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Responses of Critically Endangered migratory Swift Parrots to variable winter drought

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Abstract. Migratory birds spend a large proportion of their lives within non-breeding habitats. However, knowledge of how they respond to variable winter resources is limited, especially for small migratory species. Citizen science programs provide an effective way to collect data on small migrants over large spatio-temporal scales. Here we present survey data for the Critically Endangered Swift Parrot (*Lathamus discolor*) that were collected by hundreds of volunteers over 7 years across the species' winter range. Swift Parrots were detected in 23% of the 4035 surveys. Linear mixed models were used to examine variation in Swift Parrot abundance and correlations with climate variables. During non-drought years Swift Parrots concentrated within Victorian habitats. However, when Victoria was in drought, the response of the birds depended on the extent of drought conditions throughout the winter range. Consecutive years of drought in Victoria resulted in the population migrating over 1000 km further to drought refuge habitat in New South Wales. This study provides a rare demonstration of the large spatio-temporal responses of a migratory bird population to extreme climate conditions across its winter range. It demonstrates both variable and repeated use of winter habitats, and highlights the need for conservation management at large spatio-temporal scales.

Additional keywords: citizen science, flowering phenology, *Lathamus discolor*, migration, spatio-temporal variation, Swift Parrot.

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Introduction

The extended and often spectacular return journeys of migratory species between their breeding and non-breeding grounds have long captured the human imagination. Our current understanding of such movements is largely based on the repeated journeys of large migrants that return to the same sites to breed each year in response to predictable environmental conditions (Newton 2008). However, there is growing recognition of the complexities of migratory movements (Terrill 1990; Dingle and Drake 2007; Newton 2012) and a significant knowledge gap remains in relation to small migratory species in spatio-temporally variable environments (Dingle 2008).

Studying small migrants that undertake facultative movements is inherently difficult. This is because their movements are highly variable, they often visit areas with low human population density, satellite tracking devices are too large, small tracking devices cannot be located remotely, and the chance of recovering birds in different locations each year is low (Newton 2008). For example, of the 12 927 Yellow-faced Honeyeaters (*Lichenostomus chrysops*) ringed during autumn migration in Australia over 14 years only four (0.03%) were ever recaught at the same site (Purchase 1985). Similarly, in New York, Common Redpolls (*Carduelis flammea*) have also proven elusive, with none of the 7946 birds ringed in their wintering area ever being recaught at the same site over 18 years (Yunick 1983).

The need for basic knowledge on variable migration strategies is most pressing for threatened species, such as the Swift Parrot (*Lathamus discolor*), a small, nectarivorous species that forages in the canopy of temperate forests and woodlands. Each year the entire population of less than 2000 birds migrates from breeding grounds in Tasmania, Australia, across Bass Strait and up to 2500 km north to winter across south-eastern mainland Australia (Saunders and Tzaros 2011). Although the National Recovery Program for this species has achieved many positive conservation outcomes (Saunders *et al*. 2007) recent research indicates that the population is predicted to decline so rapidly that the IUCN now recognises the species as Critically Endangered (Heinsohn *et al*. 2015; BirdLife International 2015). Although detailed foraging studies have been undertaken within particular regions of the species' winter range (Mac Nally and Horrocks 2000; Kennedy and Overs 2001; Kennedy and Tzaros 2005; Saunders and Heinsohn 2008), the species' variable geographic distribution throughout its winter range has not previously been demonstrated. This lack of information is largely due to their small body size (<80 g), cryptic nature, small population size and broad wintering area (~1 250 000 km^2), which makes them particularly challenging to study.

One technique for addressing such spatio-temporal challenges and providing insights into variable movements of migratory species is the implementation of citizen science projects. The use of citizen science for large-scale ecological research is gaining increasing recognition for its potential to aid the collection of data over large spatial and temporal scales that would not otherwise be possible (Silvertown 2009; Dickinson *et al*. 2010, 2012). Although it is important to consider both the benefits and challenges of using such data (Dickinson *et al*. 2010; Hochachka *et al*. 2012), and the most effective ways to account for the inherent data variability or bias (Bird *et al*. 2014; Isaac *et al*. 2014), citizen science projects have provided many novel insights into landscape ecology, climate change, invasive species and conservation biology (Silvertown 2009; Dickinson *et al*. 2012).

In this study we overcame some of the major challenges of studying variable habitat use by Swift Parrots by using 7 years of data collected by volunteers across the species' winter range, providing a rare demonstration of the dynamic responses of a small migratory species to extreme and variable environmental conditions. Such knowledge is essential for improving our understanding of the species' ecological requirements as well as improving our ability to implement effective conservation measures.

