

Scarlet Honeyeater *Myzomela sanguinolenta*: An example of opportunistic irruption and nomadism heralding climate-facilitated range expansion?

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Abstract. Shifts in the traditional range of bird species are being reported globally, and often are associated with changing climate. Much conservation focus is on species that have undergone range contractions, but range expansions also can have important implications for future scenarios. Using comprehensive databases of species records, many generated through citizen science, shifts in the spatial and temporal distribution of an Australian honeyeater, the Scarlet Honeyeater *Myzomela sanguinolenta*, are investigated at the southern boundary of its range in south-eastern Australia. Historically, this boundary of the species' range was restricted to far eastern Victoria, with sporadic irruptions and vagrant records recorded infrequently further west. This study shows a recent significant increase in the spatial and temporal distribution of this species beyond its traditional range, expanding into central and western Victoria. Trends in records through time in the expansion zone display a clear shift, from vagrant and irruptive movements, to now show a pattern of regular, migratory movement behaviour. It was determined that within the expansion zone the Scarlet Honeyeater is now best considered a partial migrant. This range shift shares similarities with broader patterns of species' range shifts in response to changing climate, warranting further investigation of the climatic niche of this and other species to understand potential changes in distribution into the future.

Introduction

Geographic range boundaries of species are broadly driven by combinations of abiotic (e.g. climate), biotic (e.g. competition, species interactions and food availability) and dispersal factors (Sexton *et al.* 2009). Flying organisms, such as birds, can move extensively within the species' geographic range, and over time boundaries may be fluid and range shifts may occur. Range shifts can include range contraction (Yang *et al.* 2020; Reverter *et al.* 2023) or range expansion (Pigot *et al.* 2010; Zhang *et al.* 2023). From a species-conservation perspective, causal factors underpinning contraction in the geographic range have formed much threatened species research (Pacifi *et al.* 2020; Yang *et al.* 2020; Garnett *et al.* 2024). Alternatively, a focus on range expansion can signal changes in habitat suitability, species' behaviour or altered species' interactions, and have been explored to predict future scenarios (Capainolo *et al.* 2021; Zurell *et al.* 2024).

Geographic range expansion associated with recent changes in climate is a rich area of study (Virkkala *et al.* 2014; Massimino *et al.* 2015; Zhang *et al.* 2023), and changing species' distributions globally are likely to be in response to climate change (Guo *et al.* 2018; Rubenstein *et al.* 2023). Studies have documented bird species undergoing range shifts in response to changing climate and weather patterns (e.g. Reid 2002; Beaumont *et al.* 2006; Hällfors *et al.* 2023; Noske 2024). Interest in this field of research has benefited from the increased uptake of citizen-science activities which have contributed to exponential increases in species records over the last two decades (Mesaglio & Callaghan 2021), making exploration of such potential range shifts much more achievable and robust (van Strien *et al.* 2013; Johnston *et al.* 2020).

Changes in species range can be considered using a framework of species-movement behaviour to specify shifts or trends in spatial and temporal properties through

time. Four basic types of movement behaviour are: no movement (i.e. sedentary), one-directional movement (i.e. dispersive), regular movement between two or more sites (i.e. migration), and irregular movement between several sites (i.e. nomadism). Gilmore *et al.* (2007) considered that all movement behaviour can be described within a four-level hierarchy: movement behaviour, time, distance travelled, reason for movement. Such a hierarchy has proven useful in describing the nature of a species' movement behaviour within its range, and the following categories have been widely used to classify birds: resident, migratory, nomadic, irruptive, and vagrant (Ford 1989; Gilmore *et al.* 2007). Migratory behaviour can promote geographic range size, and can be critically important in allowing species to escape limiting conditions at their breeding location (Laube *et al.* 2013; Pigot & Tobias 2015).

The movement behaviour and patterns of species undertaking migration, or other long-distance movements, have been investigated as a corollary of determining the effects of changing climate and weather events on species. There is evidence of climate-induced poleward shifts, whereby movements and species' ranges are extending towards the poles (i.e. increasing latitude) in both the Northern (Lehikoinen & Virkkala 2016; Widick *et al.* 2023) and Southern (Quillfeldt *et al.* 2010) Hemispheres, including several Australian examples (Chambers *et al.* 2005; Beaumont *et al.* 2006; Noske 2024).

