and juveniles conforms to the maternal guidance hypothesis, whereby mothers guide young to suitable non-breeding caves and hibernation sites.

Implications. The dynamic nature of the population has implications for the management of emerging risks, including potential mortality at windfarms and the risk of white-nose syndrome. The recorded 72 km flight distance more than doubles the previous known flight distance used to inform management buffer zones. Extended congregation of large numbers of bats at maternity caves highlights resource limitation around maternity caves as a potential threat to these populations.

Introduction

Migration biology provides a ‘grand challenge’ in organismal biology with many aspects of the phenomena poorly understood (Bowlin *et al.* 2010). In addition to being challenging to study, migrating animals also provide challenges for conservation, including that they often have complex habitat requirements and a tendency to congregate in restricted areas (Fleming and Eby 2003). Migration can be defined as the seasonal movement of populations from one location to another; typically as a

two-way movement involving a return to the starting location, to seek conditions that are climatically or energetically more favourable (Fleming and Eby 2003).

Migration in bats has evolved independently in several lineages (Bisson *et al.* 2009). It may occur at regional through to long-distance scales; for example, from 50 km to over 1000 km (Fleming and Eby 2003). Bats are known to use the polarity of the earth's magnetic field for orientation and navigation (Holland *et al.* 2006; Wang *et al.* 2007). In temperate climates, migration is thought to be driven by the reproductive cycle and seasonal factors such as roost temperatures; whereas for tropical species, resource availability has a greater influence on migratory and movement behaviour (Fleming and Eby 2003). Females are more likely to migrate, and migrate over longer distances, than males: these patterns are associated with movement to (and from) summer maternity roosts with suitable conditions for raising young, and likely with energetic demands of reproduction and lactation (Fleming and Eby 2003).

Most studies of bat migration have been undertaken in Europe and North America, with relatively little known of the migratory status of bats in Africa and Asia (Popa-Lisseanu and Voigt 2009). In Australia, flying foxes (Pteropodidae) show extreme mobility, including individual movements ranging between 2268–6073 km (Welbergen *et al.* 2020). However, migration behaviour in small insectivorous bats in Australia is known only for a few species. For example, the white-striped free-tailed bat *Austronomus australis* undertakes seasonal migration, being found up to 1200 km further north from April to September (Bullen and McKenzie 2005; Churchill 2008). For the eastern bent-winged bat *Miniopterus orianae oceanensis*, banding efforts in the 1960s revealed regional seasonal migration with adult females migrating up to hundreds of kilometres to maternity caves (Dwyer 1966).

Outside of migration, small insectivorous bats typically show relatively short movement distances between roosts, and to and from foraging areas (Kunz and Lumsden 2003). For example, tracking individuals of the large-eared pied bat *Chalinobus dwyeri* showed commutes of less than 700 m from cliff roosts to foraging areas (Williams and Thomson 2019) and lactating eastern cave bats *Vespadelus troughtoni* regularly undertake inter-cave movements of less than 1.5 km (Law *et al.* 2005). Roost-switching is thought to be important to meet microclimatic requirements (Patriquin *et al.* 2016) and to maintain long-term social relationships in the

population, consistent with fission-fusion social dynamics (Willis and Brigham 2004; Godinho *et al.* 2015).

Study of migration and movement in small insectivorous bats has traditionally involved the long-term deployment of forearm bands (Hutterer 2005), but the recapture rate is low. Studies using stable isotopes and comparing genetic structure have helped to determine area of origin and migration direction (Petit and Mayer 2000; Voigt *et al.* 2012). Short-term deployment of transmitters and loggers allows for the recording of detailed information on movement patterns, but a limitation is that transmitters remain attached for an average of just nine days (O'Mara *et al.* 2014), and devices need to be less than 5% of body mass (Aldridge and Brigham 1988) when most insectivorous bat species weigh less than 30 g (Moyers Arévalo *et al.* 2020). Nevertheless, such techniques have revealed astounding data in insectivorous bats, though not without methodological and ethical challenges. For example, Weller *et al.* (2016) recorded a >1000 km round trip by a male hoary bat *Lasiurus cinereus*: the method involved using sutures to attach the loggers and therefore requires physical recapture of individuals which is often not possible or assured.

The use of passive integrated transponder (PIT) tags allows for the passive detection of individuals for their lifetime (Gibbons and Andrews 2004). By using antennas at roost sites or other regularly used locations, information can be gleaned about movement, activity and survival patterns of PIT-tagged individuals over time. PIT-tagging has been used as a wildlife marking tool since the 1980s (Gibbons and Andrews 2004) and is commonly used to study fish migration (Harding *et al.* 2019; Murauskas *et al.* 2019; Kanno *et al.* 2020). To date, this technology has not been used to investigate seasonal migration patterns in insectivorous bats.

In this study, we use PIT-tag technology and monitoring to examine seasonal population patterns, migration and movement of the southern bent-winged bat *Miniopterus orianae bassanii*, a critically endangered taxon in south-eastern Australia. Regional migration patterns of adult females in *M. orianae* have been attributed to the microclimatic conditions of caves, with those selected as maternity caves providing stable, high humidity and temperatures necessary for the young (Dwyer 1963; Dwyer and Hamilton-Smith 1965; Baudinette *et al.* 1994). Non-roosting caves have more variable, cooler temperatures and may facilitate the use of

torpor in cooler months (Hall 1982). Regional inter-cave movements are largely centred on maternity caves, with a number of non-breeding caves typically being associated with a single maternity population (Dwyer 1969).

A similar pattern of seasonal migration is thought to occur in the subspecies studied here, the southern bent-winged bat *M. o. bassanii* (Churchill 2008; DELWP 2020); although unlike the eastern bent-winged bat subspecies, significant numbers of adult males are also recorded congregating at southern bent-winged bat maternity caves (Dwyer and Hamilton-Smith 1965). The southern bent-winged bat has undergone serious population decline since the 1960s (DELWP 2020). Survival rates show lowered seasonal survival during summer and autumn in juveniles and for lactating females, with lowest survival rates coinciding with drought (Chapter 5). Population modelling predicts a continued population decline (Chapter 5), the cause of which remains uncertain, though resource limitation due to loss of foraging habitat and drought is suspected as a key threat (Chapter 5, Allinson *et al.* 2006; Bourne and Hamilton-Smith 2007; DELWP 2020). Health surveys have not revealed any pathogenic factors that could explain the severe population decline (Holz *et al.* 2018a; Holz *et al.* 2018b; Holz *et al.* 2018c; Holz *et al.* 2019a).

The southern bent-winged bat also faces two emerging threats, both of which will be influenced by migration and movement patterns. The first is windfarm development (DELWP 2020), with numerous windfarms proposed in the restricted range of the subspecies. Globally, mortality of bats from windfarms is the leading cause of multiple mortality events in bats (O'Shea *et al.* 2016) and migrating bats appear most at risk (Cryan and Barclay 2009). In Australia, there is a high degree of uncertainty around bat mortality estimates associated with windfarms (Moloney *et al.* 2019). Although deceased bats are recovered at windfarms (Hull and Cawthen 2013; Moloney *et al.* 2019), population level impacts are unknown.

The second emerging threat is the potential introduction of the pathogen causing white-nose syndrome (Holz *et al.* 2019b), which has decimated bat populations in North America (Frick *et al.* 2015). It is 'very likely/almost certain' that white-nose syndrome will be inadvertently introduced to Australia and 'likely' that it will come into contact with bats in the coming decade (Holz *et al.* 2019b). Eight species of Australian bats are considered most at risk, seven of which are already listed as

threatened species, including the southern bent-winged bat (Turbill and Welbergen 2020). Population patterns in migration and movement are important factors relating to these emerging threats, as times of inter-cave movement across the landscape may increase collision risk with wind turbines and facilitate disease spread. Information about the full seasonal activity cycle of the southern bent-winged bat is critical to inform species recovery (DELWP 2020), inform sustainable windfarm development, and strengthen potential responses to the threat of white-nosed syndrome in Australia (Holz *et al.* 2019b; Turbill and Welbergen 2020).

To address these knowledge gaps, we installed PIT antennas at a major maternity cave and a key non-breeding cave of the southern bent-winged bat in South Australia and continuously monitored activity of the PIT-tagged bat population over 3.5 years (van Harten *et al.* 2019). We expected to observe two annual migration events, to and from the maternity cave in spring and autumn, respectively, with ‘virtually all’ bats present at the maternity cave for the summer breeding season (Dwyer and Hamilton-Smith 1965). We also predicted little activity in winter, when individuals disperse to non-breeding caves for winter and undertake periods of torpor (Hall 1982).

Methods

PIT-tagging

Southern bent-winged bats were trapped and PIT-tagged at Bat Cave within the Naracoorte Caves National Park, South Australia, which serves as a major maternity and summer congregation site. Trapping occurred over six nights in 2016, and four nights in each of 2017 and 2018, at the end of the breeding season (January and February), timed to coincide with juveniles commencing flying and becoming independent. To reduce disturbance, only two consecutive trapping nights were undertaken at a time. Bats were trapped with Austbat harp traps (Faunatech, Mount Taylor) surrounding the cave entrance. Trapping continued from dusk until the early hours of the morning, catching bats as they left or re-entered the cave.

Sex and age were recorded for each of 2966 PIT-tagged bats. Age was described as juvenile (first year) or adult based on the presence or absence of a cartilaginous core at the metacarpal-phalangeal joints (Brunet-Rossinni and Wilkinson 2009). The PIT-

tag was subcutaneously injected dorsally using a sterilised 12-gauge needle and applicator (Biomark MK10 implanter and N125 needles in 2016, Biomark MK 25 Implant Guns and HPT12 Pre-load Trays in 2017–18). The injection site was sealed with a drop of surgical adhesive (3M™ VetBond™) to minimise tag loss (Lebl and Ruf 2010), and allowed to dry prior to release. All PIT-tags (Biomark HPT 12) were checked for correct function using a hand-held PIT-tag scanner (Trovan LID560 and Biomark 601), both before and after insertion. During handling and tagging, bats typically remained calm and were able to fly within minutes of the procedure. Recaptured individuals were in good physical condition, with no sign of infection or other detrimental effects (van Harten *et al.* 2020).

Monitoring of PIT-tagged individuals and data collection

PIT-tagged bats were monitored using large PIT-tracking systems (Biomark IS1001) installed at two study sites. The first system was installed within a cave passage at the Bat Cave maternity site from January 2016. The second system was installed at the entrance to a key non-breeding cave located near Glencoe, 72 km from Bat Cave. This second system was trialled short-term (e.g. a couple of nights at a time) in February 2017, with long-term monitoring subsequently occurring from April 2017 (though with intermittent power outages until June 2017, Fig. S2). The antenna systems detected any tagged individuals as they flew through the 15 m antenna loop (van Harten *et al.* 2019). When the systems were working optimally, there was a large read-range before and after the antennas and high detection success (van Harten *et al.* 2019). The system recorded data directly to USB flash drives plugged into the data logger board of the Biomark IS1001.

Data recorded included individual PIT-tag detections (date, time and PIT-tag number) and noise reports. Noise is a measure of total interference, or unwanted signal, being received by the detection system, and is known to affect detection success (van Harten *et al.* 2019). Data were collected from the caves regularly (approximately monthly) by manually retrieving the flash drives until 16 August 2019.