Materials and methods

Study area and survey design

The study area included temperate *Eucalyptus* and *Corymbia* woodlands and forests that provide winter habitat for Swift Parrots across south-eastern Australia between 25°1′S, 152°14′E and 37°6′S, 145°24′E (Fig. 1). As nectarivores, Swift Parrots are dependent on tree species that provide rich sources of carbohydrate, such as nectar from flowers or lerps (sugary secretions from psyllid insects on leaves) (Kennedy and Tzaros 2005; Saunders and Heinsohn 2008). These food resources occur scattered over vast areas and are highly variable in timing and abundance depending on each tree species' unique and variable flowering phenology (Law *et al*. 2000; Keatley and Hudson 2007).

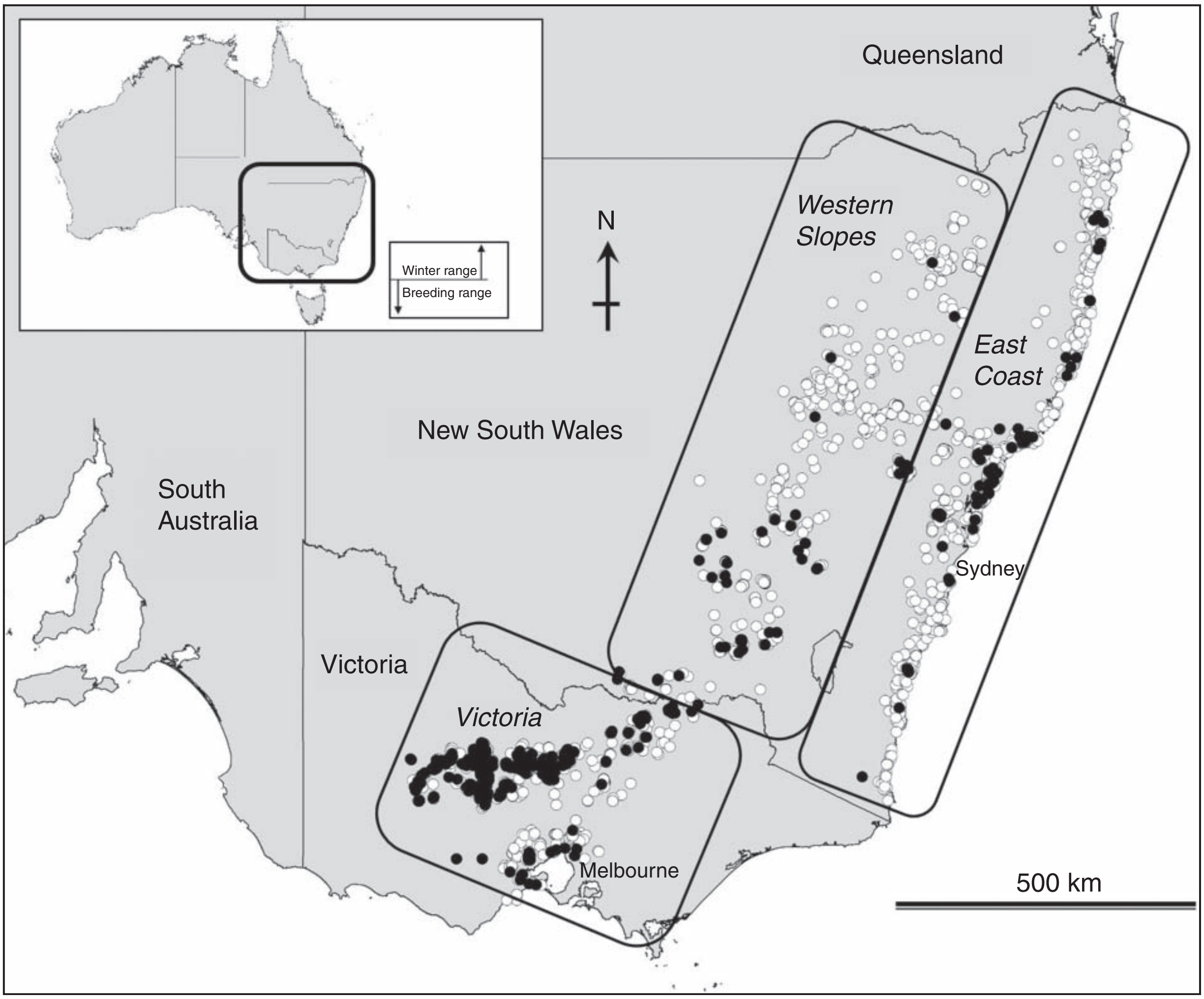

Fig. 1. Swift Parrot survey sites from 1998 to 2004 across key regions of south-eastern Australia. Regions include Victoria, and the Western Slopes and East Coast of New South Wales. Black circles represent surveys with Swift Parrots present and white circles represent nil surveys.

