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# Spatial and seasonal movement patterns of fynbos nectar-feeding bird pollinators from ring repeat records

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How species move through fragmented landscapes is critical to the resilience of ecological interactions, yet movement data are scarce for most taxa. Habitat loss and fragmentation affect the movement of nectar-feeding bird species, impacting plant-pollinator interactions. Here we use 75 years (1950–2025) of bird ringing data obtained from the South African Bird Ringing Scheme (SAFRING). Our main aims were to (i) determine the spatial movement patterns of nectar-feeding birds with varying degrees of habitat specialisation, and (ii) elucidate nectar-feeding bird movement between breeding and non-breeding seasons. The study focused on the four most abundant nectarivorous bird species in a region of the southwestern Cape, South Africa, marked by Velddrif and Witsand as the northern- and eastern-most points, respectively. These are the Southern Double-collared Sunbirds *Cinnyris chalybeus* (SDcS), Orange-breasted Sunbirds (ObS) *Anthobaphes violacea*, Malachite Sunbirds (MS) *Nectarinia famosa* and Cape Sugarbirds (CSb) *Promerops cafer*. All movements were mapped, and distances travelled during the breeding and non-breeding seasons were compared. Fire and ringing records were then assessed to determine movement in response to fire. Recaptures, resightings and recoveries were combined as ‘repeats’. No clear movement pattern was discernible, owing to an insufficient number of repeats. Repeat rates ranged from 2.8% for MS to 10.1% for CSb. The habitat-generalist MS and SDcS travelled further than the fynbos-dependent CSb and ObS. If only considering the distance between a single breeding and non-breeding season, MS travelled the farthest (28.9 km) and ObS the least (1.8 km). The concentration of ringing effort within the urban zone of influence means movement patterns between natural and transformed landscapes remain largely unknown. This highlights the need for targeted sampling across urban gradients combined with modern technology, such as GPS tracking, to fully understand pollinator movement in fragmented landscapes.

## Mouvements spatiaux et saisonniers d’oiseaux nectarivores pollinisateurs du fynbos, d’après 75 ans de données de baguage

Comment les espèces se déplacent dans des paysages fragmentés est essentiel pour la résilience des interactions écologiques, mais les données sur les déplacements sont rares pour la plupart des organismes. La perte et la fragmentation des habitats affectent les déplacements d’espèces d’oiseaux nectarivores, ce qui a des répercussions sur les interactions entre les plantes et les pollinisateurs. Nous utilisons 75 années (1950–2025) de données de baguage d’oiseaux du programme sud-africain de baguage SAFRING. Nos principaux objectifs étaient (i) de déterminer les stratégies de déplacement spatial des oiseaux nectarivores présentant différents degrés de spécialisation, et (ii) d’élucider les déplacements de ces oiseaux entre les saisons de reproduction et de non-reproduction. L’étude s’est concentrée sur les quatre espèces d’oiseaux nectarivores les plus abondantes dans une région du sud-ouest du Cap, en Afrique du Sud, délimitée par Velddrif au nord et Witsand à l’est : le Souimanga chalybé (SDcS) *Cinnyris chalybeus*, le Souimanga orangé (ObS) *Anthobaphes violacea*, le Souimanga malachite (MS) *Nectarinia famosa* et le Promérops du Cap (CSb) *Promerops cafer*. Tous les déplacements ont été cartographiés, et les distances parcourues pendant les saisons de reproduction et hors reproduction ont été comparées. Les données relatives aux incendies ont été évaluées afin de déterminer les déplacements en réponse au feu. Les recaptures, les observations et les récupérations ont été regroupées sous le terme ‘répétitions’. Aucun schéma de déplacement n’a pu être discerné, en raison d’un nombre insuffisant de répétitions. Les taux de répétition variaient de 2,8 % pour les MS à 10,1 % pour les CSb. Les espèces généralistes MS et SDcS ont parcouru de plus longues distances que les espèces dépendantes du fynbos, CSb et ObS. Si l’on ne tient compte que de la distance entre une seule saison de reproduction et une saison hors reproduction, c’est MS qui a parcouru la plus grande distance (28,9 km) et ObS la plus courte (1,8 km). La concentration des efforts de baguage dans la zone d’influence urbaine signifie que les déplacements entre les paysages naturels et les paysages transformés restent largement méconnus. Cela souligne la nécessité d’un échantillonnage ciblé sur l’ensemble des gradients urbains, combiné à des technologies modernes telles que le suivi GPS, afin de comprendre pleinement les déplacements des pollinisateurs dans des paysages fragmentés.