Analysis of population patterns using probability of encounter

To prepare the data for analysis, we first created capture-resight histories for each of the 2966 PIT-tagged bats, to produce a binary response variable (undetected/detected)

for each individual across each day of the respective study periods for each study site, with ‘day’ being defined as the 24 hours between successive middays. Plots of the capture-resight histories (detected/undetected) for each tagged individual were generated to visualise patterns at the study sites, as well as when individuals were detected at both caves in a single night.

Age functions were added such that juveniles were coded as adult on 31 December in the year of their tagging, when they were approximately 13 months old. Separate, known to be alive (KTBA) matrices, were calculated for each age by sex category (adult females, adult males, juvenile females, juvenile males). Noise readings for each antenna were averaged across each study day and were also included in the final matrices for each study site.

We used a binomial generalised additive model, implemented with the R package ‘mgcv’, to model the per-individual, daily probability of encounter as a function of *noise* + *yday* (by different individual sex and age-class parameters; see Table 2), fitted with a cyclic cubic regression spline. *Noise* is daily average noise (%) and *yday* is day of year. The spline was included to ensure continuity in the modelled response of the last and first day of year in the model. The upper limit on the degrees of freedom of the splines is given by $(k - 1)$: we assumed that $k = 3$ for the spline for *noise* which allowed for some non-linearity in detection probability as a function of environmental noise; and $k = 20$ for the spline for *yday*, which permitted a flexible response due to the day of year.

The final model for each study site were selected by comparing values of the Akaike information criterion (AIC) for alternate models incorporating different demographic variables for individuals: a) sex, b) age, c) combination of sex and age classes, and d) no demographic variable. The AIC includes a penalty for increasing complexity (i.e. number of parameters) in the model. The ‘best’ or top-ranked model is the one with the lowest AIC value (provided that the difference between the compared models is ≥ 2). The Akaike weight for each alternate model is a measure of the likelihood of that model being the best fit to the data among the set of models considered. Deviance was also compared as a measure of model fit. The chosen models for each study site were also modelled separately as yearly subsets to compare variation in patterns between years.

Observational data

Infra-red cameras were installed within the Bat Cave maternity cave in 1995, forming part of the tourist attractions for Naracoorte Caves National Park (Reed and Bourne 2013). Live footage of the bats, in multiple chambers of the cave, can be viewed from the Bat Observation Centre during visitor tours. We made use of these pre-existing cameras and tour schedule, by asking the parks staff to report any notable behaviour of the bats, such as birthing of the young. Observations were also made during visits to the study sites to collect PIT-tag data. The southern bent-winged bat is the only bat known to roost in these caves, so there was no concern about confounding these observations with other species. Observational data from the cameras and trapping effort were used to supplement the PIT-tag data by assisting with identifying the phenology of the reproductive cycle in relation to the presence/absence data provided by monitoring of the PIT-tagged population.

Results

Phenology of breeding cycle observations

Birthing at Bat Cave was observed in mid to late November (Table 1, Fig. 1a), with the first births occurring 8–10 days before mass birthing among the pregnant females in the 2015/16 and 2016/17 breeding seasons. The timing of mass birthing could not be determined in 2017/18 due to the creche being positioned out of view of the cameras. Juveniles become volant and begin emerging from the maternity cave in January, with many juveniles typically being captured for the study at the maternity cave exit from mid-January.

Table 1. Observations of births of southern bent-winged bats and juvenile development over three summer breeding seasons at Bat Cave.

Observation	2015/16	2016/17	2017/18
First pups observed in the maternity chamber	16 Nov	12 Nov	21 Nov
Mass birthing in the maternity chamber	26 Nov	20 Nov	NA
First juveniles exiting the maternity cave	9 Jan	NA	12 Jan
Large numbers of juveniles exiting the cave	15 Jan	14 Jan	19 Jan

Mating and coupling behaviour were observed on the cameras in Bat Cave on 6 May 2018 (Fig. 1b), with bats roosting as dispersed couples on the walls and ceiling of a smaller chamber extending from the main maternity chamber. In contrast, in the main maternity chamber, bats roosted in clusters or individually, as also observed at other times of the year.

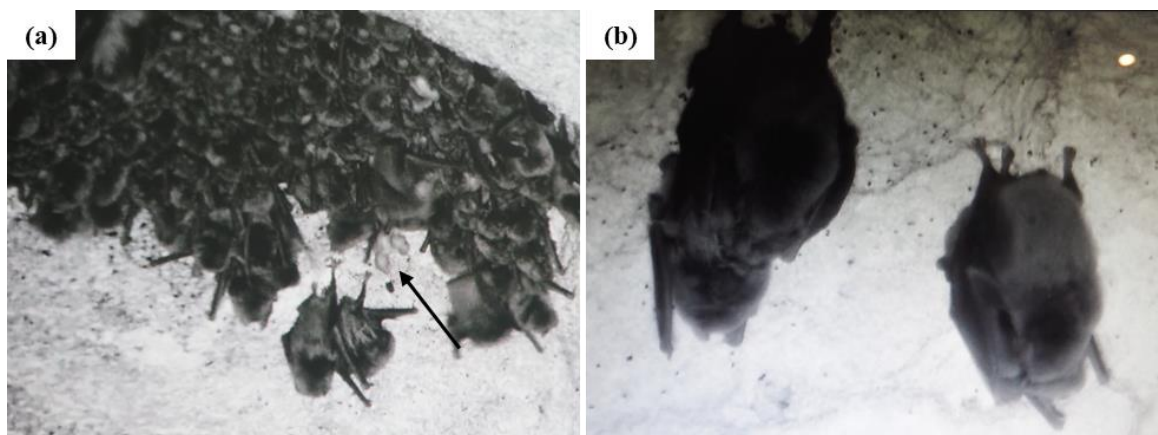


Figure 1. (a) A cluster of adult females beginning birthing in the maternity chamber at Bat Cave on 19 November 2016; mass birthing in the population occurred over the following day. On the centre-right of the frame (arrowed), two pups can be observed; one with umbilical cord and placenta still attached. (b) Mating and coupling behaviour observed in a smaller chamber extending off the main maternity chamber in Bat Cave, on the 6 May 2018. Both observations were observed remotely via infra-red video footage. Photos: Emmi van Harten.

Encounter probability

The top-ranked model for daily encounter probability of bats, as assessed by AIC values, for both study sites was the one that included the interaction of an individual's sex and age (Table 2). That is, the model that fitted separate estimates for adult females, adult males, juvenile females and juvenile males had the lowest AIC value, much lower than alternative models that included only age class or only sex. For each site, the AIC weights clearly indicated that this model was the best fit to the data among the models tested. Total deviance explained for the top-ranked models were 81.9% for Bat Cave and 52% for Glencoe. For Bat Cave, the demographic covariate (i.e. age and sex classes) accounted for 36.7% of the deviance, while for Glencoe this was 17.2%.

Table 2. Selection table comparing alternative encounter probability models with different individual covariates included for the effects of *yday*. Shown are the deviance, AIC value, Δ AIC (difference from the 'best' or top-ranked model) and Akaike weight for each model.

Model	Deviance	AIC	Δ AIC	Akaike weight
<i>Bat Cave</i>				
sex : age	124046	145705	0	1
age	158396	179982	34277	0
sex	171399	192986	47281	0
no individual covariates	196120	217671	71966	0
<i>Glencoe</i>				
sex : age	39861	51873	0	1
age	44678	56619	4746	0
sex	44699	56640	4767	0
no individual covariates	48141	60047	8174	0

Daily encounter probability (i.e. the probability that an individual known to be alive is present and detected) at Bat Cave was high in all sex and age classes from November to February (Fig. 2a). From February, encounter probability decreased in the population at Bat Cave, with the lowest encounter probability occurring in juveniles (of both sexes) and adult females in March, coinciding with a peak in encounter probability in juveniles and adult females at Glencoe (Fig. 2b). Modelled encounter probability for these three sex and age classes was similar at both study sites during this period. Activity in these classes increased again at Bat Cave around April (and decreased at Glencoe).

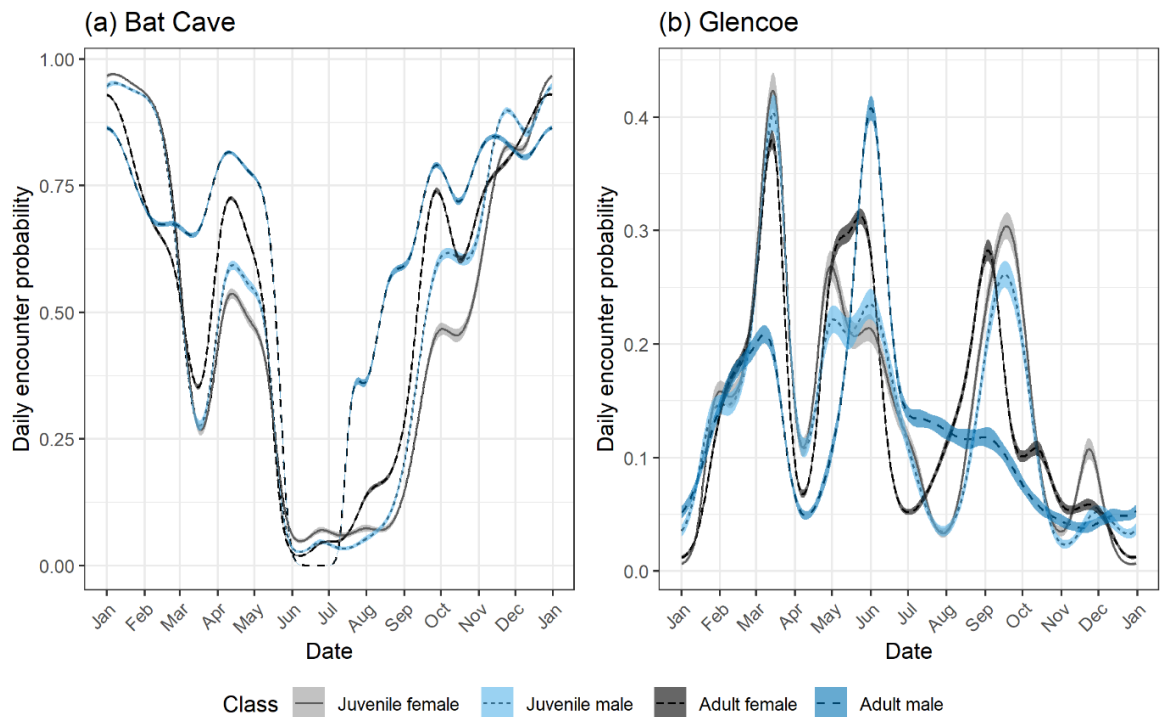


Figure 2. Daily encounter probability for southern bent-winged bats at the maternity cave, Bat Cave **(a)** and non-breeding cave at Glencoe **(b)**, South Australia (modelled effects of *yday*, where *noise* = 5%). The models are based on detections of 2966 bats PIT-tagged at Bat Cave, 1449 of which were subsequently detected at Glencoe. Ribbon width for each class represent 95% confidence intervals. Note that **(a)** and **(b)** have a different y-axis scale.

