





Seasonal population dynamics and movement patterns of a critically endangered, cave-dwelling bat, *Miniopterus orianae bassanii*

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ABSTRACT

Context. Seasonal migration and movements of bats have important implications for their conservation. 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.** We tagged a total of 2966 southern bent-winged bats 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. We used capture–resight histories to visualise population patterns and model the 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 occurred in adult females and juveniles each year: these classes left the maternity cave in late summer, when juveniles became independent, and returned in early mid-autumn, later undertaking winter dispersal. Complex underlying movements of individuals occurred throughout the year, with individuals able to fly 72 km between roosting caves in just a few hours. **Conclusions.** Seasonal movements are a key aspect of the life history of this taxon. The newly reported movement of adult females and juveniles conforms to the maternal guidance hypothesis, whereby mothers guide their young to suitable non-breeding caves and hibernation sites. In addition to seasonal movements, some individuals moved 72 km between caves multiple times over short time periods, including on successive nights. This 72-km overnight flight distance more than doubles the previous distance used to inform management buffer zones. Extended congregation of bats at the maternity cave highlights resource limitation in the surrounding area as a potential threat to this population. **Implications.** The dynamic nature of the population has implications for the management of emerging risks, including mortality at windfarms and potential rapid spread of the exotic white-nose syndrome.

Keywords: bats, encounter probability, mark–recapture, migration, *Miniopterus*, PIT tags, population modelling, wildlife tracking.

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: they often have complex habitat requirements and a tendency to congregate in restricted areas

(Fleming and Eby 2003). In bats, migration has been defined as the seasonal movement of populations from one location to another, typically as a two-way movement of > 50 km and involving a return to the starting location, to seek conditions that are climatically or energetically more favourable (Fleming and Eby 2003). However, migratory behaviour in small insectivorous bats in Australia is known only for a few species. For example, the regional seasonal migration of the eastern bent-winged bat (*Miniopterus orianae oceanensis*) often has adult females travelling distances of > 160 km to maternity caves (Dwyer 1966). Here, we examine the seasonal population patterns, migration and movements of the southern bent-winged bat (*Miniopterus orianae bassanii*), a critically endangered taxon in south-eastern Australia.

Study of migration and movement in small insectivorous bats has traditionally involved long-term deployment of forearm bands (Hutterer 2005), but recapture rates are 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 the recording of detailed information on movement patterns, but limitations include the short duration that transmitters remain attached (O'Mara *et al.* 2014), and that devices need to be < 5% of body mass (Aldridge and Brigham 1988). The use of passive integrated transponder (PIT) tags is an approach that 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), but its potential for investigating seasonal movement patterns in insectivorous bats has not yet been tested.

In this study, we use PIT-tag technology and monitoring to discover seasonal population patterns, migration, and movements of the critically endangered southern bent-winged bat to enhance its conservation. In large bent-winged bats (*M. orianae*, previously *M. schreibersii*) in Australia, regional migration of adult females has been attributed to the need to move to and from maternity caves that have suitable microclimatic conditions; those selected provide stable, high humidity and temperatures necessary for the development of young (Dwyer 1963; Dwyer and Hamilton-Smith 1965; Baudinette *et al.* 1994). Non-breeding 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, but also include a number of non-breeding caves typically associated with a maternity population (Dwyer 1969). However, most knowledge of seasonal movements of bent-winged bats in Australia has been documented from populations now described as the eastern bent-winged bat (*M. orianae oceanensis*).

The southern bent-winged bat is thought to undertake similar seasonal movements (Churchill 2008; DELWP 2020); although, unlike the eastern bent-winged bat subspecies, many adult males also congregate at maternity caves (Dwyer and Hamilton-Smith 1965). The southern bent-winged bat has undergone serious population decline since the 1960s (DELWP 2020). Survival rates assessed in 2016–2019 show lowered seasonal survival during summer (December–February) and autumn for juveniles and lactating females, with the lowest survival rates coinciding with drought in early 2016 (van Harten 2020). Population modelling predicts a continued population decline (van Harten 2020), the cause of which remains uncertain, though resource limitation due to loss of foraging habitat and drought is suspected as a key threat (Allinson *et al.* 2006; Bourne and Hamilton-Smith 2007; DELWP 2020; van Harten 2020). Health surveys have not revealed pathogenic factors that could explain the severe population decline (Holz *et al.* 2018a, 2018b, 2018c, 2019a, 2020).