**Keywords:** bird movement, bird ringing, breeding season, fire, nectarivorous birds, transformed vs protected landscapes

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## Introduction

Understanding how species move across fragmented landscapes is fundamental to conservation biology and predicting ecological responses to global change. In particular, habitat loss and fragmentation are major drivers of change in plant-pollinator interactions (Harrison and Winfree 2015; Wenzel et al. 2020). Nectarivores are amongst the most sensitive bird guilds to habitat transformation and are often more common in pristine habitat and areas with older vegetation than in transformed habitats (Lee and Barnard 2016; Sandberg et al. 2016).

In fast-growing urban areas, the loss of natural habitat leaves only small islands of isolated vegetation patches, such as urban nature reserves and greenspaces (Santos et al. 2016). These patches are surrounded by built-up areas that are relatively inhospitable to biodiversity (Fernández-Juricic and Jokimäki 2001; Santos et al. 2016), which isolate them from larger natural areas and reduce connectivity for many species (Harris and Johnson 2004; Sandberg et al. 2016). Although nectar-feeding birds are highly mobile (Ollerton 2024), some species avoid transformed areas, leading to reduced visitation of bird-pollinated plants in transformed landscapes (Geerts 2011). Such disruptions in nectarivore movement could result in dependent plant species experiencing reduced gene flow, increased inbreeding, and lower fruit and seed set (Şekercioğlu et al. 2004; Geerts and Pauw 2012; Coetzee et al. 2018), leading to reproductive failure and eventual population extinction (Thomann et al. 2013).

Habitat loss is becoming particularly serious in developing cities in Africa (Güneralp et al. 2017), and South Africa is no exception (Seymour et al. 2020). This is especially evident in the lowlands of the southwestern Cape located in the Cape Floristic Region (CFR) where natural habitat has been largely transformed by urban expansion and agriculture (Davis and Wynberg 1998). These fragmented landscapes may disrupt plant-pollinator mutualisms, although the effect varies depending on the plant and pollinator species (Harris and Johnson 2004). The CFR supports more than 300 bird-pollinated plant species, many of which are threatened or endemic, yet pollination services mostly depend on only four nectarivorous bird species (Geerts 2016; Mnisi et al. 2021): Southern Double-collared Sunbirds (SDcS) *Cinnyris chalybeus*, Orange-breasted Sunbirds (ObS) *Anthobaphes violacea*, Malachite Sunbirds (MS) *Nectarinia famosa* and Cape Sugarbirds (CSb) *Promerops cafer* (Geerts et al. 2020). Although Greater Double-collared Sunbirds *Cinnyris afer* are common in the eastern extent of the Western Cape, they do not occur throughout the study area, i.e. the southwestern Cape, from Velddrif to Witsand (SABAP2 2026). Two other species that are less common are Dusky Sunbirds *Cinnyris fuscus*, an occasional visitor, and Amethyst Sunbirds *Chalcomitra amethystina*, which have

recently been extending their range into the region (Hockey et al. 2011).