The Australian honeyeaters (Family Meliphagidae) are a prominent group of birds known to display diverse movements and patterns of residency that are often shaped by climate (Keast 1968). The Scarlet Honeyeater (also known as Scarlet Myzomela) *Myzomela sanguinolenta* is a small nectarivorous honeyeater, with its core range generally associated with subtropical and tropical eastern Australia (Higgins *et al.* 2001; Barrett *et al.*

2003) and its maximum reporting rate recorded at 26°S, 153°E (Sunshine Coast area, Queensland). At the species level, it has variously been considered resident (Keast 1968), migratory or partly migratory (Blakers *et al.* 1984; Storr 1984; Griffioen & Clarke 2002), nomadic (Morris 1975; Blaber 1995) and irruptive (Wheeler 1967). Chan (2001) classified Scarlet Honeyeaters as partial migrants, a group that showed mixes of sedentary, migrant and partial migrant tendencies in different parts of their range. Analysis of continental-scale records showed that at least part of the Scarlet Honeyeater population undertakes regular north–south migration along the eastern coast of Australia (Griffioen & Clarke 2002). At the southern limits of its distribution in Victoria, this species has generally been considered vagrant west of 147°E (Higgins *et al.* 2020). Blakers *et al.* (1984) considered it an irregular visitor west of 149°E, with no records beyond ~145°E in Victoria. Emison *et al.* (1987) described it as a summer migrant to the eastern part of the state, with vagrants occasionally recorded in north-eastern Victoria and outer eastern Melbourne. Further, a subsequent and comprehensive continent-wide survey of birds between 1998 and 2002 (Barrett *et al.* 2003) showed only one incidental record of the species west of 147°E in south-eastern Australia. Based on spatial coverage of surveys within its expected range and reporting rates within major Australian citizen-science platforms, the Scarlet Honeyeater was classified as well known and well surveyed (Backstrom *et al.* 2024).

Historic irruptions of the Scarlet Honeyeater have been recorded beyond the traditional range, including in the southern part of its distribution. Wheeler (1967) noted historic irruptions in Victoria at Lorne (~38.535071°S, 143.973567°E) in 1902 and earlier at Alexandra (~37.191261°S, 145.709394°E) in 1876. In 1985, Scarlet Honeyeaters were observed at Port Fairy (~38.387448°S, 142.226485°E) and Lower Gellibrand (~38.724520°S, 143.248625°E) along the Shipwreck Coast during a widespread irruption event in south-western Victoria (Robinson 1985). Irruptions have also occasionally been recorded within the species' traditional range, including during widespread drought conditions (e.g. Sydney, NSW, in Federation Drought, 1902; Sydney–Hawkesbury district, in 1982–1983 drought; Higgins *et al.* 2001).

The Scarlet Honeyeater has noticeably increased in numbers across central Victoria recently, regularly being reported in areas where it has not been known to occur historically (Palmer 2019; Tzaros 2021; Palmer & Farquhar 2024). Using records from comprehensive databases, the present study investigates the historic and contemporary distribution of records, examining shifts in their spatial and temporal features. This approach allows current assessment of the species' movement behaviour and provides an evidence-based method to determine any change in its residency status and geographic range. Presented is a case study of altered movement behaviour and range shift foreshadowing an expansion of a species' range in southern Australia.

Methods

Databases containing Scarlet Honeyeater records were used to explore spatial and temporal features of the species' distribution. These included Atlas of Living

Australia (ALA; ala.org.au, accessed 24 November 2023), eBird (Cornell Lab of Ornithology; ebird.org, accessed 20 November 2023) and Birddata (BirdLife Australia; birddata.birdlife.org.au, accessed 11 December 2023). Records up to the end of 2022 were used in the analysis.

The area of interest was confined to south of 36°S, near the southern limit of the species' recognised traditional range (see Figure 1). The term 'traditional range' is used to describe the species' recognised distribution (*viz* historically accepted range) based on key historic and contemporary sources that explicitly considered the distribution of Australian birds, including the Scarlet Honeyeater (Wheeler 1967; Blakers *et al.* 1984; Emison *et al.* 1987; Higgins *et al.* 2001; Barrett *et al.* 2003). At the southern boundary of its traditional range in far eastern Victoria, range depictions have generally aligned with the East Gippsland Lowlands bioregion and adjoining East Gippsland Uplands bioregion. These were used for spatial delineation of the species' traditional range in Victoria in further GIS analysis (QGIS, version 3.16), with inclusion of the small, embedded areas of Highlands–Far East and Monaro Tablelands bioregions. The area within Victoria outside this traditional range and south of 36°S was considered the southern expansion zone (termed expansion zone herein) for further analysis.