The citizen science data used in this study were collected as part of the National Swift Parrot Recovery Program from 1998 to 2004, whereby volunteers were coordinated to conduct surveys throughout the species' winter range each year for 7 years (Table 1). During this time up to 300 volunteers conducted targeted surveys twice a year, providing landscape-scale snapshots of Swift Parrot abundance and geographic distribution. Surveys occurred over one week in May and August each year to provide 'snapshots' of how the population was distributed.

Spatial and temporal variables

The study site was divided into three regions, Victoria (central Victoria from the south coast to the northern state boundary), East Coast (coastal areas east of the Great Dividing Range, New South Wales, NSW) and Western Slopes (western slopes of the Great Dividing Range, NSW) (Fig. 1). Surveys were also conducted in south-east Queensland, eastern South Australia, eastern Victoria and NSW Tablelands on the Great Dividing Range; however, the small number of surveys and very low detection rate (<5% of surveys) precluded these from being included in the analyses. Within each region 'locations' were defined by the boundaries of state forests, national parks, private properties and/or local features. Similar to the 'Area Search' technique used in the New Atlas of Australian Birds (Barrett *et al*. 2003), the survey 'sites' could be any shape and size as long as the survey was conducted within a specified time frame. Surveys were conducted using the national recovery program survey sheet (Birdlife Australia 2015) with both nil and positive surveys reported. For each survey the abundance and behaviour of Swift Parrots (flying through, perching, interacting with other species, feeding, etc) were recorded. Swift Parrots were considered present at the site only if they landed there.

To minimise false positive errors from misidentification, reported sightings of Swift Parrots were confirmed by the National Swift Parrot Recovery Program survey coordinator. We were unable to account for false negative errors. The concentration of surveys into two seasonal 'snapshots' meant that examination of arrival and departure dates was not possible.

Large-scale trends in Swift Parrot abundance were modelled using Linear Mixed Models with Poisson distribution and logarithmic link function. Explanatory variables included 'year' (1998–2004), 'region' (Victoria, East Coast and Western Slopes), and the interactions between these. 'Site' and 'location' were included in the models as random terms to avoid pseudoreplication from repeated surveys in the same place. All modelling was carried out using GENSTAT (GENSTAT Committee 2014). Best linear unbiased predictions (BLUPs) were then derived for each site in each year allowing development of spatial representations of abundance. Predictions were then mapped and smoothed using kernel density estimation in ARCview (ESRI 2005) to illustrate significant trends.

Table 1. Number of surveys within the wintering range of the Swift Parrot, 1998–2004

The annual number of surveys for each region and the percentage of surveys with Swift Parrots present each year are also shown

Year	Victoria region	East Coast region	Western Slopes region	Total no. of surveys	Percentage of surveys with Swift Parrots present
1998	275	91	109	475	35
1999	245	101	114	460	22
2000	242	130	162	534	24
2001	370	131	74	575	36
2002	234	333	95	662	17
2003	332	239	125	696	15
2004	248	258	127	633	20
Total	1946	1283	806	4035	23

Climate variables

Swift Parrot abundance was examined in relation to rainfall and temperature as these variables are associated with eucalypt flowering (Pook *et al*. 1997; Law Mackowski *et al*. 2000; Keatley *et al*. 2002) and hence food availability. Mean monthly rainfall ('rain') and maximum monthly temperature ('maxtemp') data for each site were extracted from spatially interpolated (modelled) climate surfaces developed in the ANUCLIM software package (McMahon *et al*. 1995; AGO 2002). These variables were extracted for the period six months before each survey since the preceding conditions at each site influence the phenological cycles of key feed tree species (Pook *et al*. 1997; Law *et al*. 2000; Keatley *et al*. 2002). The modelled climate surfaces are based on mean monthly climate data from 2500 Bureau of Meteorology weather stations across Australia and the national digital elevation model of AUSLIG (2000). All site coordinates and extracted climate data had a spatial resolution of ~1 km (AGO 2002). Regional rainfall conditions were classified into four categories in relation to the mean monthly rainfall (derived from 16 years of climate data from 1990 to 2005). These categories included 'wet' (more than 115% of mean rainfall), 'average' (90–115% of mean rainfall), 'dry' (65–90% of mean rainfall) and 'drought' (less than 65% of mean rainfall) conditions.

The effects of climate on Swift Parrot abundance were developed for each year, as well as all years combined, using Linear Mixed Models with Poisson distribution and logarithmic link function. Explanatory variables in the climate models included 'year', 'region', 'rain' and 'maxtemp'. Model terms were also added in varying order to confirm consistency of effects.