The movement of these four nectarivorous bird species in response to anthropogenic changes and seasonal floral resources requires more attention. Fraser et al. (1989) studied the movements of avian nectarivores in predominantly natural areas around Cape Town, documenting movements of 4.5–161 km by MS, 1–60 km by CSb, 1–34 km by SDcS, and 4–7 km by ObS. The greatest distances were recorded by MS, primarily during post-fledgling dispersal. Fraser et al. (1989) had some limitations: a small sample size (11 CSb, 10 MS, 3 ObS, 3 SDcS), a short timeframe (six years: 1984–1989), and a focus solely on natural areas. More recent studies have examined seasonal movements of MS particularly in non-urban environments (De Swardt 2001; Symes et al. 2001; Bonnevie et al. 2023); however, none of these studies took place in the southwestern Cape. On a national scale, Darroll et al. (2024) presented the following maximum distances travelled by nectarivorous bird species using the South African Bird Ringing Scheme (SAFRING) database: CSb (365 km recovery), MS (161 km recapture), ObS (38 km recapture) and SDcS (65 km recapture). Although this provides maximum distances travelled, movement between breeding and non-breeding areas and across fragmented landscapes where resources are scarcer (Baldock 2020) is largely unknown.

Nectar-feeding bird movements are driven by seasonal flowering patterns and consequent food availability (Fraser 2014; Schmid et al. 2016; Bonnevie et al. 2023). In the southwestern Cape, these birds form breeding territories primarily during the wet winter months (Geerts et al. 2020) and may leave their territories to find food in the dry season, returning to the same localities the following breeding season (Skead 1967; Calf et al. 2003). Early observations of CSb documented short-distance seasonal movements (< 3 km) between breeding and non-breeding areas, with individuals showing strong site fidelity by returning to the same breeding territories annually, between mid-January and early April (Broekhuysen 1959). More recent tracking has revealed greater variability in movement strategies: and whilst most movement is over small distances, some CSb travel 160 km in search of flowering *Protea* plants between breeding seasons (Mackay et al. 2017), with one record reaching 365 km (Hockey et al. 2005). While many CSb individuals may be nomadic, Altwegg and Underhill (2006) found two strategies employed by CSb in response to food availability in the non-breeding season, namely visiting the same sites annually or finding new nectar-producing sites each year. This range of movement strategies, from localised to long-distance, improves their likelihood of encountering isolated habitat patches (Fraser 1997). In southeastern South Africa, MS have been

documented to migrate from high to low elevations during winter months (Symes et al. 2001), being found in the Drakensberg montane forests in summer and descending to low elevation aloe patches in winter (Bonnievie et al. 2023). Their movements in other parts of the country, and in particular in transformed landscapes, are less well understood. The movements of ObS are also influenced by resource availability as during autumn–winter (the breeding season) they may become more common on the lower slopes when *Erica* and *Protea* species are flowering (Fraser et al. 1989). The larger species, such as CSb (Male: 36.8 g; Female: 32.2 g; and MS (18.4 g; 15.2 g) (Rose et al. 2020) require higher nectar volumes and energy intake (Lotz and Nicolson 2002) than the smaller SDcS (8.2 g; 7.4 g) and ObS (9.7 g; 8.6 g) (Rose et al. 2020). Although body size and distance moved were positively correlated for three weaver species (Oatley and Underhill 2001), spatial and temporal nectar availability more accurately influence nectarivore movements (Fraser et al. 1989), and therefore bird mass is not considered here.

SDcS were found to occur throughout the urban gradient, whereas CSb and ObS mostly avoid built-up areas, and MS rarely travel more than 1 km from natural vegetation (Pauw and Louw 2012). However, MS are not restricted to fynbos, unlike the fynbos-dependent CSb and ObS (Le Roex 2020; Darroll et al. 2024). In a fragmented landscape, the distance between vegetation patches may impact ObS movement (Cloete 2023). Since SDcS are generalists, they are able to exploit various habitats and food sources in fragmented patches (Cloete 2023). It is therefore hypothesised that the habitat-generalist MS and SDcS will move less than CSb, whilst ObS are expected to have the most restricted movement.