Consistency in the submission of species records in Australia and their locational accuracy has greatly increased in recent decades, becoming more consistent from the period of the Royal Australasian Ornithologists Union's first atlas (1977–1981; Blakers *et al.* 1984). Therefore, scrutiny of spatial and temporal patterns has been limited to records from 1976 onwards. Other time periods have been applied in some analyses. For example, a delineation between years pre-2000 and post-2000 was applied, as the year 2000 aligned with the initiation of the new bird atlas (Barrett *et al.* 2003) and, from this time onwards, there have been >1000 locational records of the species each year (pre-2000, mean of 579 records annually *c.f.* mean 4767 records annually post-2000).

A classification of movement behaviour, adapted from Gilmore *et al.* (2007), was used in the contemporary assessment of the Scarlet Honeyeater's status in south-eastern Australia. Table 1 describes the criteria used in the present classification.

Evidence of range shifts and any altered movement behaviour was sought by analysing patterns in the spatial and temporal distribution of records through time. Spatial spread was measured using a grid of 0.5° × 0.5° cells of latitude and longitude overlying the expansion zone. The number of cells with Scarlet Honeyeater records was the response variable and the strength of evidence was calculated using Mann–Kendall's *tau* correlation for time series data (Kendall package: McLeod 2022) in R Studio (version 4.3.2; RStudio Team 2019). The temporal span of Scarlet Honeyeater occupancy within the annual cycle was measured by determining the number of dates each year that the species was recorded in the expansion zone. The number of dates that Scarlet Honeyeaters were recorded was the response variable and the strength of evidence was again calculated using Mann–Kendall's *tau* correlation for time series data in R Studio. Other temporal features examined were distribution of records within a year, with comparisons across traditional range and expansion zone, and between historic and more recent time periods (pre-

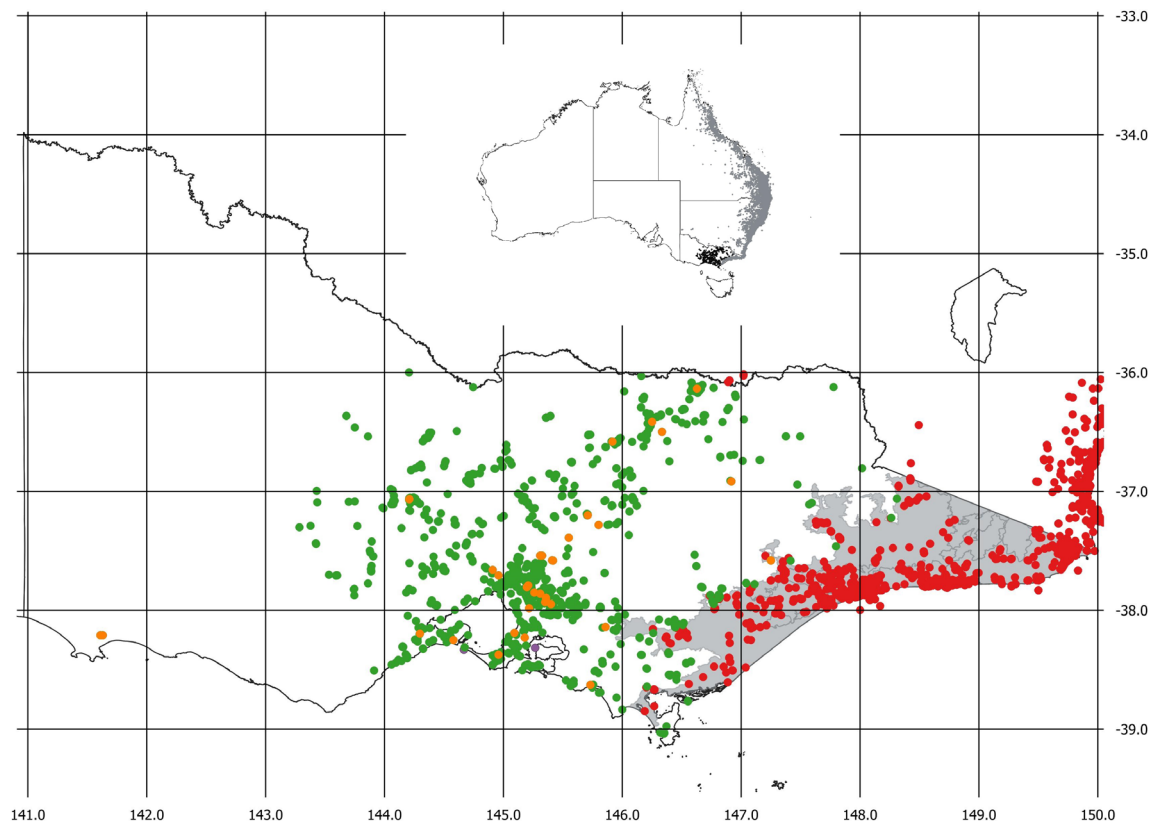


Figure 1. Scarlet Honeyeater distribution in Australia (inset) and in the southern extent of its range south of 36°S (main map). For Australia-wide distribution (inset), black dots represent records in the expansion zone; all other records in grey. In Victoria (main map), red dots show records in the species’ traditional range (represented by the grey-shaded area) for all years. Orange (pre-2000 records) and green (post-2000 records) dots show records in the expansion zone.