Results

Swift Parrots were detected in 23% of the 4035 surveys, with between 460 and 696 surveys conducted each year (Table 1). Swift Parrot abundance during individual surveys varied from 0 to 260 birds (mean 4.125 ± 0.23, standard error) with the mean abundance of Swift Parrots per survey in any region ranging from 0 to 10.8 birds (Fig. 2). In 2 years (2001 and 2002) the mean flock size (10.8 and 10.3 birds per survey respectively) was much greater than the mean flock size (5.7 birds per survey) over the whole study period (Fig. 2*a, b*). Swift Parrots repeatedly used habitats within each winter region, with large concentrations occurring within the Victorian and East Coast regions (Fig. 3).

Spatial and temporal winter distribution

Over the 7-year study period there was significant spatio-temporal variation in the distribution of Swift Parrots across their winter range (Table 2). Although Swift Parrots used

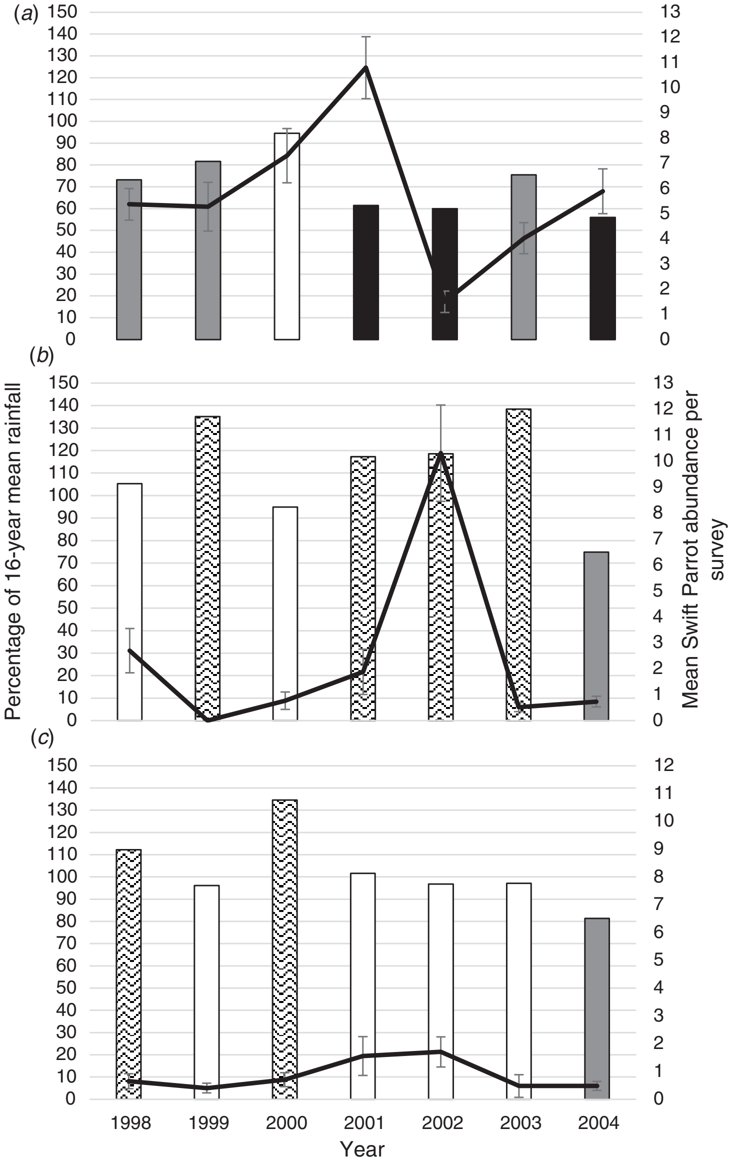

Fig. 2. Mean Swift Parrot abundance per survey (black line +/– standard error) and percentage of 16-year mean rainfall (black = drought, grey = dry, white = average, pattern = wet) for each winter region ((*a*) Victoria, (*b*) East Coast and (*c*) Western Slopes) from 1998 to 2004.

Victorian habitats each year (Fig. 2*a*), there were detectable annual shifts between different habitats within this region (Fig. 3). Small numbers of Swift Parrots also occurred within the Western Slopes region each year and the East Coast region supported Swift Parrots in 6 of the 7 years (Fig. 2). The most notable large-scale spatial variation occurred in 2002 when most of the population migrated over 1000 km further north-east than in other years (Fig. 3*f*). This large influx of Swift Parrots into coastal habitats of NSW corresponded with a large decrease in the number of Swift Parrots in Victorian regions (Fig. 2*a, b*). Within each region, the same locations were used repeatedly by Swift Parrots over the study period, as indicated by a high within-term correlation for the random term 'location' in the model, $r = 0.86$, albeit on an irregular basis.