The southern bent-winged bat faces two emerging threats, both influenced by migration and movement patterns. First, there are numerous windfarms within its restricted range, and many more are proposed (Moloney *et al.* 2019; DELWP 2020). Globally, collision with wind turbines 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, although deceased bats are recovered at windfarms (Hull and Cawthen 2013), there is a high degree of uncertainty around mortality estimates and population level impacts are unknown (Moloney *et al.* 2019). A 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 (Cheng *et al.* 2021). A risk assessment found that 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, including the southern bent-winged bat (Turbill and Welbergen 2020). Knowledge of the seasonal activity cycle of the southern bent-winged bat is critical to inform both species recovery (DELWP 2020) and 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 used these data to address three predictions: first, that there are 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); second, that the timing of movements will vary by age

and sex class; and third, that there is little activity in winter when individuals are expected to disperse to non-breeding caves 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 (37°21'S, 140°47'42"E), a major maternity and summer congregation site (current population estimated at approximately 30 000 individuals). 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 10–14 Austbat harp traps (Faunatech, Mount Taylor, Vic., Australia), set exterior to the fencing 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 in the metacarpal–phalangeal joints (Brunet-Rossini and Wilkinson 2009). The PIT-tag (Biomark HPT 12, 12.5 mm, <0.1 g) 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 2017–2018). 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 (van Harten *et al.* 2020). All PIT-tags 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. Re-captured 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 was installed at the entrance to a key non-breeding cave located near Glencoe, 72 km south of Bat Cave. This second system was trialled short-term (e.g. 2–3 nights at a time) in February 2017, with long-term monitoring commencing in April 2017 (though with intermittent power outages until

June 2017). The antenna systems detected any tagged individuals as they flew through the loop formed with the flexible, 15-m long antenna (van Harten *et al.* 2019). When the systems were working optimally, there was a large read-range (up to 105 cm) 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 system.

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 downloaded from the systems regularly (approximately monthly) by manually retrieving the flash drives until 16 August 2019, with over 2.1 million unique detections recorded.

Analysis of population patterns using probability of encounter

We defined probability of encounter as the probability that an individual known to be alive was both present and detected. Thus, for an age/sex class in the population, an increasing value of encounter probability (from 0 to 1) reflects an increasing proportion of that age/sex class that is likely to be present and detected at the respective cave. We used models of encounter probability data to address the three predictions: (1) that annual migration occurs to and from the maternity cave; (2) that the timing of movements varies between age and sex classes; and (3) in winter months, individuals disperse to non-breeding caves.

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 (detected/undetected) for each individual across each day of the respective study periods for each cave. ‘Day’ was defined as the 24 h between successive middays. Plots of the capture–resight histories (detected/undetected) for each tagged individual were generated to visualise patterns at the two caves, as well as to identify 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 tagging, when approximately 13 months old. 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 cave.

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 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 cave was selected by comparing values of the Akaike information criterion (AIC) for alternate models that incorporated different demographic variables for individuals: (1) sex, (2) age, (3) combination of sex and age classes, and (4) no demographic variable. The AIC includes a penalty for increasing complexity (i.e. number of parameters) in the model. 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. The top-ranked model is the one with the lowest AIC value, and can be compared with other models by the difference in AIC values and AIC weights with the top-ranked model. Deviance explained was used as a measure of model fit. The chosen models for each cave were also modelled separately as yearly subsets to compare variation in patterns among 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 (Panasonic WV-SPN631) and tour schedule by asking the National Park staff to report any notable behaviour of the bats, such as birthing of the young. Observations were also made during visits to Bat Cave to collect PIT-tag data. The southern bent-winged bat is the only bat taxon known to roost in this cave, so there was no concern about confounding observations with other species. Observational data from the cameras and from trapping, together with presence/absence data from PIT-tag monitoring, were used to identify the phenology of the reproductive cycle.

Results

Phenology of the breeding cycle

Birthing at Bat Cave was observed in mid to late November (Table 1, Fig. 1a). The first births occurred 8–10 days before mass birthing by pregnant females in the 2015/2016 and 2016/2017 breeding seasons. In 2017/2018, the timing of mass birthing could not be determined due to the creche being positioned out of view of the cameras. Juveniles commenced flying and began emerging from the maternity cave in January, with many juveniles captured 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, Naracoorte Caves National Park, South Australia.