Over winter, from May, daily encounter probability at Bat Cave fell steeply to ~0–0.05 at the beginning of June (Fig. 2a). Compared to the other sex and age classes, encounter probability in adult males at Bat Cave decreased later and increased earlier, meaning that there was only approximately one month (~June) where few bats were detected at Bat Cave. Following the influx of bats at Glencoe in May–June associated with dispersal from the maternity cave, winter was also associated with a drop in encounter probability at this non-breeding cave; this could be due to lowered winter activity or use of other non-breeding caves. Nevertheless, regularly activity was still detected at Glencoe and it was not uncommon to detect hundreds of bats per day at this study site in June and July. Adult males maintained higher encounter probability at Glencoe over winter (e.g. encounter probabilities > 0.1) than other sex and age classes, until beginning their earlier return to Bat Cave (~July). Adult females became more active at Glencoe around the beginning of August, with the daily encounter probability for spring peaking at this site at the beginning of September. Daily encounter probability in juvenile classes began increasing approximately one month after adult females but rose faster, peaking at Glencoe in mid-September.

There was a staged increase in activity at Bat Cave between the sex and age classes in late winter and early spring, with some variation in timing evident between years (Fig. 3). Encounter probability in adult females increased later than adult males, followed by the juvenile cohorts. For example, encounter probability in adult males was 0.25 at the beginning of August in each of the first three years, whereas adult females reached the same encounter probability in mid-August to the beginning of September in the same years. Both adult classes returned to Bat Cave considerably earlier in the final year (2019), reaching 0.25 in mid-July and beginning of August for males and females, respectively. Caution must be taken when interpreting results in late spring due to a series of system issues and power outages (occurring around October 2016, November 2017 and November 2018, Supplementary data, Fig. S1) which likely influenced the drop in encounter probability during these periods – as such, population patterns at this time of the year remain less clear. However, encounter probability at Glencoe also varied considerably between the two years of spring monitoring at this location (Fig. 3b, 2017 and 2018) and is not associated with any known system issues or outages at this time of year (Supplementary data, Fig. S2).

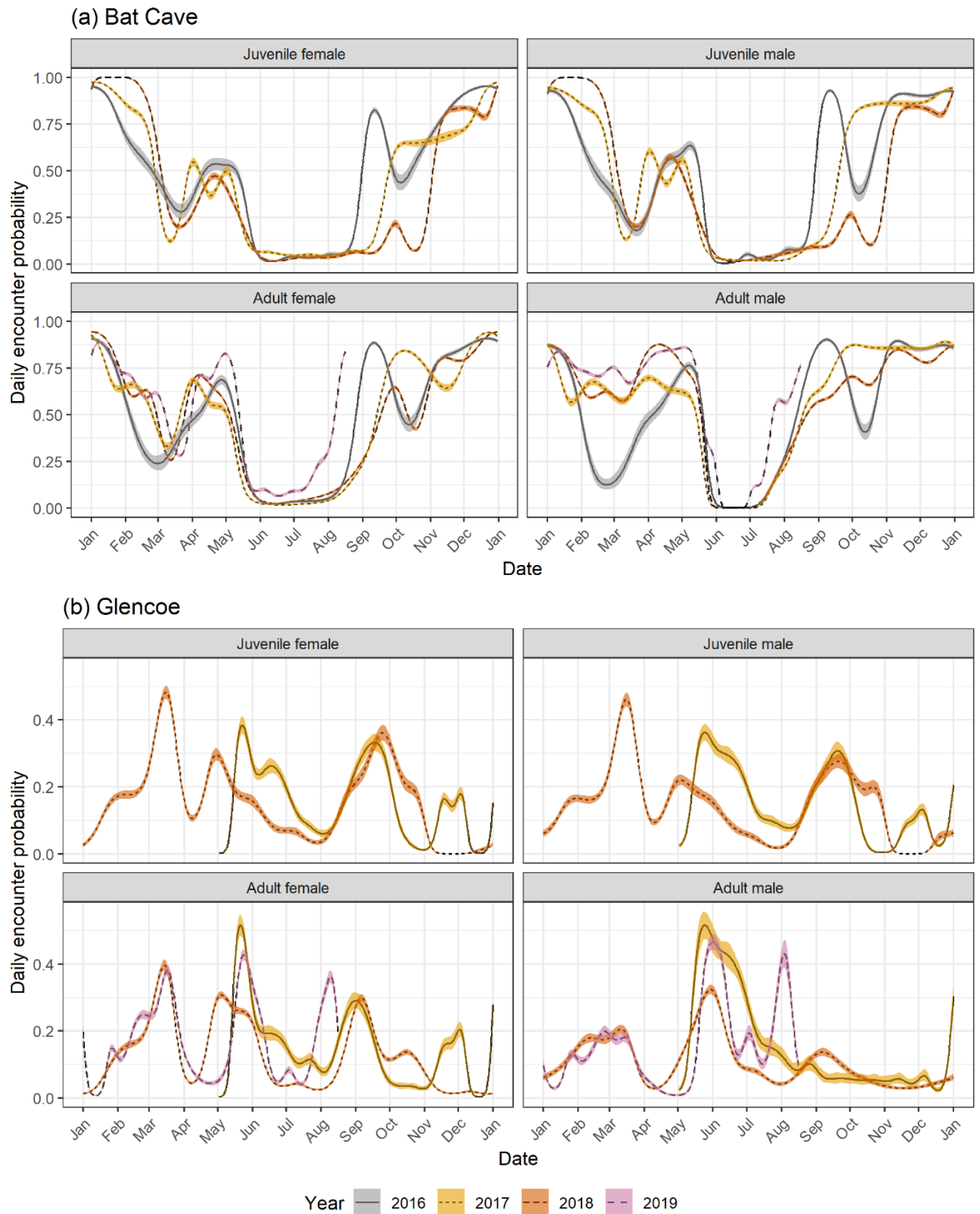


Figure 3. Variation in daily encounter probability for southern bent-winged bats over the study years at the maternity cave Bat Cave (a) and non-breeding cave at Glencoe (b), South Australia (modelled effects of *yday*, where *noise* = 5%). Models are based on data collected at Bat Cave from January 2016 to August 2019 and Glencoe from May 2017 to August 2019. Ribbons width for each class represent 95%

confidence intervals. Note, as no bats were tagged in 2019 only adult (≥ 1 year old) classes are known for that year.

Despite some variation in timing, the general seasonal patterns among the sex and age classes were maintained across years. A notable exception was in early 2016, when adult males showed a fall in encounter probability in February and March at Bat Cave that is not shown in the following three years. It is possible that this was caused by detection issues at Bat Cave during this period, which were resolved in May 2016 (van Harten *et al.* 2019). This period also corresponded with severe drought conditions and may therefore suggest some plasticity in behaviour in adult males in relation to resource availability (a flexibility that is unlikely to be possible for breeding adult females until juveniles are independent). Unfortunately, as the system at Glencoe was not established until 2017, we are unable to determine if adult males were present at this non-breeding cave during this time.

Visualising individual detection histories across the tagged population demonstrated that the observed changes in encounter probability were associated with individuals moving between the two caves, with clear seasonal movement patterns evident (Fig. 4). This includes the aforementioned synchronous patterns of encounter probability for juveniles and adult females in early autumn.

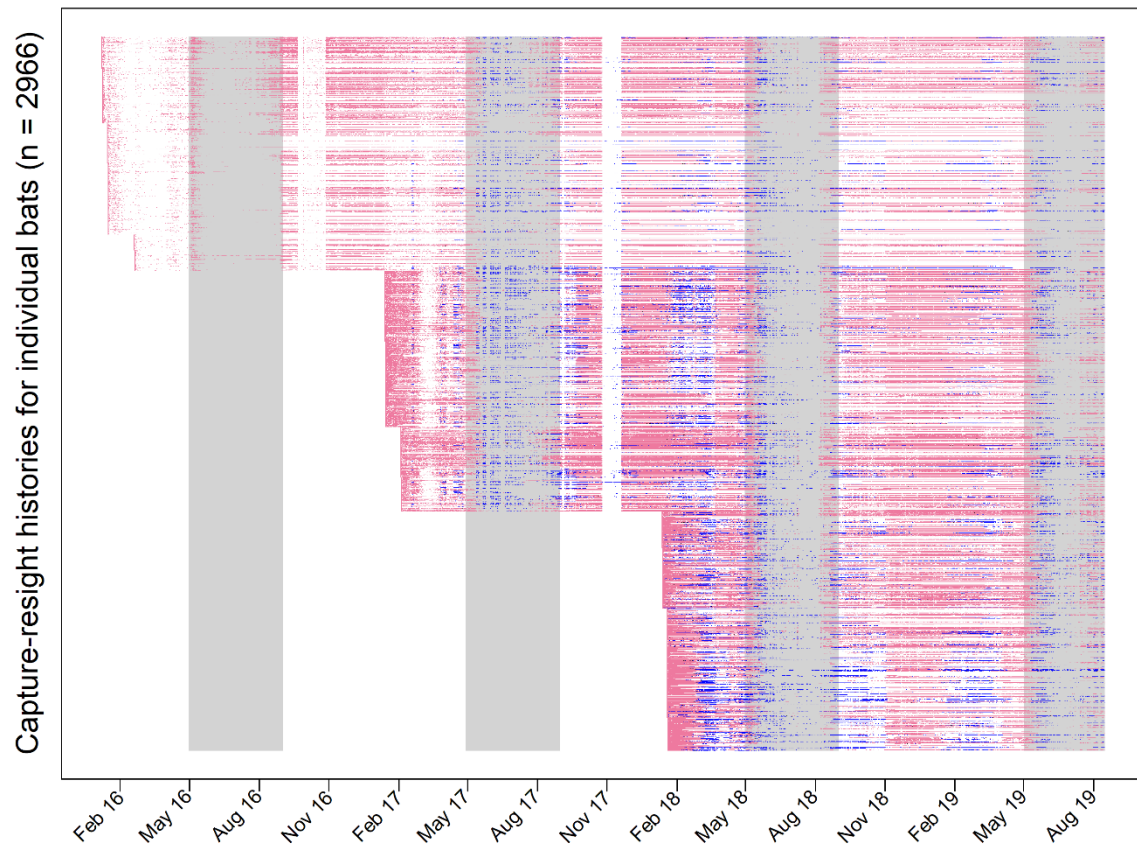


Figure 4. Capture-resight histories of all PIT-tagged individuals at Bat Cave (red) and Glencoe (blue) over the 3.5-year study period. Each of the 2966 tagged bats is represented as an individual row on the y-axis, with initial capture and subsequent daily detections indicating presence at the respective caves marked in red and blue. The data occur in blocks because individuals were tagged over three years and seven trapping events. The Glencoe PIT-antenna system was installed from April 2017. Some absences (white) are due to system issues such as power outages or high ‘noise’ (signal interference) – these occurrences are outlined in the Supplementary material, Figs. S1 and S2. Grey shading indicates the winter months of May to August, when little activity was expected (due to use of torpor and dispersal to numerous non-breeding caves).

Direct movements between the study sites

In addition to the seasonal population movements, direct movements between the two monitored caves were detected throughout the year and in all seasons, indicating the underlying dynamic nature of the cave populations, even during peak occupancy periods at the respective caves (Fig. 5). Individuals were able to fly the 72 km between the two sites in a single night. The nightly occurrence of such ‘direct flights’ detected peaked during the early autumn, autumn-winter and winter-spring population movements (Fig. 5).