2000 vs post-2000) to determine any altered patterns in movement behaviour.

To explore potential triggers for any Scarlet Honeyeater range shift, annual rainfall within the expansion zone (annual total rainfall for Victoria, from Bureau of Meteorology climate data), and from the core part of the species’ Australian range (annual total rainfall for Sunshine Coast, Queensland, from Bureau of Meteorology climate data) were correlated with total number of records and number of days recorded in the expansion zone.

Results

There is strong evidence that the Scarlet Honeyeater has extended its range beyond the south-western boundary of its traditional range in Victoria over the past two decades, and now regularly occupies an area west of 146°E to ~143°E, hereafter termed the expansion zone (Figure 1). There have been additional isolated records further west, including the westernmost outlier at Port Augusta, South Australia (137°E), and in south-western Victoria, including Cobboboonee National Park and Hamilton (141°E).

Table 1. Species population status defined by movement behaviour criteria.

<i>Movement status</i>	<i>Movement</i>	<i>Time</i>	<i>Distance</i>	<i>Evidence expected</i>
Resident	Sedentary, no movement	Present always	Very short distance	Regular records, all times, across range
Migratory	Consistent to and from movement	Regular, within year	Long distance	Regular, consistent records, separate breeding and non-breeding areas in range
Nomadic	Less predictable, frequent movement between multiple sites	Semi-regular, within year	Local to long distance	Semi-regular records, lack of large time gaps, short return times, within range
Irruptive	Irregular, high numbers, tracking highly productive sites	Greater than 1 year	Long distance	Irregular records, large numbers of individuals involved, medium–large time gaps, sometimes outside range
Vagrant	Accidental	Greater than 1 year	Long distance	Inconsistent occurrence, very few individuals, outside range, large time gaps

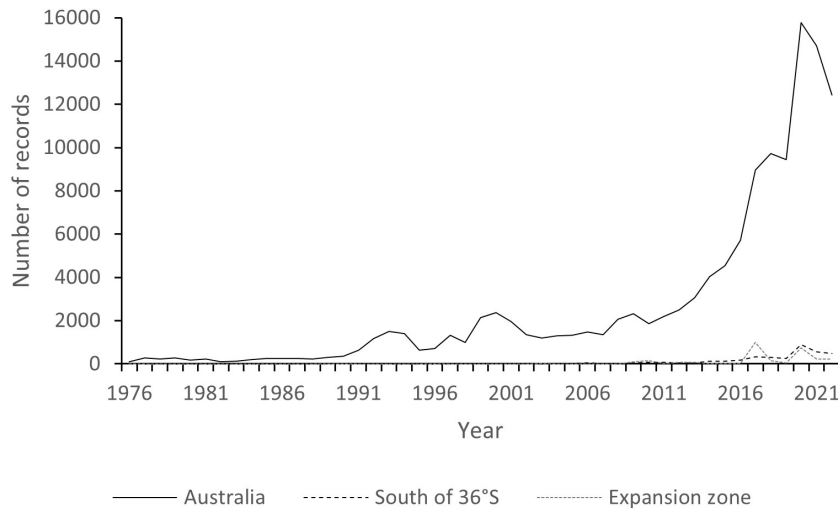


Figure 2. Number of Scarlet Honeyeater records within Atlas of Living Australia since 1976. Records are shown for three areas of interest: (a) Australia-wide, (b) at the southern extent of the species' range (south of 36°S not including expansion zone), and (c) expansion zone.

Across the Scarlet Honeyeater's Australian distribution, the number of records has increased since 1976, displaying an exponential increase over the previous two decades (Figure 2). In the First Atlas (1977–1981), there were just 2217 records for Australia, and just 32 in Victoria. In comparison, for 2022 alone, the ALA database (ala.org.au; accessed 1 August 2024) contained 12,440 records of the Scarlet Honeyeater from Australia (9.4% of all-time records), with 510 records from Victoria.