Observation	2015/2016	2016/2017	2017/2018
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

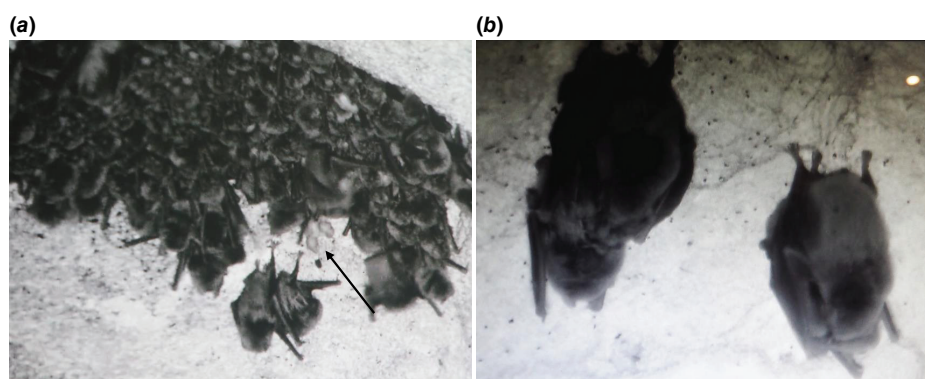


Fig. 1. (a) A cluster of adult females beginning birthing in the maternity chamber at Bat Cave on 19 November 2016; mass birthing in the population occurred over the following day. On the centre-right of the frame (arrowed), two pups can be observed, one with umbilical cord and placenta still attached.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

Mating and coupling behaviour were observed during the day on the cameras in Bat Cave on 6 May 2018 (the only observation) (Fig. 1b), with bats roosting as dispersed

Table 2. Selection table comparing alternative encounter probability models with different individual covariates included for the effects of γ_{day} .

Model	Deviance	AIC	Δ AIC	Akaike weight
Bat Cave				
Sex:age	124 046	145 705	0	1.0
Age	158 396	179 982	34 277	0.0
Sex	171 399	192 986	47 281	0.0
No individual covariates	196 120	217 671	71 966	0.0
Glencoe				
Sex:age	39 861	51 873	0	1.0
Age	44 678	56 619	4746	0.0
Sex	44 699	56 640	4767	0.0
No individual covariates	48 141	60 047	8174	0.0

Deviance, AIC value, Δ AIC (difference from the 'best' or top-ranked model) and Akaike weight for each model.

couples on the walls and ceiling of a smaller chamber extending from the main maternity chamber. In contrast, in the main maternity chamber that day, bats roosted in clusters or individually, the typical pattern at other times of the year.

Encounter probability

For each study site, the top-ranked model for the daily encounter probability of individuals, as assessed by AIC values and AIC weights, 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 (Table 2). AIC weights clearly indicated that, for each site, this model was by far the best fit to the data among the models tested. Total deviance explained by the top-ranked models were 81.9% for Bat Cave and 52% for Glencoe, respectively. For Bat Cave, the demographic covariate (i.e. age and sex classes) accounted for 36.7% of the deviance, and for Glencoe this was 17.2%.

Daily encounter probability (i.e. the probability that an individual known to be alive is present and detected) at Bat Cave was high for all sex and age classes from November to February (Fig. 2a). From February, encounter probability decreased at Bat Cave, with the lowest encounter probability