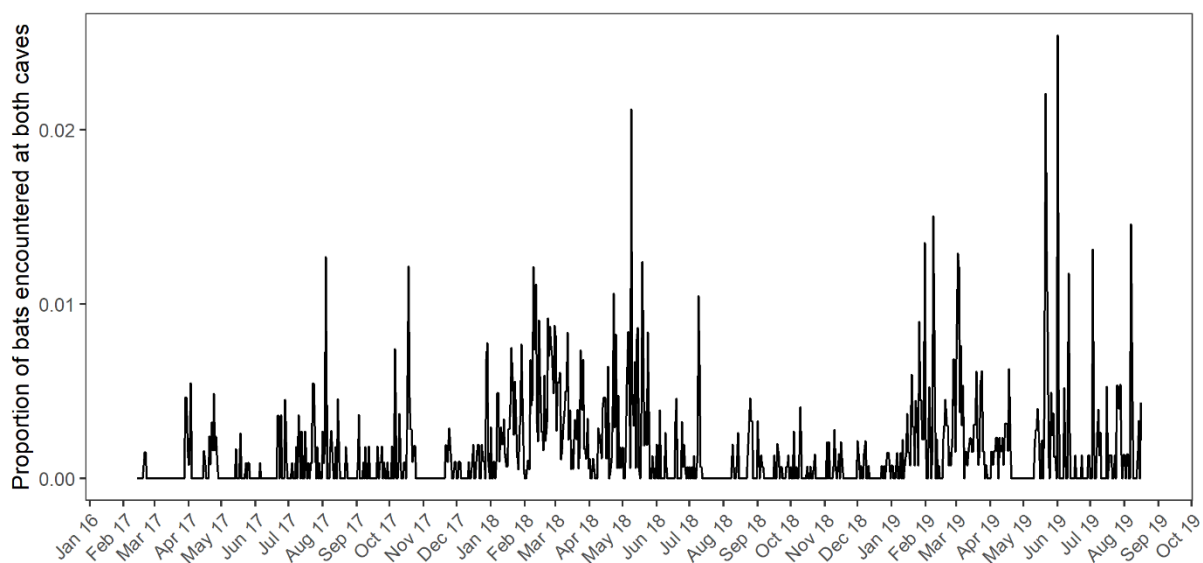


Figure 5. The nightly proportion of PIT-tagged southern bent-winged bats detected at both study sites on the same night (of the total population known to be alive each night). The study sites, Bat Cave and Glencoe, South Australia, are located 72 km apart.

Detailed analysis of individual movements is beyond the scope of this chapter: however, data exploration showed that individuals demonstrated complexity in movement patterns and that seasonal inter-cave movements were not necessarily ‘one-way’ regional migrations (Fig. 6). For example, an adult female in early August (late winter) 2017 flew the 72 km from Glencoe to Bat Cave in 3.2 hours, returning to Glencoe the following night in 3.5 hours. This female was then not detected for two nights, then subsequently flew again from Glencoe to Bat Cave, this time in 5.5 hours, and returned to Glencoe on the following night in 4.2 hours.

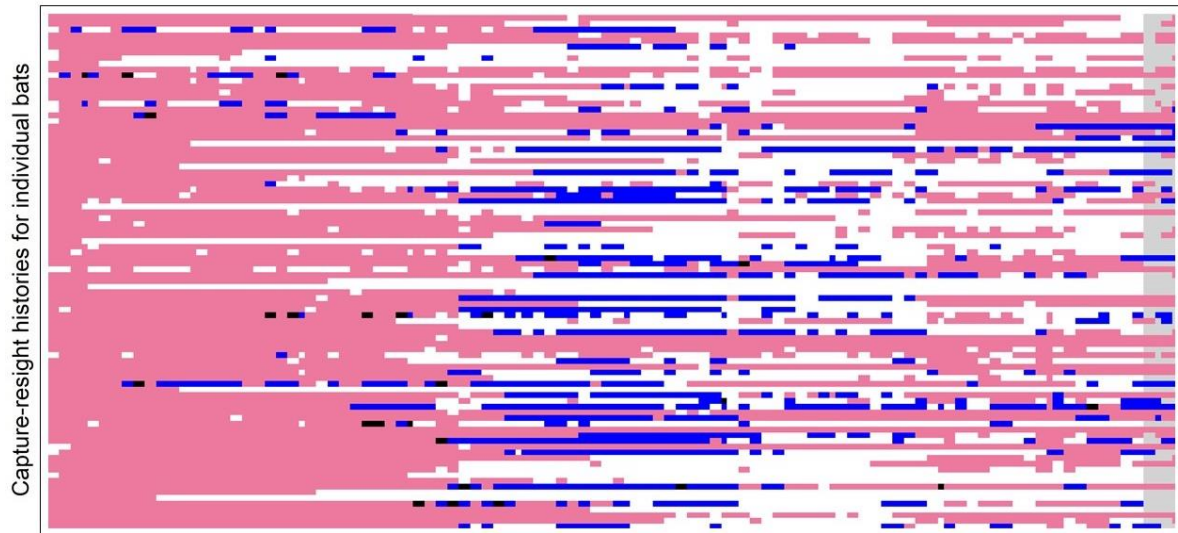


Figure 6. An example of detail taken from Fig. 4. Rows represent the capture-resight histories for approximately 90 PIT-tagged individuals from mid-January to the beginning of May 2018. Grey shading on the right of the image indicates the start of May. Pink represents presence/detection at Bat Cave (the maternity cave), blue indicates presence/detection at Glencoe (non-breeding cave), black shows occurrences where an individual was detected at both caves on the same night and white indicates absence or lack of detection.

Discussion

Migrating bats face a number of conservation challenges, but detailed knowledge of the migration patterns of bat species is limited, particularly outside of Europe and North America (Fleming and Eby 2003; Popa-Lisseanu and Voigt 2009). *Miniopterus orianae* has been described as migrating regionally, after the first banding efforts revealed seasonal movements in the order of 280 km (Purchase and Hiscox 1960). The focus of this study was to describe the phenology of the seasonal congregation and migration events undertaken by the southern bent-winged bat *M. o. bassanii*. Using PIT-tag technology, we identified seasonal patterns among the population's age and sex classes, and use these to bring together the full seasonal cycle of the subspecies for the first time.

Seasonal breeding cycle and population movements

The encounter probability of PIT-tagged individuals confirmed that the southern bent-winged bat population at Bat Cave peaks over the summer breeding season. Massed birthing of bats occurred in November, and presence at the maternity cave remained high among all sex and

age classes over the subsequent summer months. Juveniles began flying in January. Lactation rates decreased in early February, suggesting the bats are being weaned at this time (Chapter 5).

Following juvenile independence, we identified a previously undescribed movement event in southern bent-winged bats, occurring in each study year. This event peaked in mid-March, with bats moving away from the maternity cave (coinciding with increased detection at Glencoe), and then returning to Bat Cave in April. This inter-cave movement was primarily undertaken by juveniles and adult females, with these population classes having almost identical encounter probability patterns at the study sites during this time. This behaviour is consistent with the maternal guidance hypothesis (Stumpf *et al.* 2017), whereby mothers guide their offspring to known roost sites, including hibernacula. In wild free-ranging bats, individuals use a combination of cognitive processes to localise roosts (Hernández-Montero *et al.* 2020). *Myotis bechsteinii*, for example, uses spatial memory to re-localise previously occupied roosts: however, social information significantly improves success in localising unfamiliar roosts (Hernández-Montero *et al.* 2020). Maternal guidance of young to roosts has long been proposed (e.g. Fenton 1969), and the hypothesis has been supported by observations from proximity sensors (Ripperger *et al.* 2019) and genetic studies (Stumpf *et al.* 2017) showing females and young of *Nyctalus noctule*, *Myotis daubentonii* and *Myotis nattereri* roost-switching together, or being located together at ‘swarming’ sites, significantly more than is expected by chance (‘swarming’ behaviour at particular caves is thought to be associated with mating in some bat populations (Parsons *et al.* 2003; Rivers *et al.* 2005; Bogdanowicz *et al.* 2012)).

After the short-term movement to the non-breeding cave by southern bent-winged bats in late summer to early autumn, most adult females (daily encounter probability >0.7) and many juveniles (daily encounter probability >0.5) returned to the maternity cave in April through to May. An opportunistic observation of mating behaviour at Bat Cave in early May suggests that adult females return to mate with adult males; this coincides with the timing of conception recorded in the population (Crichton *et al.* 1989). Southern bent-winged bats are not thought to be reproductively mature until their second year, as described for eastern bent-winged bats by Dwyer (1963), with some corroborative evidence from a small sample of recaptured female southern bent-winged bats in this study (Chapter 5). However, it is possible that many first-year bats return to Bat Cave as part of their socialisation and learning, or due to attachment to their mothers or social group. Migrating bat species are

more commonly documented mating at, or on route to, swarming sites and hibernacula (Fleming and Eby 2003). In this population, autumn swarming has not been observed and the presence of males at maternity caves could explain the mating behaviour observed. For example, in *Myotis daubentonii*, mating behaviour varied depending on the proportion of males at maternity caves; at roosts with few males, females mated at swarming sites, whereas at mixed maternity roosts females mated with males at the maternity site (Angell *et al.* 2013). However, further observation of mating in southern bent-winged bats are needed to draw conclusions, as bats may also mate at non-breeding caves and at other times.

The southern bent-winged bat has been described as entering periods of torpor over winter months from mid-May to mid-September, including deeper hibernation from June to mid-August (based on observations at caves when collecting specimens during these months) (Crichton *et al.* 1989). We anticipated near-zero detection of PIT-tagged bats over June and July, but contrary to our expectation it was not uncommon to detect hundreds of bats per day at Glencoe during these months. Encounter probability was significantly reduced from mid-June through July (Fig. 2), though adult males remained more active than adult females over winter, possibly to increase mating opportunities and due to males having no need to conserve body condition for spring pregnancy (Turbill 2006; Czenze *et al.* 2017).

In spring, return to Bat Cave is gradual and staged among sex and age classes, with adult males returning first, then adult females, and finally the juveniles from the previous breeding season. By October, daily encounter probability approaches similar levels observed before winter dispersal for all groups, suggesting that natal philopatry in the population is high in both sexes. Indeed, our results show just one month at Bat Cave (~June) where few bats are detected at the maternity cave.

Whilst this research re-shapes understanding of seasonal population patterns in the southern bent-winged bat, some elements of this understanding appear unchanged over the last ~50 years. For example, Dwyer and Hamilton-Smith (1965) reported that juveniles had dispersed from Bat Cave by the end of February in 1962 and 1963, timing which coincides with our observation of late summer-early autumn movement in juveniles and adult females before returning to Bat Cave. Codd *et al.* (2003) reported a decline in bats at Bat Cave through May, coinciding with winter dispersal; and Hamilton-Smith's cave journal records (unpublished data) noted that the low number of bats present in mid-August 1964 were all males, which aligns with the observation in this study of adult males returning to Bat Cave before females.