Within the expansion zone, historic records (pre-2000) were very sparse (Figure 2). For example, before 1980 there was a total of 22 records and in 1980–2000 just 19 records. Since 2000, the regularity of records ($n = 2888$) in the southern part of the species' range has increased. In all years post-2008, there are records (increasing to hundreds each year since 2017) in the expansion zone. Before 2008, few records (maximum 11 records) occurred in this zone in any annual cycle, with records in only some years.

There is very strong evidence of an increasing spread of the Scarlet Honeyeater in the expansion zone, represented by the number of $0.5^\circ \times 0.5^\circ$ cells occupied within a year, which displays an increasing trend through time (Figure 3a); (Kendall's $\tau = 0.639$, $df = 22$, $P < 0.001$). This

is evidence that the Honeyeaters are regularly occupying more areas and achieving more saturated coverage of the expansion zone.

There is also very strong evidence of increasing occupation of the expansion zone through time, represented by the number of days that Scarlet Honeyeaters were recorded in the zone within an annual cycle, which displays an increasing trend through time (Figure 3b) (Kendall's $\tau = 0.633$, $df = 22$, $P < 0.001$).

Across the annual cycle, Scarlet Honeyeaters have been recorded in all months, with ~80% of records in October–January (Figure 4). Historically, there was strong evidence indicating regular local movements or migration into the Victorian part of the traditional range predominantly during spring–summer (Emison *et al.* 1987). In recent years in the expansion zone, most records have also been during spring–summer but records from 2008 onwards show a shifting trend towards increasing length of time in this zone (Figure 5), alongside the increasing geographical spread of records already shown. The emerging trend is highlighted by the period 2021 to the present (November 2024), where Scarlet Honeyeaters have continuously been recorded in all months in the expansion zone (Figure 5).

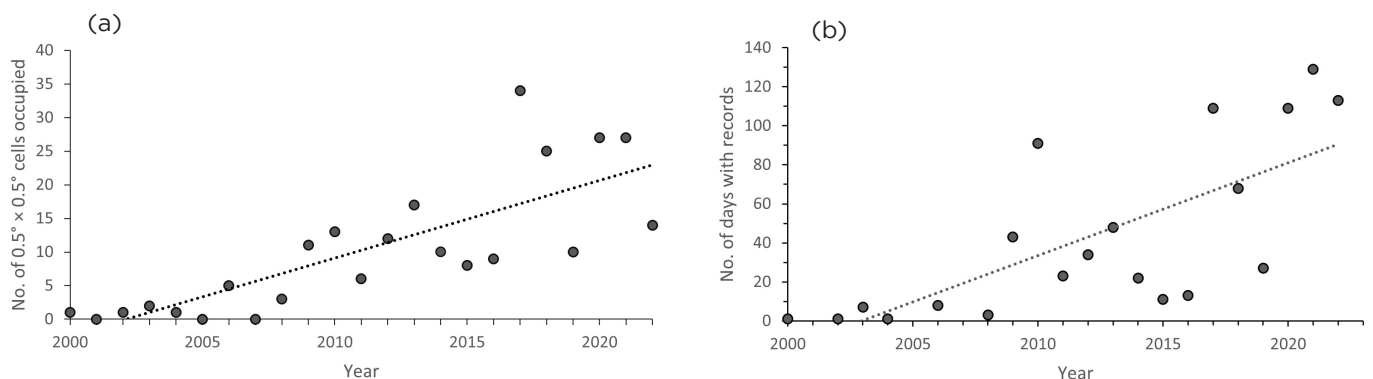


Figure 3. Evidence of spatial and temporal spread of the Scarlet Honeyeater in the expansion zone: (a) number of $0.5^\circ \times 0.5^\circ$ cells occupied, and (b) number of days in each year since 2000 that the Scarlet Honeyeater has been recorded.