Winter climate conditions

Initially all years were combined in a single model to examine the overall effects of climatic variables on Swift Parrot abundance. All terms ('year', 'region', 'rain' and 'maxtemp') contributed significantly to the model, either as individual terms and/or when interacting with other terms (Table 3). Given the significant interactions between the fixed terms and the high interannual variability, additional models were also developed separately for each year. In these annual models, none of the interactions between terms contributed significantly to the model and therefore only the individual fixed terms are presented (Table 3).

Regional drought conditions were experienced in 3 (2001, 2002 and 2004) of the 7 years; however, the response of the

Table 2. Geographic distribution models: terms and interactions for Swift Parrot abundance in relation to regions and years (1998–2004)
d.f., degrees of freedom

Abundance	Wald statistic (d.f.)	*P*
Year	64.63 (6)	<0.001
Region	31.71 (2)	<0.001
Year × Region	105.25 (12)	<0.001

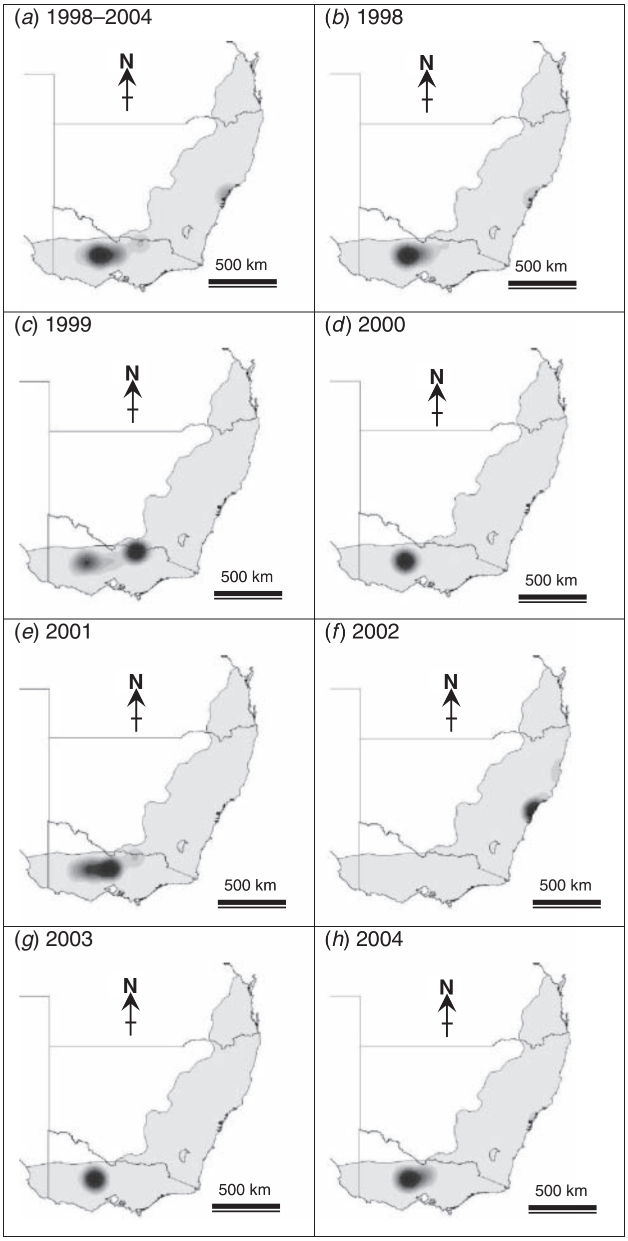

Fig. 3. Spatial and temporal variability of Swift Parrot abundance. Shading represents the predicted likelihood of Swift Parrot abundance (ranging from 0 to 9.7 birds) per survey on a continuous scale ranging from low (light shading) to high (dark shading) abundance. Scales are approximate. Due to the potential for false negative data, predicted abundance values of zero were included as low abundance.