Inter-cave movement and flight distance

Movements between roosts, and to and from foraging areas, by insectivorous bats are typically less than several kilometres (Kunz and Lumsden 2003); though some studies record maximum flight distances between 10 to 35 km (Barclay *et al.* 2000; O'Donnell 2001; Lumsden *et al.* 2002; Bourne 2010), particularly in fragmented areas. This study recorded numerous movements between the two study sites (72 km), in the same night and individuals can fly the distance in just a few hours. These flight distances more than double the previously recorded maximum flight distance by southern bent-winged bats (35 km, Bourne 2010) which is used to inform buffer zones around caves for conservation. The number of these 'direct flights' detected questions the assumption that southern bent-winged bats use transition caves as 'stop-overs' *en route* to maternity caves (Churchill 2008; DELWP 2020), as originally described for the eastern bent-winged bat (Dwyer 1964). Caves mid-distance between the maternity and key non-breeding cave may be more important as general roosting sites rather than transition caves specifically, though such sites may perhaps serve as 'stopovers' for bats moving longer distances or in adverse weather.

Dwyer and Hamilton-Smith (1965) suggested that virtually all southern bent-winged bats within this region congregated at Bat Cave for the breeding season. This was supported by observations of the approximate equivalence in adult sex-ratios and apparent desertion of non-breeding caves (Dwyer and Hamilton-Smith 1965). Our results show that whilst the greater proportion of bats do congregate at Bat Cave, there is an underlying turn-over occurring in the population, and in addition to the main seasonal movements, inter-cave movements between the maternity cave and Glencoe non-breeding cave can occur all year-round. Thus, not all movement detected was consistent with definitions of seasonal migration (e.g. Fleming and Eby 2003); for example, data exploration showed that movements by some individuals involved moving back and forth between the caves on successive nights. There are ~80 non-breeding caves in the southern bent-winged bat's distribution, including at least 48 caves in south-east South Australia (Thompson 2017; DELWP 2020), and it is probable that similar patterns also occur between Bat Cave and at least some of these caves.

Preliminary short-term PIT-tag data from other non-breeding caves in the lower south-east of South Australia demonstrate movement occurring between Glencoe and these other non-breeding caves (unpublished data). Further study, ideally by monitoring a number of roosting caves, is needed to fully characterise these movement patterns. However, a shift in language

from ‘regional migration’ to ‘population movement’ may be more fitting for the southern bent-winged bat in the future.

The drivers behind inter-cave movements are not entirely clear. Maternity caves provide warm and humid microclimatic conditions for raising young (Dwyer and Hamilton-Smith 1965; Baudinette *et al.* 1994). However, southern bent-winged bats use the Bat Cave maternity cave for much of the year, so it likely also fulfills other requirements for the population; for example, acting as a population ‘social hub’, and at certain times of the year, a mating site. As previously discussed, some movement to non-breeding caves (i.e. the newly identified movement event in adult females and juveniles) may be associated with the young’s cognitive learning of the location of non-breeding sites. The use of these non-breeding sites has been attributed to the cooler microclimates that facilitate the use of torpor (Hall 1982); however, resource availability may also be a driver. Codd *et al.* (2003) suggested that dispersal away from Bat Cave for the winter may be associated with decreased prey in the area. The non-breeding cave near Glencoe is within vicinity of vegetated areas and wetlands that may provide important foraging resources. This could explain the continued movement to this key non-breeding cave, even during the summer months when the bat population in this region was thought to remain at the Bat Cave maternity site (Dwyer and Hamilton-Smith 1965).

Implications for emerging threats and conservation

A notable finding in this study is the extended length of congregation of southern bent-winged bats at Bat Cave, rather than only over summer breeding months. This clearly highlights the importance of adequate resource availability in the vicinity of this major maternity cave, which needs to support a large population almost all year round. Drought and loss of foraging habitat have both been identified as key threats to the southern bent-winged bat (DELWP 2020). Approximately 90% of native vegetation in its distribution has been cleared (DELWP 2020) and lower survival rates for juveniles and lactating females occur in the drier seasons of summer and autumn, with highest mortality during drought (Chapter 5).

This study demonstrates that the times of lower survival in summer and autumn are also times of significant seasonal movements, undertaken predominantly by juveniles and adult females. This highlights the possibility of mortality associated with movements undertaken by these population cohorts. Alternatively, if other threats such as availability of food resources are the main drivers of decline and mortality, and disproportionately affect survival

of adult females and juveniles, then any additional mortality risk during seasonal movement may further disadvantage these vulnerable population classes (e.g. if windfarms were developed on flight routes between maternity caves and key non-roosting sites).

The population congregation and movement patterns identified in this study have important implications for the potential development of windfarms in this region and mitigation strategies (e.g. Peste *et al.* 2015). For example, bat activity may be underestimated if pre-construction monitoring is undertaken only short-term, or during summer when juveniles are still dependent on adult females at maternity caves. Autumn is a time when bats are more frequently found dead at windfarms, both in Australia (Hull and Cawthen 2013; Moloney *et al.* 2019) and internationally (Cryan and Barclay 2009). If pre-construction surveys therefore targeted the autumn period but are undertaken short-term (e.g. only in April), significant levels of bat activity occurring could still be missed. Monitoring over a full seasonal cycle (i.e. at least one year) would provide greater understanding of bat activity at a site and more comprehensively inform mitigation strategies.

The high level of inter-regional movement also has implications for potential responses to white-nose syndrome. If the pathogen is introduced to Australia and comes into contact with southern bent-winged bats, it would likely spread quickly through the entire distribution. Hibernating bats are susceptible to white nose-syndrome because infection causes a cascade of physiological effects which lead to bats arousing more frequently from torpor, and thereby depleting valuable fat reserves (Reeder *et al.* 2012; Verant *et al.* 2014). There is a high diversity of torpor use among species and individuals (Geiser 2020), with torpor best being described as a continuum from short-term daily torpor bouts to hibernation (e.g. longer-term, multiday torpor bouts) (McNab and O'Donnell 2018). It has been suggested that 'shallow hibernators' with relatively high levels of winter activity (e.g. characterised by more frequent arousals from torpor) may have a lower susceptibility to white-nose syndrome (Johnson *et al.* 2012).

More research is needed to examine the length and frequency of torpor bouts in southern bent-winged bats, and other Australian bats, to adequately assess their hibernation ecology and associated susceptibility to white-nose syndrome (Holz *et al.* 2019b; Turbill and Welbergen 2020). Our finding of higher than expected winter activity parallels results in other studies that some species of temperate bats are more active in winter than previously thought (Hope and Jones 2012; Johnson *et al.* 2016; Zahn and Kriner 2016), including in

subzero temperatures (Christie and Simpson 2006; Lausen and Barclay 2006). We recommend that further studies employ additional methods such as temperature transmitters to describe torpor expression in Australian bats, to adequately inform bat conservation and white-nose syndrome response strategies.

Globally, many bat species are threatened with extinction (Frick *et al.* 2020), and in Australia 62% of cave-dwelling bats are listed as threatened or near-threatened (Chapter 2). The seasonal population patterns in the critically endangered, southern bent-winged bat highlight the conservation challenges associated with migrating or highly mobile species, particularly a reliance on congregating in specific and restricted areas, combined with complex and broadscale habitat needs (Fleming and Eby 2003; Welbergen *et al.* 2020). The higher than expected mobility in the southern bent-winged bat is consistent with the literature revealing dynamic movement in some bat species, readily moving across regional, state and international jurisdictional boundaries (Hutterer 2005; Voigt *et al.* 2012; Welbergen *et al.* 2020). This highlights the need for conservation and management initiatives to be distribution-wide to address threats to bat populations such as habitat loss (Frick *et al.* 2020), windfarm development (O'Shea *et al.* 2016; Frick *et al.* 2017) and white-nose syndrome (Frick *et al.* 2015; Holz *et al.* 2019b; Turbill and Welbergen 2020), to ensure effective conservation into the future.

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Supplementary material

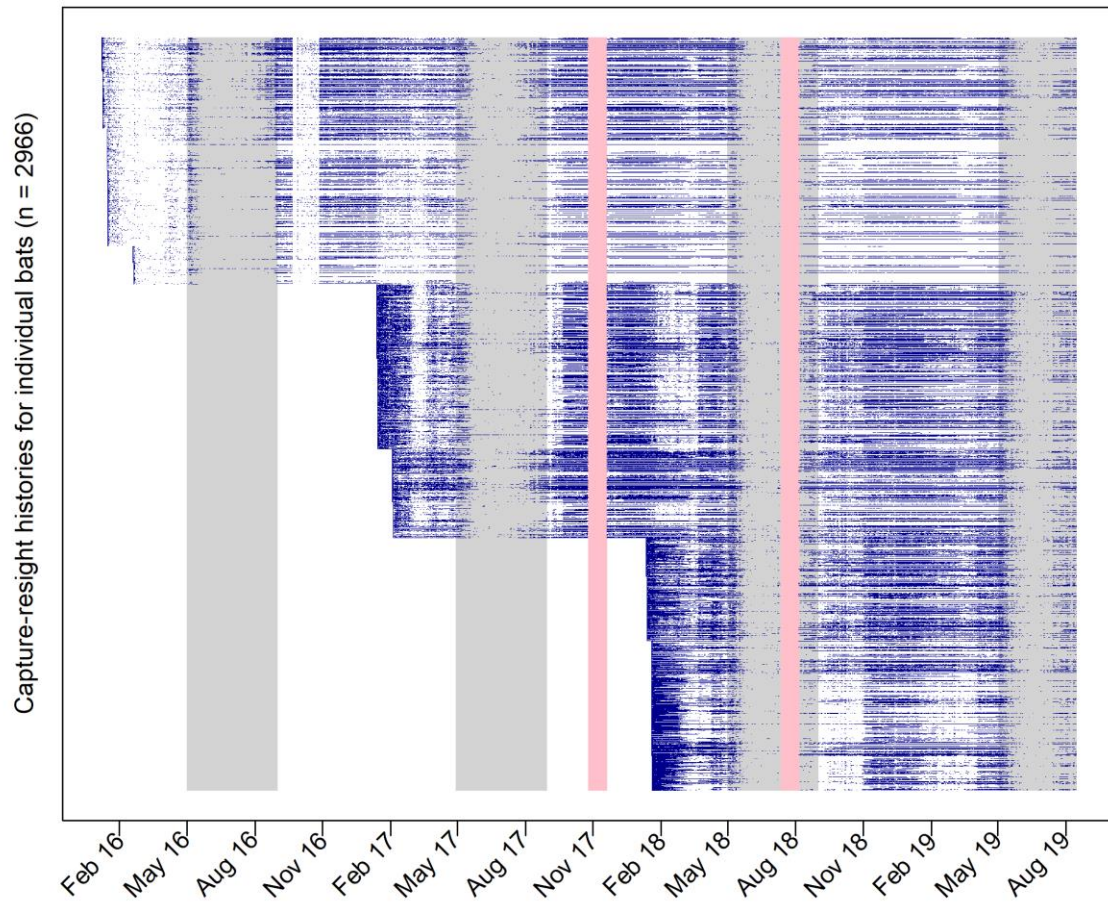


Figure S1. Capture-resight histories of all PIT-tagged individuals at Bat Cave over the study period. Each of the 2966 tagged bats is represented as an individual row on the y-axis, with initial capture and subsequent daily detections/presence at Bat Cave marked in blue. Missing data due to power outages are marked in pink. High noise levels (signal interference) affected detection success prior to May 2016 and during October–November 2016 (van Harten *et al.* 2019). Grey shading indicates the winter months May to August, when little bat activity was expected.