Fire also impacts nectar-feeding bird movement as the richness and abundance of these birds decrease significantly in post-fire Mountain Fynbos with loss of food resources (Fraser et al. 1989; Geerts et al. 2012; Lee and Barnard 2014; Sandberg et al. 2016) even though visitation rates to flowers in post-fire environments increase (Mantintsilili et al. 2025). In response to fire, both CSb and ObS have been observed to switch from their preferred Mountain Fynbos habitat to marginal feeding areas (Fraser et al. 1989; Fraser and McMahon 1992). ObS were common in all natural fynbos vegetation types of the Cape Peninsula, except those burnt within the previous year, whereas CSb only occur in older vegetation because they specialise on Proteaceae, which only begin to flower prolifically at ~4 years of age (Geerts et al. 2020; Le Roex 2020). Once *Protea* and *Erica* species have fully matured post-fire, nectarivore numbers may increase again (McMahon and Fraser 1988). Studies on this topic are limited, particularly for SDcS and MS. Furthermore, whether ring recapture and recovery data can be linked to fire history in the CFR is largely unknown.

The aim of this study is therefore to use existing bird ringing data to determine the spatial and seasonal movement of nectar-feeding birds in the southwestern Cape, from Velddrif to Witsand. We ask: (i) What are the spatial movement distances and patterns of the four main nectar-feeding bird species in the southwestern Cape, and do these differ among species with different degrees

of habitat specialisation?, (ii) Do movement distances of nectar-feeding birds in the southwestern Cape differ between breeding and non-breeding seasons, and are these seasonal patterns consistent across all four species?, and (iii) What do 75 years of ringing records in the southwestern Cape reveal about the movement of nectar-feeding birds in relation to fire events, and does the spatial distribution of ringing effort constrain our ability to detect post-fire movement? We hypothesise that ringing data can reveal long-distance movements that vary seasonally with breeding patterns and floral resource availability.

## Methods

### Study area and study species

The study area falls within the greater southwestern Cape located in the CFR. For the purpose of this study, the furthest point to the east was Witsand (34°23' S, 20°50' E) and to the north was Velddrif (32°36' S, 18°18' E). This region of the CFR has a Mediterranean climate, experiencing mild wet winters and hot dry summers with maximum temperatures ranging from 28.7–46.1 °C (Rebelo et al. 2006). Annual rainfall quantity (mm) in the CFR is highly variable, averaging 480 mm, but ranging from 30 to 3 000 mm (Goldblatt 1997; Bradshaw and Cowling 2014). As one moves from west to east in the Cape, rainfall seasonality shifts from being predominantly in the winter to more evenly spread throughout the year, and even marginally summer rainfall in the eastern extents (Rebelo et al. 2006). Considering this variation, we restricted our assessment to an area with similar rainfall patterns to ensure consistency.

The study species for this study are as follows: CSb, MS, ObS and SDcS. Although Dusky Sunbirds are vagrants in the study area, and Amethyst Sunbirds are currently extending their range into the region, records of their movements and sightings are too limited, with no repeat occurrences in the southwestern Cape, to allow meaningful comparisons. They were therefore excluded from the analyses.

The four target species are monogamous, typically breeding during the wet season (Skead 1967) and partially into the dry season. Studies have classified the breeding season of SDcS as peaking in June–October, ObS in April–October, MS in May–November, and CSb in March–August in the southwestern Cape (Skead 1967; Craig and Hulley 1994; Chittenden et al. 2016). For the purpose of bird movements in this study, we consider the breeding season as March to August for CSb and May to October for the sunbird species. These breeding months are further supported by Irons et al. (2023) who compared the annual probability of moult and the presence of a brood patch for our focal species.