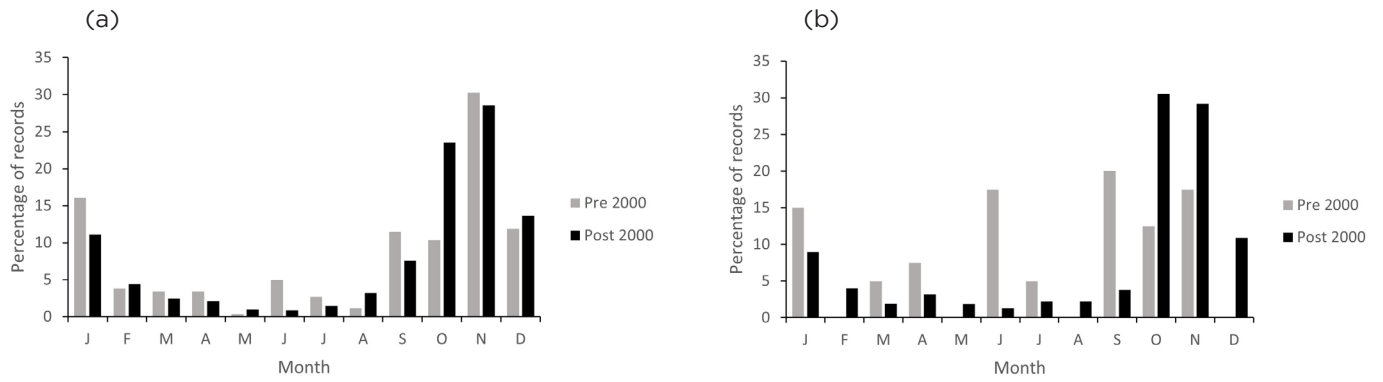


Figure 4. Distribution of records of Scarlet Honeyeaters across months in south-eastern Australia: (a) south of 36°S, and (b) in the expansion zone.

Year	Month											
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
2009												
2010												
2011												
2012												
2013												
2014												
2015												
2016												
2017												
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2022												
2023												

Figure 5. Months with records of the Scarlet Honeyeater (shaded grey) in the expansion zone during the period of continuous yearly records since 2009.

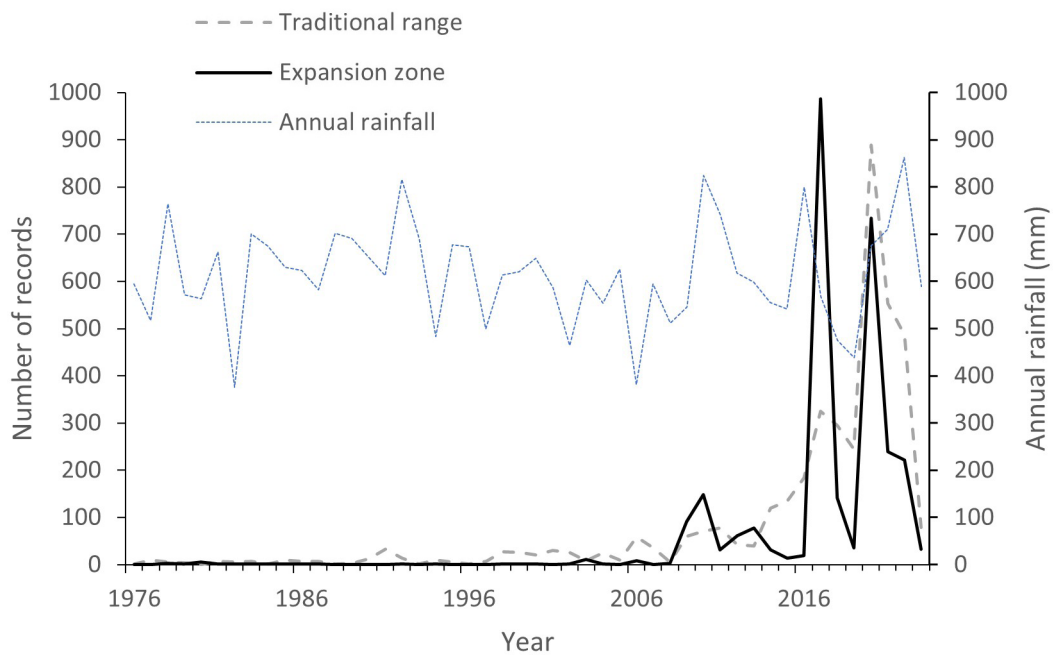


Figure 6. Number of Scarlet Honeyeater records in Australia south of 36°S between 1976 and 2023. Numbers of records in traditional range and expansion zone are shown separately. Annual rainfall for Victoria is shown for the same period.

In the region considered the southern boundary of the species' traditional range, there was no obvious difference in the distribution of the percentage of records across months between the pre- and post-2000 periods (Figure 4a), which showed a pattern expected for a migratory (or partially migratory) species, with a regular seasonal change in occurrence. However, in the expansion zone pre-2000, records were inconsistent and irregular in the annual cycle (Figure 4b), aligning with criteria for irruptive or vagrant movement behaviour. Post-2000, there is a clearer seasonal pattern in records, with most records (~80%) in October–January (Figure 4b), indicating a more regular, repeated pattern of movement, more closely aligning with criteria expected for migratory movement behaviour.