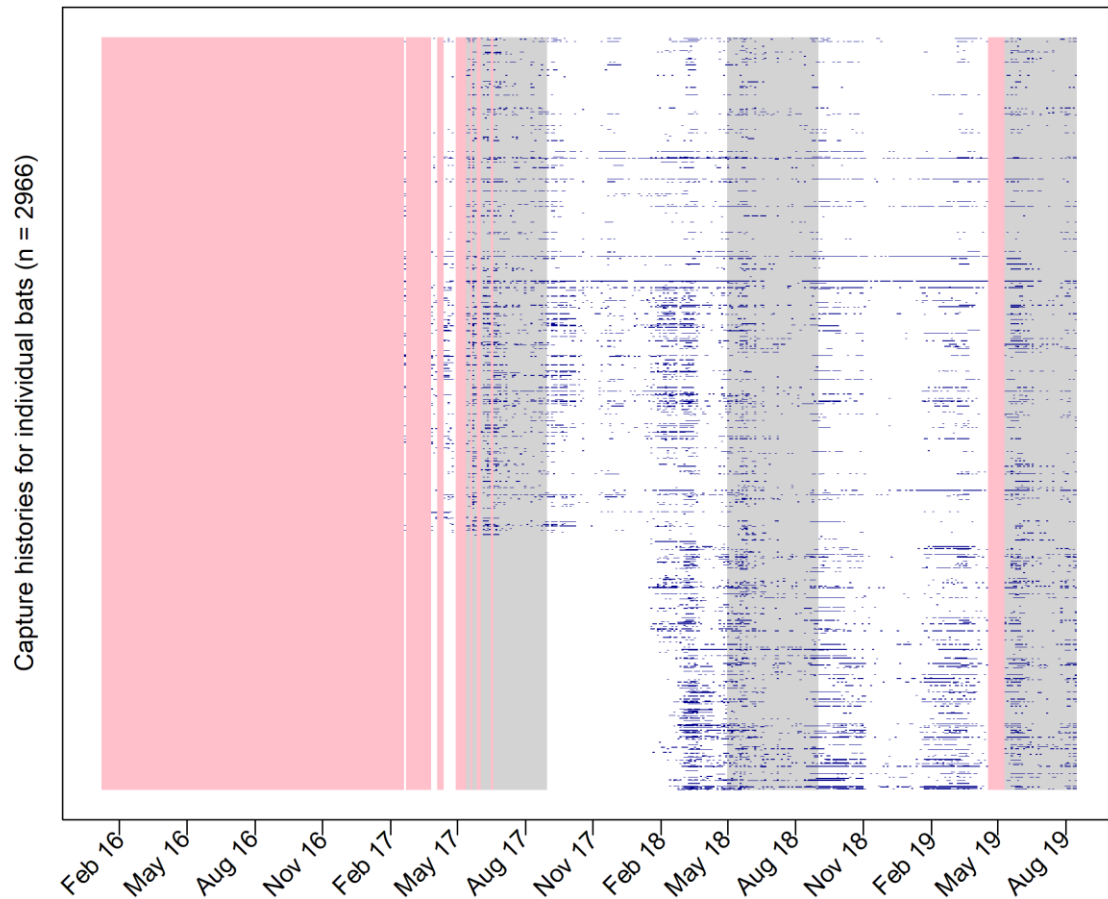


Figure S2. Capture-resight histories of all PIT-tagged individuals at Glencoe over the study period. Each of the 2966 tagged bats is represented as an individual row on the y-axis, with daily detections/presence at Glencoe marked in blue. Pink shading indicates the time prior to the Glencoe system being permanently installed and missing data due to power outages. Grey shading indicates the winter months of May to August, when little bat activity was expected.

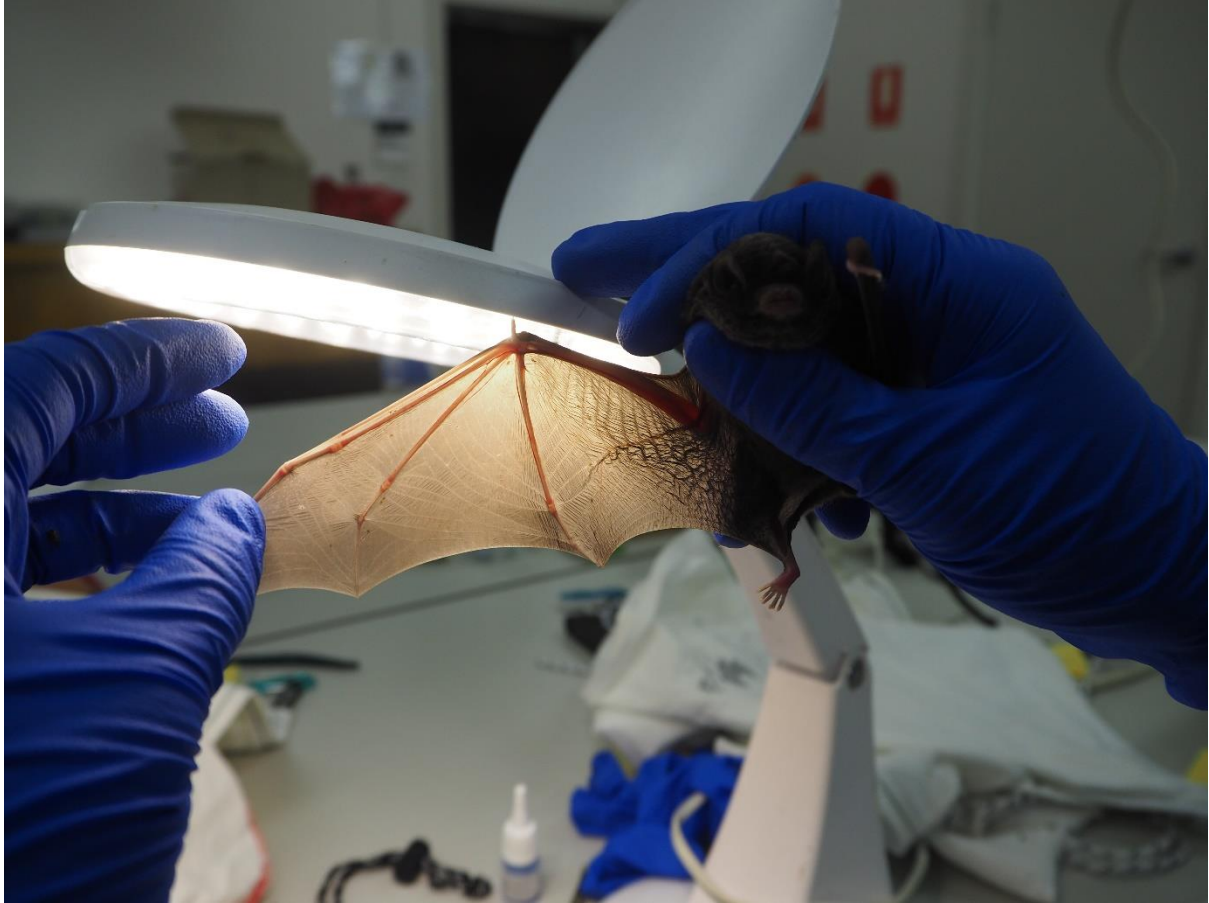


Figure 1. Age was assessed by transilluminating the metacarpal-phalangeal joints in the wings. In this individual, the visible bands/gaps (with more light passing through compared to the bone) and smooth shape of the joints indicate that it is a juvenile; adults have a round cartilaginous core. Photo: Emmi van Harten.

Thesis overview

Bats are diverse group of mammals (Simmons and Cirranello 2020) that provide globally important ecosystem services (Kunz *et al.* 2011). However, more than half of the world's bat species assessed for conservation status have unknown or decreasing population trends (Frick *et al.* 2020). There is a similarly concerning state of knowledge of bat species in Australia (Chapter 2). This thesis has focused one such taxon of concern in Australia, investigating the population dynamics of the critically endangered, southern bent-winged bat *Miniopterus orianae bassanii*, with the purpose of informing conservation and recovery. Table 1 provides an overview of the objectives for each data chapter and the key findings presented.

Table 1. Objectives and key findings for each data chapter presented in this thesis.

Data chapter	Objective	Key findings
Chapter 3	Investigate the use of passive integrated transponder (PIT) tag technology and develop methods for passively monitoring flying bats in large cave-passages, without interrupting the flight path of the bats.	<ul style="list-style-type: none"> - A 15m long PIT-antenna was optimised to create a c. 8 m² vertical detection plane. PIT-tags were detected up to 105 cm either side of the antenna plane. - Post-installation monitoring determined that the antenna did not hinder the flight path of the bats. - Large PIT antennas are highly sensitive to environmental ‘noise’ (unwanted signal perceived by the system). The probability of encountering a tagged bat decreased with increasing noise. - Initial high levels of noise could largely be mitigated by earthing the systems, increasing the daily probability of encounter from <0.2 (noise level ≥30%) to 0.7–0.8 (noise level 5%–15%). Systems using large antennas should be earthed as standard protocol. - Quantified noise metrics should be included as covariates influencing the probability of detection in statistical analysis of marked populations. - Passive resight rates of tagged individual were high with over 1.4 million individual detections and 97% of individuals being detected at least once.
Chapter 4	Following PIT-tagging and application of surgical adhesive, determine any potential effects on recaptured southern bent-winged bats (including body mass and recovery of the PIT-tag injection site).	<ul style="list-style-type: none"> - In subsequent trapping events, a small number of individuals were physically recaptured enabling investigation of the impact of the PIT-tagging procedure. - All recaptured bats ($n = 52$) were in good body condition based on body mass. - Change in body mass after PIT-tagging and associated use of surgical adhesive was not significant for most recaptured individuals, except for six bats that followed the same pattern of lowered body mass as untagged bats from the same capture period. - No signs of infection or irritation were observed. - Temporary, localised fur loss occurred at the injection site. Fur re-growth was observed in recaptured bats three to six weeks after tagging. - Most bats ($n = 10$) recaptured one to two years after tagging showed no external signs of tagging. Fur at injection sites of two individuals had re-grown white instead of brown.

		<ul style="list-style-type: none"> - PIT-tagging and the use of surgical adhesive appeared to be a safe marking method in this study.
Chapter 5	Investigate the survival rate of PIT-tagged southern bent-winged bats and predict population trends at the major maternity site, Bat Cave.	<ul style="list-style-type: none"> - The survival model providing the best fit for ‘apparent’ survival included the variables of age, sex, female reproductive status and the interaction between year and season (i.e. fitting separate estimates for each season over the study period). - Bats exhibited lowest apparent survival over summer and autumn. Apparent survival was particularly low for reproductively active adult females in summer (when lactating) and juveniles in autumn (after weaning). - Winter survival was high for all population classes. - Apparent survival rates were markedly lower in summer and autumn of 2016, which corresponded with severe regional drought conditions. Such dry conditions may be affecting the viability of this critically endangered population. - Juvenile sex ratios were close to 50:50, except in 2017 when there was statistically significant ($P<0.01$) male bias (55:45). - Lactation status in a small number of recaptured females tagged as juveniles appears to confirm previous assumptions of female reproductive maturity at two years of age. Two females were recaptured at one year old and were classed as pre-parous; a further two females were recaptured at two years old and were classed as lactating. - Exponential rates of population growth (r) were calculated using apparent survival estimates for each study year and various combinations of additional parameters and assumptions (e.g. juvenile sex ratios, breeding probabilities, tag loss rates and emigration). All calculations of r predicted population decline under the apparent survival rates experienced in 2016, with the baseline value as low as -0.603. Predicted rates of decline were markedly smaller for 2017 and 2018, though all r values were negative unless including a permanent migration rate of at least 0.1 (double the expected rate). Overall, calculations of r suggest continued population decline at Bat Cave.