Table 3. Effect of major climatic variables and region on Swift Parrot abundance in the climate models (1998–2004)
d.f., degrees of freedom

Year	Fixed term	Wald statistic	d.f.	*P*
All years (1998–2004)	Year	66.86	6	<0.001
	Region	34.18	2	<0.001
	Rainfall	1.48	1	0.223
	MaxTemp	6.70	1	0.010
	Year × Region	103.35	12	<0.001
	Year × Rainfall	64.20	6	<0.001
	Regions × Rainfall	6.92	2	0.031
	Year × MaxTemp	21.56	6	0.001
	Regions × MaxTemp	6.12	2	0.047
	Rainfall × MaxTemp	2.21	1	0.137
1998	Region	14.80	2	<0.001
	Rainfall	6.14	1	0.013
	MaxTemp	2.21	1	0.137
1999	Region	10.26	2	0.006
	Rainfall	0.01	1	0.925
	MaxTemp	0.41	1	0.520
2000	Region	20.80	2	<0.001
	Rainfall	0.81	1	0.369
	MaxTemp	0.23	1	0.631
2001	Region	22.37	2	<0.001
	Rainfall	0.39	1	0.532
	MaxTemp	1.08	1	0.299
2002	Region	5.02	2	0.081
	Rainfall	9.04	1	0.003
	MaxTemp	3.12	1	0.078
2003	Region	28.00	2	<0.001
	Rainfall	0.73	1	0.394
	MaxTemp	0.00	1	0.994
2004	Region	25.62	2	<0.001
	Rainfall	1.52	1	0.218
	MaxTemp	2.97	1	0.085

birds varied markedly between years (Fig. 2). In 2001, region had a strong significant effect on Swift Parrot abundance (Table 3), whereby Swift Parrots concentrated within Victoria during drought conditions, even though there were average to wet conditions elsewhere (Fig. 2*a*).

Alternatively, in 2002 when drought conditions in Victoria had prevailed for 2 consecutive years, rainfall had a significant positive effect on Swift Parrot abundance (Table 3). During this year, prolonged drought conditions in Victoria coincided with wet conditions on the East Coast where large concentrations of Swift Parrots occurred (Fig. 2*a*, *b*). Although wet conditions occurred in the East Coast region in 4 of the 7 years, a large influx of Swift Parrots into this region occurred only following 2 consecutive years of drought conditions in Victoria (Fig. 2*a*, *b*).

In 2004, region again had a strong significant effect (Table 3), with Swift Parrots predominantly concentrating in Victorian habitats when dry to drought conditions were prevalent throughout their winter range (Fig. 2).

In the remaining 4 years (1998, 1999, 2000 and 2003), region was the only variable with a significant effect on Swift Parrot abundance (Table 3). Although Victoria experienced dry conditions during three of these 4 years, the birds continued to concentrate in this region, with smaller numbers of birds using the other regions, which experienced average to wet rainfall conditions each year (Fig. 2). Interestingly, over the study period Victoria experienced drier than average conditions in most years, the East Coast experienced wetter than average conditions in most years and the Western Slopes rainfall was consistent with the long-term average (Fig. 2).

Discussion

This study provides a rare demonstration of large-scale spatio-temporal responses of a small migratory bird population to variable climatic conditions throughout their winter range. Our results demonstrate interannual variation in winter distribution, large-scale drought-related movements, as well as repeated use of sites over 7 years.

Spatio-temporal variation in winter distribution

This study is the first to compare the spatial distribution of a population of small migratory birds through a series of wet and dry years across their winter range. The annual shifts between different combinations of Victorian habitats each year are likely to reflect the unique and variable flowering phenology of each key tree species used for food (Law *et al*. 2000; Keatley and Hudson 2007). For example, in Victoria food tree species such as red ironbark (*Eucalyptus tricarpa*), fail to flower once every 12.5 years at some sites but almost twice as often (every 6.4 years) at other sites (Keatley and Hudson 2007). Similarly, in the East Coast region flowering periodicity and intensity are highly variable between tree species and sites, ranging from annual to no flowering over a 10-year period (Law *et al*. 2000). Complex interactions between habitat quality and the quantity of nectar produced each year is also an important factor that may influence migratory movements because Swift Parrots have been found to prefer high-quality mature woodland rather than regrowth (Kennedy and Overs 2001; Kennedy and Tzaros 2005). This is likely to be due to mature woodland flowering more reliably (Wilson and Bennett 1999) and producing more than twice as much sugar per hectare as regrowth forest and 10 times as much sugar per hectare as recently logged forest (Law and Chidel 2008). However, even when a tree species flowers reliably, the nectar volumes and sugar concentrations within the flowers may vary significantly depending on local environmental conditions (Law and Chidel 2008).