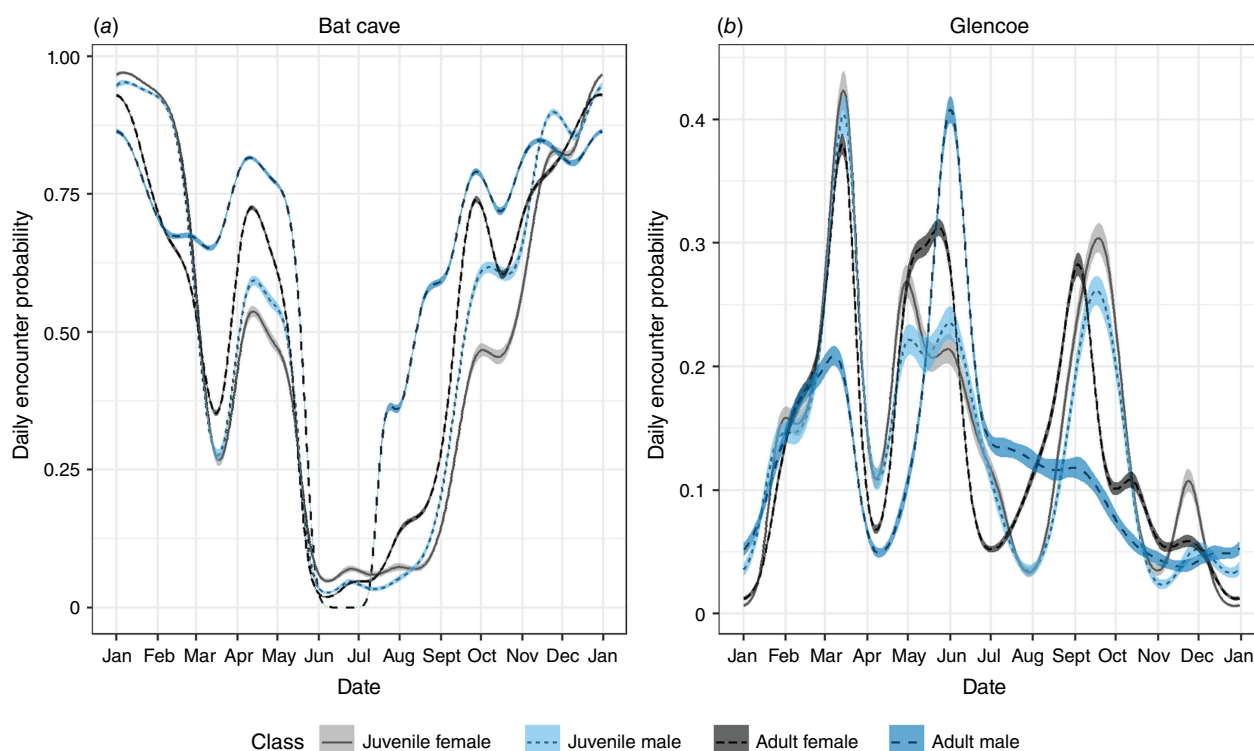


Fig. 2. Daily encounter probability for age and sex classes of the southern bent-winged bats at two sites: (a) the maternity cave, Bat Cave; and (b) the non-breeding cave at Glencoe, South Australia (modelled effects of γ_{day} , where $noise = 5\%$). The models are based on detections of 2966 bats PIT-tagged at Bat Cave over 3.5 years, 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.

for autumn months 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 caves during this period. Activity in these classes increased again at Bat Cave around April (and decreased at Glencoe).

Over winter, from May, the daily encounter probability at Bat Cave fell steeply to ~ 0 –0.05 at the beginning of June (Fig. 2a). Compared with the other sex and age classes, encounter probability of adult males at Bat Cave decreased later and increased earlier, such that there was only approximately 1 month (\sim June) when few bats were detected at Bat Cave. Following an influx of bats at Glencoe in May–June, associated with dispersal from the maternity cave, the winter months also experienced a drop in encounter probability at this non-breeding cave, likely due to lowered winter activity or use of other non-breeding caves. Nevertheless, regular activity was still detected at Glencoe and it was not uncommon to detect hundreds of bats per day at the entrance of this cave 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 (\sim 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 1 month after that of adult females but rose faster, peaking at Glencoe in mid-September.

At Bat Cave, there was a staged increase in activity between sex and age classes in late winter and early spring, with variation in timing evident among years (Fig. 3). Encounter probability of adult females increased later than adult males, followed by the juvenile cohorts. For example, encounter probability of adult males was 0.25 at the beginning of August in each of the first 3 years, whereas adult females did not reach the same encounter probability until mid-August to early September in the same years. Both adult classes returned to Bat Cave earlier in 2019, reaching 0.25 in mid-July and the beginning of August for males and females, respectively. Caution must be taken when interpreting results for late spring due to a series of system issues and power outages (occurring around October 2016, November 2017 and November 2018, Supplementary Fig. S1), which likely influenced the drop in encounter probability during these periods – thus population patterns at this time of the year remain less clear. However, encounter probability at Glencoe also varied considerably between the 2 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 Fig. S2).

Despite variation in timing (Fig. 3), the general seasonal patterns among sex and age classes were maintained across years. A notable exception was in early 2016, when adult

males showed a decline in encounter probability in February and March at Bat Cave that is not shown in the following 3 years. This may have been caused by detection issues at Bat Cave during this period, resolved in May 2016 (van Harten *et al.* 2019). This period also corresponded with severe drought conditions that may have affected movement behaviour in adult males.

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 patterns of movement evident (Fig. 4). This includes the aforementioned synchronous patterns of encounter probability for juveniles and adult females in early autumn.

Direct movements between caves

In addition to seasonal population movements, direct movements between the two monitored caves were detected throughout the year, in all seasons, even during peak occupancy periods at the respective caves (Fig. 5). Individuals were able to fly the 72 km between caves in a single night. The nightly occurrence of detecting such ‘direct flights’ peaked during the early autumn, autumn–winter and winter–spring population movements (Fig. 5). For example, 35 individuals were recorded at both caves on the same night in early May 2018, equating to just over 2% of the tagged population known to be alive at that time.