Chapter 6	Describe the full seasonal cycle of activity of the southern bent-winged bat, including identifying migration and congregation events undertaken by the population's sex and age classes.	<ul style="list-style-type: none"> - Southern bent-winged bats congregate at the maternity site at Bat Cave for most of the year; based on over 3.5 years of monitoring, there is only approximately one month (~June) where few bats are present. - Movements between Bat Cave and a key non-breeding cave at Glencoe (72 km south) occur all year round, even during peak occupancy periods at Bat Cave. - Bats can fly between the maternity cave and the Glencoe non-breeding cave in just a few hours (e.g. as little as 3.2 hours). - Mass birthing was observed in November in each breeding season over three years. Juveniles began emerging from the maternity cave in January. Mating behaviour was observed in early May. - Different regional movement patterns were identified between the population's different sex and age classes, with major seasonal movement events identified each year. While some variation in timing was evident between years, the general population patterns for sex and age classes did not change. - A movement event was undertaken by juveniles and adult females in late summer and early to mid-autumn, with these classes being detected at Glencoe during this period, before returning to Bat Cave. This movement may be associated with mothers guiding their young to non-breeding caves. - In winter, bats were expected to be seldom detected at the study sites due to dispersal to numerous non-breeding caves and use of prolonged periods of torpor. The population dispersed from Bat Cave through May, coinciding with a peak in bat activity at Glencoe. After this initial activity at Glencoe, encounter probability decreased over winter at both caves; however, some bat activity was still detected throughout the cooler months (particularly at Glencoe). There was a staged return to the maternity cave among the sex and age classes from July through spring, with adult males returning first. Overall, the movement patterns of the population were more dynamic than expected.
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One of the challenges in studying the ecology and population dynamics of insectivorous bats is that many have low recapture rates and are exceptionally small in size (Moyers Arévalo *et al.* 2020). This severely limits options for using technology such as transmitters and bio-loggers due to weight restrictions and ethical considerations (Aldridge and Brigham 1988). The use of passive integrated transponder (PIT) tags is a technique that offers a solution to these problems. PIT-tags (<0.1 g) are injected under the skin (Fig. 2) and carried by the individual for a lifetime. Subsequent detection of PIT-tagged individuals can be undertaken remotely by using antennas (usually at roosts), significantly increasing ‘recapture’ rates compared to traditional mark-recapture methods (Ellison *et al.* 2007). However, a limitation has been the read-range or detection distances, with animals typically needing to pass within centimetres of the antennas to be detected (Gibbons and Andrews 2004).



Figure 2. The candidate, Emmi van Harten, injecting a PIT-tag subcutaneously into a southern bent-winged bat. Photo: Steve Bourne.

This study provides a robust contribution to the literature on use of PIT-tag methods in wildlife research (Table 1). First, methods and recommendations were documented for optimising PIT-tag detection using large antennas, allowing bats to be detected in flight and creating larger detection areas than previously thought possible (Chapter 3). Importantly, these methods did not require altering the flight path of the bats by changing the mouth or passage of the cave, as used in other studies (Britzke *et al.* 2014; Adams and Ammerman 2015), because such changes are not tolerated by all species, including bent-winged bats in Australia (Thomson 2002). The results of this work suggest there is much potential for the use of this technology with other species, particularly cave-dwelling bats, which are disproportionately threatened and susceptible to disturbance (Chapter 2). When the antenna was working optimally, detection success was very high, resulting in exceptionally high resight rates and millions of detections, creating rich capture-resight histories ideal for studying population dynamics of wildlife (Chapter 3).

In a survey of small mammal researchers, more than 70% stated that they intended to use PIT-tagging as a marking method in the future; but respondents agreed that additional studies are needed to inform the use of such methods for capture-mark-recapture/resight studies (Jung *et al.* 2020). PIT-tagging generally has not been associated with negative effects on body condition, survival or reproductive success in small mammals (Rao and Edmondson 1990; Rigby *et al.* 2012). However, health and recovery following PIT-tagging and the application of surgical adhesive to the injection site (as per the recommended procedure for PIT-tagging bats (Kunz and Weise 2009)) has thus far not been adequately documented. One unpublished PIT-tagging study using surgical adhesive on little brown bats *Myotis lucifugus* reported no signs of infection ‘or physical distress’ was based on observations of just five recaptured individuals (Horn 1998). PIT-tagging (with application of Vetbond as per this study) in Kuhl's pipistrelle *Pipistrellus kuhlii* also found no changes in body condition in 14 bats recaptured 0–2 years after tagging (Locatelli *et al.* 2019). The largest known sample size is for Daubenton's bat *Myotis daubentonii* (without use surgical adhesive), with 38 individuals recaptured with PIT-tags and no signs of lowered body mass or apparent impacts on reproductive success (Rigby *et al.* 2012).

This study significantly increases the number of PIT-tagged individuals that have been recaptured in the wild and had their subsequent recovery documented. During

the three-year study, recovery of 52 recaptured individuals was assessed (Chapter 4), with no signs of infection, irritation, or lowered body mass as a result of the procedure, although temporary localised fur loss occurred at the injection site. The use of PIT-tagging and surgical adhesive appears to be a safe method. Continued documentation of marking effects in a variety of species is important so that researchers can fully consider potential welfare impacts for their study species (Murray and Fuller 2000).

Using the methods developed, documented and assessed in Chapters 3 and 4, monitoring of the PIT-tagged population was undertaken to investigate the population dynamics of the southern bent-winged bat. This insectivorous, cave-dwelling bat has experienced serious historical decline (Chapter 1), however, the cause of the decline has remained unclear and the current population trend was unknown (DELWP 2020). For example, it was unknown whether the population has stabilised or whether decline is ongoing. Survival rates in the population, as examined in this study, showed that apparent survival is associated with a multitude of factors (Chapter 5). Bats experienced lower survival in the drier seasons of summer and autumn, lactating females and juveniles experienced lower apparent survival than adult males and non-reproductive females (potentially due to having lower energy costs than lactating females), and lowest survival in all population classes coincided with drought conditions in the region in 2016. Survival rates and other parameters, including juvenile sex ratios and female reproductive maturity as determined in this study, were used to model the current population trajectory under different assumptions for each study year. Virtually all calculated rates of population growth were negative, indicating ongoing decline in the population. Projected rate of decline was most severe under the survival rates estimated for 2016.

Taken together, the results suggest that resource limitation is likely to be a key influence affecting population viability, probably due to drought and extensive habitat loss in the region (Chapter 5). This is supported by the approximate timing of severe historical population decline and regional habitat loss (clearance of natural vegetation, wetland drainage, and loss of wetlands due to lowered groundwater levels) (PIRSA 2017; Harding *et al.* 2018; DELWP 2020); the population's reliance on extended congregation at maternity caves (Chapter 6); evidence of mortality during previous drought events (Bourne and Hamilton-Smith 2007; DELWP 2020); health surveys

revealing no apparent signs of ill health from pathogenic factors (Holz *et al.* 2018a; Holz *et al.* 2018b; Holz *et al.* 2018c; Holz *et al.* 2019a); and conclusions from other researchers that resource limitation as a result of habitat loss is a likely driver of decline in the southern bent-winged bat (Allinson *et al.* 2006; Holz 2018).

In addition to understanding past and current population trends and threats, information is needed about the ecology of the southern bent-winged bat to assess and manage the potential impacts of emerging risks (DELWP 2020). These risks include elevated mortality associated with windfarm development, and the possible introduction of the pathogen causing the disease white-nose syndrome – the two leading causes of multiple mortality events in bats globally (O’Shea *et al.* 2016). Numerous windfarms are in planning stages in the range of the southern bent-winged bat, and white-nose syndrome has been assessed as almost certain to be inadvertently introduced to Australia and likely to come into contact with bats in the coming decade (Holz *et al.* 2019b).

Previously, much of the life-history of the southern bent-winged bat has been presumed to be similar to the eastern bent-winged bat *Miniopterus orianae oceanensis* (DELWP 2020). However, monitoring the PIT-tagged southern bent-winged bat population in this study has revealed population patterns that differ from the eastern bent-winged bat. For example, Dwyer (1963; 1966) describes eastern bent-winged bats using maternity caves for a significantly shorter period, with adult females forming maternity colonies in mid to late spring (October and November) and leaving in early autumn (March). In the southern bent-winged bat population, both males and females congregate at the maternity caves (Dwyer and Hamilton-Smith 1965). Adult males return to Bat Cave from mid-winter, adult females from late-winter and juveniles follow in spring. Mass dispersal associated with winter behaviour largely occurs in May (late autumn) (Chapter 6). In addition, this study highlighted a previously unknown movement event undertaken by juveniles and adult females, with these cohorts temporarily leaving the maternity cave in late summer and returning early to mid-autumn. This event is possibly explained by the ‘maternal guidance’ hypothesis, whereby mothers guide their young to other roosting sites (Stumpf *et al.* 2017). These seasonal population patterns add to further understanding of the distinctions between the eastern and southern bent-winged bat taxon, which also

include genetic differences (Cardinal and Christidis 2000) and differences in mean echolocation frequencies (Conole 2000).

Overall, the cave populations were more dynamic than previously thought. Individuals flew the 72 km between the major study sites in just a few hours and, in addition to the main regional movement events identified, underlying turn-over occurred in the population all year round. The 72 km flight distance more than doubles the current management ‘buffer zones’ that had previously been determined by radio-tracking of a small number of individuals (Bourne 2010). The findings add to literature showing remarkable dynamic mobility in some bat species, emphasising the need for conservation and management initiatives to be implemented across regional, state, and sometimes international, jurisdiction boundaries (Voigt *et al.* 2012; Welbergen *et al.* 2020).

These findings on mobility have major implications for risk associated with windfarm development, highlighting the potential susceptibility of southern bent-winged bats to additional mortality at windfarms, with population movements coinciding with periods of lowered survival (Chapters 5 & 6). Autumn is also the period that bats are more commonly found dead at windfarms in south-eastern Australia (Moloney *et al.* 2019). The findings also have implication for the potential threat of white-nose syndrome. If the pathogen is introduced to Australia and this region, the high level of movement and underlying turn-over in the bat population means that the disease would likely spread quickly through the population.

The seasonal population patterns and dynamic nature of the southern bent-winged bat population help explain the fluctuations identified in fly-out counts undertaken at maternity caves (Lear 2012; Lumsden *et al.* 2019). Ongoing monitoring programs form a key component of the National Recovery Plan for the southern bent-winged bat, with the purpose of detecting changes in population trends and evaluating whether conservation initiatives are successful (DELWP 2020). The encounter probability models developed in this thesis can be used to help pin-point suitable timing of such counts in the future (e.g. when all population classes are present at Bat Cave), to ensure that population monitoring can accurately document population trends to inform species recovery.