Therefore Swift Parrots must use a migration strategy that permits them to winter in different combinations of habitats each year. This includes the ability of the population to use different combinations of habitat types across Victoria in response to variable resource availability in most years, as well as undertake major spatial shifts north-east to coastal NSW when prolonged, adverse conditions occur within key wintering habitats. Such strategies may reflect a combination of basic migration decision rules where birds undertake obligate (endogenous) migration to their wintering habitats, then facultative (exogenous) migration to other sites if conditions are found to be unfavourable (Terrill 1990). This may be a similar strategy to that used by coexisting Regent Honeyeaters (*Anthochaera phrygia*), whereby they have a specific directional orientation in spring followed by a period of no specific directional orientation in winter (Cooke and Munro 2000). However, this strategy appears to differ from that of Yellow-faced Honeyeaters, another small migratory species that coexists with Swift Parrots, given that they appear to have two specific orientation phases during the non-breeding season, which are likely to be endogenously controlled (Munro *et al*. 1993). There is increasing recognition of the diversity of migratory species that respond to such variable and extreme environmental conditions (Newton 2012) and the strategies they use, including the use of variable migratory routes, stopover sites, multiple wintering sites (McKinnon *et al*. 2013) and individual prospecting or ranging behaviour (Roshier *et al*. 2008). For example, the annual migration of individual white storks between Europe and Africa over 10 years demonstrated variable interannual migration strategies (Berthold *et al*. 2002). The Red-billed Quelea (*Quelea quelea*) in Africa (Ward 1971; Cheke and Tratalos 2007; Cheke *et al*. 2007; Oschadleus and Underhill 2008) and the Bobolink (*Dolichonyx oryzivorus*) in South America (Renfrew *et al*. 2013) have also been shown to undertake spatio-temporally dynamic movements in direct response to rainfall and primary productivity patterns.

Repeated use of habitat

Although Swift Parrots often move in spatio-temporally dynamic ways, they are also often found at the same sites between years. Repeated use of the same sites may lead to improved knowledge of spatial and temporal resource availability in particular areas, and an enhanced capacity to avoid predation (Hancock and Milner-Gulland 2006). In this study, the importance of repeated use of sites is highlighted, albeit at more variable temporal scales than the annual cycles found for many Palaearctic and Nearctic migrants (e.g. Ketterson and Nolan 1990; Hestbeck *et al*. 1991; Belda *et al*. 2007). However, the North America Black Brant (*Branta bernicla nigricans*) provides an example of a migrant that also displays a high level of site fidelity at wintering sites between years, but then undertakes additional variable movements to different sites throughout the winter (Lindberg *et al*. 2007).

Variable cycles make it more difficult to detect repeated use of sites in the short term, which is of concern when such information is used as a basis for conservation of threatened migratory species. For example, when studies are not conducted over sufficiently long periods for the target species, there is a risk that repeated use of sites may not be detected (e.g. Mac Nally and Horrocks 2000; Berthold *et al*. 2004), potentially underestimating the importance of some habitats for conservation. Therefore, this study highlights the conservation challenges for highly mobile species and the importance of identifying, prioritising and protecting habitats throughout their range (Martin *et al*. 2007).

Responses to drought

Our study also provides a rare demonstration of the responses of a small migratory bird population to variable drought conditions, and the importance of drought refuge habitat. Climatic variability and periods of drought are an inherent part of the Australian environment (Nicholls 1991; Hunt 2009; Ummenhofer *et al*. 2011) and have influenced the spatial and temporal distribution of food sources (Nix 1976) as well as the number and behaviour of migratory birds (Chan 2001; Griffioen and Clarke 2002; Dingle 2004). Despite the important role winter drought conditions play in population limitation for migratory species

(Winstanley *et al*. 1974; Newton 2004) a significant knowledge gap remains in relation to winter distribution patterns, habitat use and foraging ecology (Vickery *et al*. 2014). That is, studies have tended to focus on subsequent population declines and carry-over effects on reproductive success within breeding areas (e.g. Norris *et al*. 2004; García-Pérez *et al*. 2014; Ockendon *et al*. 2014) and altered timing of return migration to stopover sites and breeding grounds (e.g. Saino *et al*. 2007; Rockwell *et al*. 2012). There have been only limited studies within winter habitats that have examined the responses of migratory species to drought conditions (e.g. Sherry and Holmes 1996; Latta and Faaborg 2002; Saunders and Heinsohn 2008) and these primarily examine the responses at a limited number of sites rather than across the winter range of a migratory species (e.g. Jaksic and Lazo 1999; Herremans 2004; Cueto *et al*. 2008).

However, the current study included some of the most extreme drought years on record in Australia (Nicholls 2004), providing an excellent opportunity to examine responses of migratory birds to extreme climate conditions. Although there were 3 years of drought in Victoria, the response of the Swift Parrot population varied depending on spatial and temporal extent of climate conditions throughout their winter range, and the carry-over effect of climate conditions from the preceding year.