Although the number of records shows a strong seasonal bias, with most records during spring–early summer, there is an emerging pattern of year-round presence of at least some individuals in the expansion zone (Figure 5). This is evidence that at least some birds remain in the expansion zone all year, despite the majority likely moving out of the region, and moving northwards along the eastern coast, as described by Griffioen & Clarke (2002). The Scarlet Honeyeater is now best considered a partial migrant in the expansion zone.

There have been two obvious irruptions in Victoria in the past decade, with influxes of Scarlet Honeyeaters during spring in 2017 and 2020. Each of these irruptions resulted in a spike in records of the species spreading across central Victoria (Figure 6).

There was no strong evidence that the amount of rainfall within a year ($r = 0.016$, $df = 15$, $P = 0.953$) or in the year before ($r = 0.280$, $df = 15$, $P = 0.294$) influenced the extent of the area occupied by the Honeyeaters in the expansion zone. At the range level, amount of rainfall within a year ($r = -0.117$, $df = 15$, $P = 0.655$) or in the year before ($r = 0.028$, $df = 15$, $P = 0.914$) in the core part of the species' range in eastern Australia also showed no strong evidence of influencing the extent of the area occupied by the Honeyeaters in the expansion zone. There was no strong evidence that rainfall within a year ($r = 0.391$, $df = 15$, $P = 0.134$) or in the year before ($r = 0.273$, $df = 15$, $P = 0.306$) influenced the extent of time the Honeyeaters occupied the expansion zone. Further, amount of rainfall within a year ($r = 0.313$, $df = 15$, $P = 0.222$) or in the previous year ($r = -0.273$, $df = 15$, $P = 0.428$) in the core part of the species' range in eastern Australia also showed no strong evidence of influencing the number of days within a year that the Honeyeaters spent in the expansion zone.

Discussion

The Scarlet Honeyeater has undergone a range shift, displaying a range expansion from its southern boundary in recent years. Although there are historic records from parts of the expansion zone, these have been considered irregular irruptive or vagrant records (Wheeler 1967; Blakers *et al.* 1984; Higgins *et al.* 2001) and generally outside the species' traditional range. Such records from the most recent decades (post-2000) show that the regularity of occurrence in the region exceeds the criteria expected for irruptive movement behaviour (large fluctuations, irregular presence: Table 1). The pattern of records within years in the expansion zone instead meets criteria expected for

migratory movement behaviour, with smaller numbers of birds remaining in the area throughout the year; therefore, the population is best considered partially migratory in the expansion zone. Most records occur in September–January (Austral spring–early summer) in each year, which matches patterns previously documented in the southern part of the species' traditional range (Emison *et al.* 1987; Higgins *et al.* 2001; Griffioen & Clarke 2002).

Range expansion in Meliphagidae has previously been reported (McAllan & Lindsey 2016). The Spiny-cheeked Honeyeater *Acanthagenys rufogularis* was shown to increase its range ~200 km eastwards over several decades in Australia, extending beyond the Great Dividing Range in the process (McAllan & Lindsey 2016). In that case, the Spiny-cheeked Honeyeater displayed a sedentary pattern, moving into and occupying the newly expanded area year-round. Other nectarivores, including Musk Lorikeet *Glossopsitta concinna* and Rainbow Lorikeet *Trichoglossus moluccanus* (Psittaculidae), have greatly increased their range and abundance in recent decades in Victoria and other states, emanating from populations establishing in urban areas (Fitzsimons *et al.* 2003; Smith & Lill 2008). Smith & Lill (2008) attributed their increase in abundance and distribution in Melbourne, Victoria, to enhanced food availability associated with abundant and prolonged flowering of ornamental eucalypts.

Interactions between food availability and changing climate have been used as evidence of predicted impacts of climate change on birds (Stillman *et al.* 2021; Nägeli *et al.* 2022). Honeyeater movement behaviour has been closely linked to food availability (McGoldrick & Mac Nally 1998; Saunders *et al.* 2003), and climate has been shown to influence the phenology of flowering of eucalypts, a key food resource for honeyeaters (Hudson *et al.* 2010). The diet of the Scarlet Honeyeater is mainly nectar (Higgins *et al.* 2001, 2020), and food availability likely has a significant role in the range expansion observed, but this requires further investigation. Wood (2008) found numbers of Scarlet Honeyeaters varied independently of tree-flowering levels in Wollongong, NSW, across a span of 19 years. Observations of the Scarlet Honeyeater in the expansion zone, near Ballarat, Victoria (37.672616°S, 143.887807°E), showed that the birds concentrated feeding in flowering Drooping Mistletoe *Amyema pendula pendula* among eucalypts in multiple years (GCP pers. obs.). This was in forest and woodland environments, including Scentbark *Eucalyptus aromaphloia*, Messmate *E. obliqua*, and Broad-leaved *E. dives* and Narrow-leaved Peppermint *E. radiata*, none of which were flowering during the period that the Honeyeaters were present.