Detailed analysis of individual movements is beyond the scope of this paper. However, individuals demonstrated complexity in movement patterns and 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 h, returning to Glencoe the following night in 3.5 h. This female was then not detected for two nights, then subsequently flew again from Glencoe to Bat Cave, this time in 5.5 h, and returned to Glencoe on the following night in 4.2 h.

Discussion

In this study, we have provided new insights into the phenology of the seasonal congregation and movements of the southern bent-winged bat. 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. We interpret this knowledge in relation to the conservation of this critically endangered taxon, particularly in relation to emerging threats.

Seasonal breeding cycle and population movements

The encounter probability of PIT-tagged individuals confirmed that the population at Bat Cave peaks over the

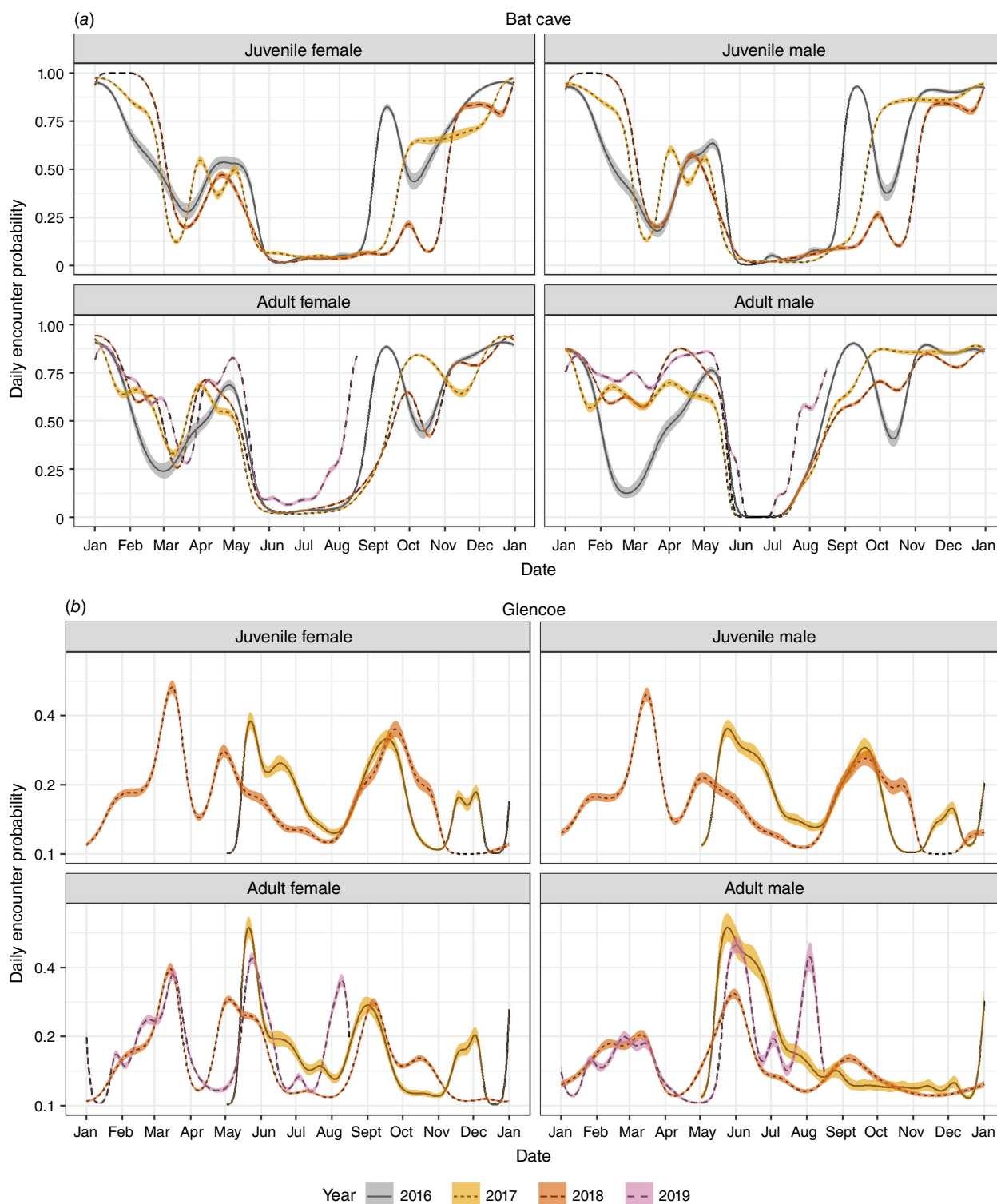


Fig. 3. Annual variation in daily encounter probability for age and sex classes of the southern bent-winged bats over the study years at two sites: (a) the maternity cave Bat Cave; and (b) the non-breeding cave at Glencoe, South Australia (modelled effects of yday, where noise = 5%). Models are based on data collected at Bat Cave from January 2016 to August 2019 and Glencoe from May 2017 to August 2019. Ribbon width for each class represents 95% confidence intervals. Note, because no bats were tagged in 2019 only adult (≥ 1 year old) classes are known for that year.