That is, in years when drought conditions occurred in Victoria but the preceding year was relatively wet, Swift Parrots continued to concentrate in Victorian habitats, possibly due to the long phenological cycles of key feed tree species and the consequential carry-over effects between years. For example, *Eucalyptus* species, which are a major source of nectar throughout the Swift Parrot range, develop flower buds up to 21 months before flowering (Porter 1978; Law and Chidel 2008). Although both rainfall and temperature have been demonstrated to influence budding and flowering of *Eucalyptus* species (e.g. Law *et al.* 2000; Hudson and Keatley 2013) for flowering to commence, buds must reach a particular maturity (Hudson and Keatley 2013) then and a complex set of cyclical climate conditions need to occur over subsequent months (Hudson *et al*. 2011). As a result, the quality and quantity of nectar produced varies between different species, conditions and years (Law *et al*. 2000; Law and Chidel 2008). Interestingly, Pook *et al*. (1997) suggest that some tree species attain greatest nectar production during winter drought conditions. That is, as long as there are preceding conditions that promote budding, trees may allocate available starch resources to flowering rather than to growth during drought conditions (Pook *et al*. 1997).

However, conditions of extreme or prolonged drought can also lead to abortion of buds and less flower and nectar production (Pook *et al*. 1997; Law *et al*. 2000). In this study, during the second consecutive year of drought in Victoria, a large proportion of the Swift Parrot population migrated substantially longer distances in search of food resources. That is, they concentrated in small, fragmented patches of habitat within suburban areas of coastal NSW (Saunders and Heinsohn 2008), ~1000 km further north-east of their most commonly used sites in Victoria. During these 2 drought years Swift Parrots also occurred in more concentrated flocks than in other years, including mass roosting congregations (Saunders and Heinsohn 2008). Such social groups usually form when the benefits of association exceed the competitive and health costs of existing close to other individuals (Krause and Ruxton 2002), and is likely to be highly beneficial when drought conditions are severe but unevenly distributed across the landscape (Németh and Moore 2014; Silk *et al*. 2014). Potential benefits of such concentrations include improved social information about resource acquisition while reducing risks and uncertainties during migration (Hancock and Milner-Gulland 2006; Németh and Moore 2014). Such concentrations have previously been demonstrated for migratory species in both the Palaearctic (e.g. Berthold *et al*. 2002; Markovets and Yosef 2005; Belda *et al*. 2007) and Nearctic migratory systems (e.g. Hestbeck *et al*. 1991; Warkentin and Hernandez 1996).

By using a combination of both social information and direct experience of local environmental conditions, migrants can rapidly attenuate or intensify individual behavioural responses at a time when personal energetic demands are large (Cornelius *et al*. 2010). Interestingly, specific apparent drought refuges used by a large portion of the Swift Parrot population (up to 400 birds or 16% of the population) during drought conditions had previously been used by only a small number of birds (less than 10 parrots) during non-drought years. It is possible that their knowledge provided the basis for population-wide responses to variable environmental conditions across the broad landscape. However, if the combined knowledge of individuals in the population plays an important role in the population's capacity to respond to variable conditions, it is concerning that as this Critically Endangered population continues to decline the population's capacity to respond to such situations is likely to be reduced.

Furthermore, although most of the population was able to migrate further and locate coastal drought refuge habitat, they were likely to have to contend with additional stressors. These include the extra physiological demands of having to migrate substantially longer distances, increased mortality from collisions with surrounding built suburban structures (Pfennigwerth 2008; Saunders and Tzaros 2011) and increased competition and aggression for limited resources from a variety of other nectarivorous and aggressive suburban species (Grey *et al*. 1998; Saunders and Heinsohn 2008; Bennett *et al*. 2014*a*). At least some of these potential stressors may result in poorer body condition and hence reduced fitness for return migration and subsequent breeding. However, the movement capacity of Swift Parrots, as demonstrated here, indicates that this species may be better placed to deal with drought than many resident species currently considered more secure. For example, the response of resident woodland birds to the same drought conditions within the same Victorian habitats indicates significant population declines given their inability to move vast distances and the amplification of the effects of land-use change and interspecific interactions (Mac Nally *et al*. 2009; Bennett *et al.* 2014*b*, 2015).

Conclusion

This study provides critical insights into the dynamic responses of a small migratory bird species across its winter range to extreme and variable environmental conditions. It is also of particular importance given that the Swift Parrot population has continued to decline significantly since the surveys were conducted over 10 years ago and the species is now considered Critically Endangered (Heinsohn *et al*. 2015). It highlights the importance of drought refuge habitat to avoid resource bottlenecks, and maintaining a network of habitats within and between different regions throughout the winter range to ensure there are sufficient resources available each year. The combination of repeated as well as variable use of habitats over time, and the potential importance of social information on population movements, provides an important contribution to the growing knowledge of synergies between migratory systems around the world.

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