Scarlet Honeyeater records increased in number and became regular each year in the southern expansion zone following the breaking of the Millennium Drought in 2009. The 2017 irruption across central Victoria occurred during an extended period of extensive drought throughout the species' traditional range along Australia's eastern seaboard (Tzaros 2021). Historic irruptions in the expansion zone (e.g. Wheeler 1967) have occurred during periods of intense drought in New South Wales and southern Queensland (e.g. Federation Drought, 1895–1902). The amount and reliability of rainfall has long been associated with the degree of residency in Australian Meliphagidae (Keast 1968). In a bird-banding study in south-eastern Queensland, the trapping rates of Scarlet Honeyeater

each month were negatively associated with rainfall amount (Blaber 1995). Changing climate has already been linked with changed movement behaviour for the Scarlet Honeyeater in Australia. In the Blue Mountains, west of Sydney, Scarlet Honeyeater arrival dates are now earlier than previously, with the birds arriving 1.9 days earlier per year, the highest rate of change recorded among migrating species in that local bird community (Smith & Smith 2012).

The Scarlet Honeyeater is undergoing a phase of becoming a regular component of bird communities in the expansion zone. Occurrences have shifted from vagrant and nomadic patterns to regular and repeated occurrences of birds at the same locations in multiple years or consecutive years at some sites, including Greater Bendigo National Park (37.523821°S, 144.379941°E), You Yangs Regional Park (37.948607°S, 144.415542°E), Brisbane Ranges National Park (37.859180°S, 144.226064°E) and near Buninyong, central Victoria (37.672360°S, 143.886795°E). Their movement behaviour is migratory, predominantly being spring–summer migrants, with at least some birds present in the expansion zone at any time in the year. The Scarlet Honeyeater breeding period is typically spring–summer (Higgins *et al.* 2001). There is little available evidence of breeding activity in the expansion zone. Historically, a breeding attempt was recorded at Mitcham, suburban eastern Melbourne (Emison *et al.* 1987) but no confirmed records of recent breeding in the expansion zone were uncovered. However, recent observations of adults carrying nesting material (12 November 2023: GCP pers. obs.) and feeding young birds (3 January 2024: GCP pers. obs.) have been made in the expansion zone.

The range expansion displayed by the Scarlet Honeyeater shares similarities with recent range shifts observed for the Eastern Koel *Eudynamis orientalis* (Limparungpatthanakij *et al.* 2020), Brown Gerygone *Gerygone mouki* (Appleby & O'Brien 2015), Australasian Figbird *Specothes vieillotii* (Menkhorst *et al.* 2017) and Common Cicadabird *Endolisoma tenuirostre* (Palmer & Farquhar 2024) in the southern parts of their range, within the Scarlet Honeyeater expansion zone considered here. It is congruent with patterns of poleward shifts that have been reported for birds worldwide as a response to changing climate (Quillfeldt *et al.* 2010; Lehikoinen & Virkkala 2016; Widick *et al.* 2023).

The exponential increase in the number of records of the Scarlet Honeyeater since 2000 is the result of the uptake of citizen-science platforms like iNaturalist in Australia, and globally, which have contributed to much higher rates of reporting (Mesaglio & Callaghan 2021). Undoubtedly, there are expected to be historic records of Scarlet Honeyeater from the expansion zone that have not been captured by the methods used in the current study, including personal observations of ornithologists and birdwatchers and some records published in newsletters of local birdwatching groups. However, there has been considerable effort by others to retrospectively add such records to platforms like eBird and the Atlas of Living Australia, and there is evidence of such records among those considered here. Further, across two atlas periods (1977–1981 and 1998–2002), high survey effort with extensive coverage of the expansion zone across multiple years resulted in very few records ($n = 8$ records) of the species in the expansion zone overall (Blakers *et al.* 1984; Barrett *et al.* 2003). So, although the methods used have limitations for consideration of

numbers of individuals and density patterns through time because of uneven sampling and availability of records, the spatial and temporal patterns identified are clearly robust. The current climatic niche of the species may be a strong predictor of species' response to climate change, driving range shifts in many taxa (Rushing *et al.* 2020; Hällfors *et al.* 2023), and warrants investigation to understand the mechanisms and potential extent of range expansion for the Scarlet Honeyeater into the future.

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