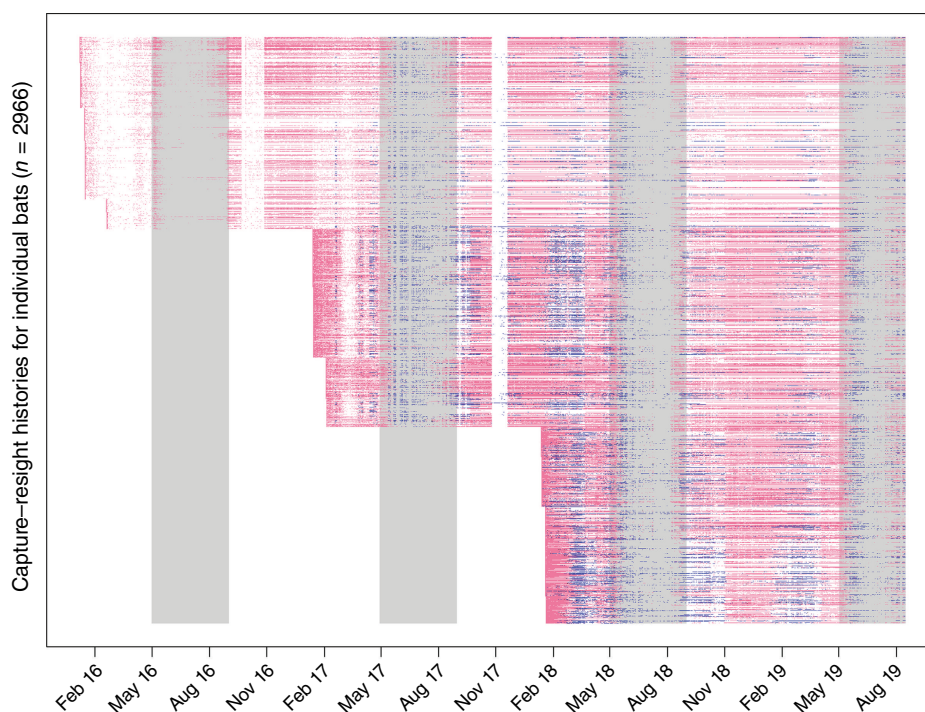


Fig. 4. Capture-resight histories of all PIT-tagged individuals at Bat Cave (pink) and Glencoe (blue) over the 3.5-year study period. Each of the 2966 tagged bats is represented as an individual row on the y-axis, with initial capture and subsequent daily detections indicating presence at the respective caves marked in pink and blue. The data occur in blocks because individuals were tagged over 3 years and seven trapping events. The Glencoe PIT-antenna system was installed in 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 Figs S1, 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). Occurrences where individuals were detected at both caves in a single night are marked in black. Distinct seasonal movement patterns are evident in the population. This figure also highlights the vastness of the dataset and the complexity of inter-cave movements by individuals over the study period. For an example of finer detail, see Fig. 6.