Finally, given the parlous state of knowledge about population trends in bats globally (Frick *et al.* 2020), and the high proportion of cave-dwelling species listed as threatened or near-threatened in Australia (Chapter 2), this study provides knowledge and approaches for understanding population dynamics of other species more broadly and informing biodiversity conservation efforts in the Anthropocene. For example, the use of unique identifiers for each individual enabled ecological patterns to be documented for different population classes – these patterns proved important in understanding the complexity of seasonal survival and movements of southern bent-winged bats (Chapters 5 & 6). Numerous bat species regularly share roosts with other bat species (e.g. Churchill 2008). The approach adopted in this study would also enable behavioural comparisons to be made between species and could enhance understanding of population trends in interspecific roosts over time. For example, the PIT-tag monitoring technique would allow for monitoring of a single, elusive species of conservation concern even though several other species are present (where the use of emergence counts using infra-red or thermal imagery is unable to facilitate such distinctions). These possibilities are important because effective conservation of bat species will require sustained efforts to assess population status and trends and address data deficiencies across the globe (Frick *et al.* 2020).

Recommendations: conservation actions and research priorities

Habitat loss is a key threat to global biodiversity; more than 500,000 terrestrial species are at risk of extinction unless their habitats can be protected and restored (IPBES 2019). Globally, the two most important habitats for bats are forests and subterranean features, such as caves (Frick *et al.* 2020). Habitat requirements for the southern bent-winged bat include suitable roosting caves (including maternity caves and non-breeding sites), as well as foraging habitat. Although the caves used by the southern bent-winged bat have faced a number of threats (DELWP 2020), such as alteration for guano mining and being used as rubbish dumps, conservation efforts have resulted in some caves being restored (Baudinette *et al.* 1994) and cleaned out (Bourne 2015); and many caves are now being protected through working with landholders and inclusion in reserves. Bat Cave, the maternity cave with the largest current and historical population of the southern bent-winged bat, is located within the

Naracoorte Caves National Park and World Heritage Area. Recent protection of the second major maternity cave near Warrnambool has been a key success for conservation of the southern bent-winged bat, protecting the site from land use that may have resulted in cave collapse (DELWP 2020). Diminished foraging resources is more difficult to rectify, yet resource limitation as a result of drought and loss of foraging habitat are suspected as likely contributors to mortality and decline in the southern bent-winged bat (Chapter 5).

Wetlands provide important foraging habitat for bats in Australia, particularly in dry landscapes (Blakey *et al.* 2018). Both treed/forested areas and vegetated wetlands are thought to be favoured foraging habitats of the southern bent-winged bat (DELWP 2020). Urgent protection and restoration of such foraging habitats is needed in the southern bent-winged bat range. Given the extended congregation of the population at Bat Cave (Chapter 6) and lower survival in juveniles and lactating females (Chapter 5), if survival is being impacted by resource limitation, habitat restoration within the foraging range (e.g. 35 km, Bourne 2010) of maternity caves is likely to provide the most benefit and have greatest impact on population recovery. Such restoration may also be able to help buffer some of the impacts of droughts, which are becoming more frequent and severe in the region (Rashid and Beecham 2019) and may be having a severe impact on population viability. Annual survival rates in this study were reduced by approximately 37% during the year coinciding with drought, compared to the subsequent study years. This is concerning for population viability, particularly given the reliance on high levels of annual survival in the population dynamics of bat populations (Schorcht *et al.* 2009; O'Shea *et al.* 2011), and the drastic rates of decline estimated in southern bent-winged bats during drought conditions (Chapter 5).

It is important that habitat restoration also considers the habitats of prey species; that is, habitat required for the full life-cycle of insectivorous prey species, which may extend beyond direct foraging habitat (Arrizabalaga-Escudero *et al.* 2015). The diet of the southern bent-winged bat appears to be comprised almost entirely of Lepidoptera (Kuhne 2020). However, further research is needed to investigate foraging requirements and prey species of the southern bent-winged bat (and the abundance, distribution and habitat requirements of these prey species) (DELWP 2020).

An excellent example of habitat rehabilitation in the region is the restoration of Mt Burr Swamp, near Mt Gambier, South Australia (Thompson 2017). The property had historically been drained for agriculture, as has occurred with most wetlands in south-east South Australia (PIRSA 2017). Restoration led by Nature Glenelg Trust since 2016 has included creating a weir to prevent surface water from flowing out of the main wetland, thus ensuring Mt Burr Swamp retains water. Progressive revegetation of riparian plant species around the swamp is also occurring (B. Haywood, pers. comm. 2020). In just three years since works began, many species of conservation significance have been confirmed at the site, including the southern bent-wing bat which was captured at the property during a harp-trapping survey in 2019 and is presumed to forage at the site (R. Thompson, pers. comm. 2020). The restoration of Mt Burr Swamp provides a successful example that could be used as a model for other locations.

The protection of the troposphere (airspace) as habitat is also critical (Diehl 2013; Voigt *et al.* 2018). A key movement event in southern bent-winged bats is undertaken by juveniles and adult females at a time when survival is already lowered in these population classes, suggesting that this movement may be associated with increased mortality risk. Additional mortality risk from a planned increase in windfarm development may further disproportionately impact these vulnerable population cohorts (Chapter 6). Conservation initiatives associated with future windfarm development should include cross-border (South Australia and Victoria) implementation of policy and guidelines (Voigt *et al.* 2012), adequate pre-construction monitoring of bat activity (including effective survey design and careful data interpretation, as acoustic monitoring may underestimate true bat activity (Mills and Pennay 2018)), appropriate mitigation strategies (Peste *et al.* 2015; Hayes *et al.* 2019) and building trust among stakeholders (Straka *et al.* 2020) to ensure that windfarms are truly sustainable for both renewable energy production and biodiversity conservation.

Conservation actions to protect bat species require funding and research but despite a large proportion of bat species in Australia being listed as threatened (Chapter 2), bats are under-studied and conservation measures not adequately funded (Fleming and Bateman 2016). Whilst some of these issues are likely a product of the challenges in studying these species (e.g. Chapter 2 & 3), bats also face cultural prejudices, as well

as fear of risk of disease from bats (Lunney and Moon 2011). Sensationalised media reporting and scientific articles that highlight bats as a public health concern and carriers of disease (e.g. without reference to beneficial ecosystem services) can decrease support for bat conservation (López-Baucells *et al.* 2018), and can even fuel calls for culling and ‘dispersal’ of bat colonies. Community involvement is integral to successful recovery of threatened species (Garnett *et al.* 2018) and harnessing such support will likewise be critical for conserving the southern bent-winged bat and ensuring that the species can flourish in the wild.

Community education is an important tool for changing negative perceptions of bats (Lunney and Moon 2011; Hoffmaster *et al.* 2016). Community education is especially important within the current context of the global COVID-19 pandemic (Fenton *et al.* 2020; MacFarlane and Rocha 2020). Whilst the origin of the SARS-CoV-2 (the virus causing COVID-19) remains uncertain, phylogenetically, the closest known related coronavirus is found in a species of horseshoe bat (Zhou *et al.* 2020). The link between bats and COVID-19 has fuelled fear and persecution of bats and eroded support for bat conservation (MacFarlane and Rocha 2020). Bats have specially developed responses to living with zoonotic viruses, possibly as a result of mechanisms to mitigate oxidative stress incurred from flight (Brook and Dobson 2015). However, perceptions that bats may carry more zoonotic viruses than other taxa is misleading; recent study shows that zoonotic risk is actually homogenous among taxonomic orders of mammals and birds and is instead a product of their respective species richness (i.e. greater diversity of species results in increased diversity of zoonoses) (Mollentze and Streicker 2020). The major underlying cause of wildlife disease outbreaks such as the COVID-19 pandemic is human activity, for example by increasing ‘spill-over’ events of zoonoses to humans through continued encroachment into wildlife habitats (Jones *et al.* 2013; Johnson *et al.* 2020), and by accelerating subsequent spread through globalisation (Fenton *et al.* 2020). To that end, it is important that communication from the scientific community avoids (directly or inadvertently) repeating or reinforcing misleading information and the normalising of negative attitudes and actions towards bats (MacFarlane and Rocha 2020). Community education should seek to emphasise the importance of bats to local communities, (such as agricultural pest control), dispel common myths and misunderstandings, as well as communicating species-specific messages (e.g. the

decline in the southern bent-winged bat) to foster community support, funding opportunities and conservation action.

Finally, it is vital that further research and monitoring of the southern bent-winged bat continues. Adaptive management will be critical as new knowledge is obtained and management actions are developed, refined, and implemented (DELWP 2020). This study has highlighted several areas where further study could assist recovery.

- Expansion of PIT-tagging and monitoring with antennas to further sites in the southern bent-winged bat distribution, including in Victoria, to enhance understanding of movements, population structure and change in population trends over time. In particular, this would provide greater understanding of the level of movement occurring between the populations associated with each maternity cave, which has thus far thought to be minimal, but could alter population growth estimates if the rate of such movements are much higher than previously thought.
- Determine survival rates in the maternity population near Warrnambool to clarify whether survival patterns in this population differ from the results of the present study. Logistical difficulties of the Warrnambool maternity cave precluded this site from the current study; however, with appropriate funding, PIT-tag monitoring may be possible at key nearby non-breeding caves.
- Determine survival rates in juveniles before they become volant and the proportion of adult females breeding each year. Pre-volant juvenile survival rates remain a knowledge gap due to the bats in this study being captured and PIT-tagged following emergence from the maternity cave. Together with counts that are being undertaken of the clusters of pups at maternity caves (Lumsden *et al.* 2019), these investigations would help inform whether breeding success is influencing population dynamics.
- Examine diet preferences (across the distribution and over the full-seasonal cycle), foraging behaviour and historical landscape change to better understand foraging requirements, the impact of habitat loss and the habitat requirements of prey species. This would allow for better evaluation of the threat of diminished foraging availability for the species and the most effective actions to alleviate this threat.

- Further research the potential risk of mortality associated with windfarms (especially, but not exclusively, during autumn movement events coinciding with lower survival), appropriate mitigation strategies and effective monitoring strategies for informing windfarm development and management.
- Further study of winter activity, including length and frequency of torpor bouts. More information is needed to better understand susceptibility of southern bent-winged bats to white-nose syndrome (which impacts bats during hibernation) and to refine response strategies (Holz *et al.* 2019b; Turbill and Welbergen 2020).
- Investigate the potential population impacts of climate change (including increased severity and frequency of droughts) and potential management strategies to reduce these impacts.

To summarise, this study has investigated the use of PIT-tag technology in wildlife research and contributed to understanding of the population dynamics of the southern bent-winged bat, to inform recovery of this critically endangered species. Key conservation actions recommended are:

- Immediate protection and restoration and protection of foraging habitat, especially within foraging range of maternity caves.
- Protection of the troposphere as habitat, particularly ensuring that windfarm development does not increase mortality
- Community education and engagement to foster support for conservation action
- Continued research to further inform and refine recovery actions

Recent adoption of the National Recovery Plan and establishment of a National Recovery Team provide hope that the current declining trajectory of the southern bent-winged bat can be halted with collaborative recovery efforts. Given the concerning population trajectory of the southern bent-winged bat, urgency in action is of upmost importance. As we have learnt from recent Australian extinctions, acting fast prevents extinction: we need to implement recovery actions soon while there still is an opportunity to act (Martin *et al.* 2012; Woinarski *et al.* 2017).

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