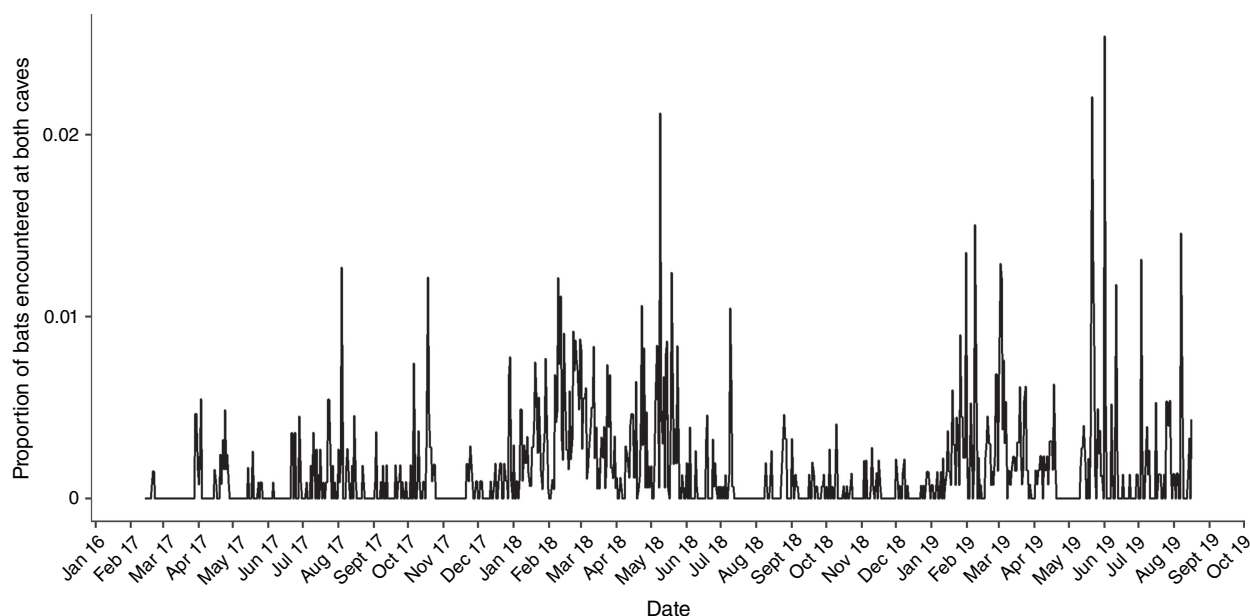


Fig. 5. Nightly proportion of PIT-tagged southern bent-winged bats (of the total population known to be alive each night) detected at both caves on the same night. The caves, Bat Cave and Glencoe, South Australia, are located 72 km apart.



Fig. 6. An example of detail 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. Although clear seasonal population patterns emerged in the encounter models developed (Fig. 2), the detail in this dataset shows that individual presence/absence and movements are complex and are not confined to only two-way seasonal movements or ‘migrations’.

summer breeding season. Mass birthing occurred in November, and presence at the maternity cave remained high among all age and sex classes over the subsequent summer months. Juveniles began flying in January. Lactation rates decreased in early February (van Harten 2020), suggesting the bats are being weaned at this time.

Following juveniles becoming independent, a previously undescribed movement event occurred in autumn months each 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, which had almost identical encounter probability patterns at the two caves 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). For example, the Bechstein’s bat (*Myotis bechsteinii*) 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 for several northern hemisphere species by observations from proximity sensors (Ripperger et al. 2019) and genetic studies (Stumpf et al. 2017).

After this short-term movement to the non-breeding cave 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). *Miniopterus orianae* are thought to not reach reproductive maturity until their second year (Dwyer 1963; van Harten 2020). 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 commonly documented mating at, or on route to, ‘swarming’ sites and hibernacula (Fleming and Eby 2003). In this population, autumn swarming (see Parsons et al. 2003) has not been observed, and the presence of males at maternity caves could explain the mating behaviour described. For example, in Daubenton’s bats (*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). Further observation of mating in southern bent-winged bats is needed to draw conclusions, because they 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 expectation it was not uncommon to detect hundreds of bats per day active 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, 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, the return to Bat Cave was gradual and staged among age and sex classes: adult males returned first, then adult females, and finally juveniles from the previous breeding season. By October, daily encounter probability approached similar levels to that observed before winter dispersal for all groups, suggesting that natal philopatry in the population is high in both sexes. There was just 1 month at Bat Cave (~June) when few bats were detected at the maternity cave.

Although this research re-shapes understanding of seasonal population patterns in the southern bent-winged bat, there are elements consistent with other observations 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 that 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 (unpubl. 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 daily/nightly movements to and from foraging areas by insectivorous bats are typically less than several kilometres ([Kunz and Lumsden 2003](#)). For example, tracking individuals of the large-eared pied bat (*Chalinolobus 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](#)). However, some studies have recorded maximum nightly flight distances from 10 to 35 km ([Barclay *et al.* 2000](#); [O'Donnell 2001](#); [Lumsden *et al.* 2002](#); [Bourne 2010](#)), particularly in fragmented habitats. In this study, we recorded numerous movements between the two caves (72 km) in the same night, with individuals able to fly this distance in just a few hours. These flight distances more than double the previously recorded maximum flight distance by the southern bent-winged bat (35 km, [Bourne 2010](#)), which has been used to inform buffer zones around caves for conservation.

[Dwyer and Hamilton-Smith \(1965\)](#) suggested that almost all southern bent-winged bats in this region congregate 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 most bats do congregate at Bat Cave, but there is an underlying turnover occurring within the population. In addition to the main seasonal movements, inter-cave movements between the maternity cave and Glencoe non-breeding cave occur all

year-round. Thus, not all movement detected was consistent with the definition of seasonal migration (e.g. [Fleming and Eby 2003](#)), notably the movements by some individuals back and forth between the caves on successive nights. There are ~80 non-breeding caves known in the southern bent-winged bat's distribution, including at least 48 caves in south-east South Australia ([Thompson 2017](#); [DELWP 2020](#)). Similar movements probably also occur between Bat Cave and some of these caves. Preliminary PIT-tag data from other non-breeding caves in the lower south-east of South Australia demonstrate movement occurring between these sites and Glencoe (unpubl. data). Simultaneous monitoring of a number of non-breeding caves is needed to characterise these movement patterns. We suggest that a shift in terminology from regional 'migration' to 'movement' is appropriate for the southern bent-winged bat.

The drivers for inter-cave movements are not clear. Maternity caves provide warm, 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 population requirements; for example, acting as a 'social hub', and at certain times of the year, a mating site. The use of non-breeding sites has been attributed to cooler microclimates that facilitate 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 local area. The non-breeding cave at Glencoe is close to vegetated areas and wetlands that may provide important foraging resources. This may explain continued movement to this key non-breeding cave (previously assumed to be a 'wintering cave'), even during summer months when the regional population was thought to remain at the Bat Cave maternity site ([Dwyer and Hamilton-Smith 1965](#)).

Implications for emerging threats and conservation

The extended congregation of the southern bent-winged bat at Bat Cave highlights the importance of adequate resources in the vicinity of this major maternity cave to support a large population almost year-round. Drought and loss of foraging habitat have 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 ([van Harten 2020](#)). These times of lower survival in summer and autumn coincide with the timing of significant seasonal movements, undertaken predominately by juveniles and adult females. Any additional mortality associated with such movements (e.g. due to collisions with wind turbines) would further disadvantage these vulnerable population classes.

Population congregation and movement patterns have important implications for the development of windfarms within the range of the southern bent-winged bat, and their mitigation strategies (Peste *et al.* 2015). For example, the risk associated with bat activity in the vicinity of proposed windfarms may be underestimated if pre-construction monitoring is undertaken only short-term, or during summer when juveniles still depend on adult females at maternity caves. Autumn months are 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 target the autumn period, but for only a short period (e.g. only in April, when many bats returned to the maternity cave), significant levels of bat activity could be missed. Monitoring over a full seasonal cycle would provide greater understanding of bat activity and more comprehensively inform mitigation strategies.

The high level of movement also has implications for potential responses to the risk of white-nose syndrome. If the pathogen causing white-nose syndrome is inadvertently introduced to Australia and comes into contact with southern bent-winged bats, it will likely spread quickly through the entire distribution. Hibernating bats are susceptible because infection causes a cascade of physiological effects which lead to bats arousing more frequently from torpor, and thereby depleting fat reserves (Reeder *et al.* 2012; Verant *et al.* 2014). It has been suggested that bat species that are 'shallow hibernators', with relatively high levels of winter activity (e.g. characterised by more frequent arousals from torpor), have a lower susceptibility to white-nose syndrome (Johnson *et al.* 2012). 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), including in subzero temperatures (Christie and Simpson 2006; Lausen and Barclay 2006). Further knowledge of the length, frequency and other characteristics of torpor bouts in the southern bent-winged bat, and other Australian bats, is needed to adequately assess their hibernation ecology, associated susceptibility to white-nose syndrome and appropriate response strategies (Holz *et al.* 2019b; Turbill and Welbergen 2020).

Globally, many species of bats are threatened with extinction (Frick *et al.* 2020): in Australia, 62% of cave-dwelling bats are listed as threatened or near-threatened (van Harten *in press*). The seasonal population dynamics and movement patterns of the critically endangered southern bent-winged bat highlight the conservation challenges associated with 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 of the southern bent-winged bat is consistent with other studies of dynamic movement in some bat species, 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 if they are to adequately address threats such as habitat loss (Frick *et al.* 2020), the risk of mortality from 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), and the need to ensure effective conservation into the future.

Ethics approval

All animal capture and handling procedures and data collection were carried out under ethics approval from the La Trobe University Animal Ethics Committee (Project Number AEC15-67) and in accordance with relevant guidelines and regulations prescribed by the South Australian Department of Environment and Water (Research Permit Number U26453).

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. Thomas Prowse is an Associate Editor of *Wildlife Research*. Despite this relationship, he did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor of this journal. The authors have no further conflicts of interest to declare.

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