### Bird ringing data

Bird ringing data from 1950 to February 2025 were obtained for all four nectarivorous bird species from the South African Bird Ringing Unit (SAFRING) at the FitzPatrick Institute of African Ornithology, University of Cape Town. SAFRING is the central database for all bird ringing records in southern Africa and other parts of Africa. As of 2019, more than 2.6 million bird ringing records have been captured on the SAFRING database, primarily by citizen scientists (Rose

et al. 2020). Data were filtered to the southwestern Cape. SAFRING data lack precise coordinates as locations are standardised to only include degrees and minutes. Omitting the seconds results in an error radius of 1.8 km. Ringers were thus contacted through SAFRING to provide precise decimal coordinates for their ringing locations. Where coordinates could not be verified, they were approximated using the location description provided, together with the available degrees and minutes.

For the remaining coordinates, i.e. those without site descriptions, a sensitivity analysis was carried out to determine whether the 1.8 km inaccuracy would influence the results. This was done by measuring the distance between sites using the midpoint, northwest corner, southeast corner, and a random point within the one-minute square and comparing travel distance averages between these different methods. The analysis showed no influence on the overall averages; thus, these coordinates were retained.

The data were then summarised as the total number of captures and repeats recorded at new locations, the average period (months) between repeats, the average distance travelled per species between different locations, and the maximum distances travelled by each species. 'Recaptures' typically refer to birds re-caught during ringing, 'resightings' refer to identification of the individual without capture, and 'recovery' refers to birds found dead (Lebreton 2001; EURING 2025). However, since this study focuses on the location where the birds were present rather than the method of detection, 'repeats' here include all three categories. One set of coordinates located within the sea was relocated to the nearest terrestrial location. Duplicated sightings were excluded from the dataset. Distance was measured as the shortest distance between two locations, even if the pathway extended partly over the ocean (i.e. False Bay). Since the average territory size of the target species ranges from 6.4 to 12 km<sup>2</sup> with an average diameter of 2.5–2.9 km (Wolf and Wolf 1976; Calf et al. 2003), only records with distances  $\geq$  3 km were used to determine bird movement and to calculate the average distances travelled, since shorter distances likely represent territorial movement or repeat records at the same site. However, all distances were used to compare movement between and within the breeding and non-breeding seasons because limited movement was expected during the breeding season due to territoriality. The MS dataset in the southwestern Cape spanned 69 years (1955–2024; total number of bird ringing records in the southwestern Cape,  $n = 2\ 839$ ), SDcS 72 years (1953–2025;  $n = 7\ 815$ ), Obs 72 years (1952–2024;  $n = 3\ 676$ ), and CSb 75 years (1950–2025;  $n = 12\ 461$ ) (Table 1).

Repeat records were also assessed against historical fire records obtained from South African National Parks for the Cape Peninsula, Table Mountain National Park (TMNP) (1962–2022), and Cape Nature for the Boland Mountains (1932–2025) to determine whether wildfires influenced the movement of nectar-feeding birds. Specifically, bird ringing repeat records at new locations were compared to wildfire history to determine whether birds moved away after a fire occurred, where they moved to, and when they returned post-fire. Fires were filtered to those that occurred in the southwestern Cape, including only large ( $> 1\ 000$ – $5\ 000$  ha)

**Table 1:** Summarised ringing data of four nectar-feeding bird species in the southwestern Cape of South Africa. The period of ringing, total captures and repeats (i.e. individuals observed or captured more than once via bird ringing), total repeat rate (%) (recaptured or resighted birds as a percentage of the total number of captured birds), total recapture rate (%) (birds only recaptured as a percentage of captured birds), repeats with a new location, the respective repeat rate (percentage of repeat records with a new location relative to the total repeats), recapture rate (%) with new location, and the repeat rate equal to or exceeding a distance of 3 km relative to the total repeats. The average period between repeats and average distances between repeats with a new location are also provided, as well as the maximum travel distances

| Species                          | Ringing period       | Total captures | Total repeats | Total repeat rate (%) | Total recapture rate (%) | Repeats with new location | Repeat rate (%) with new location | Recapture rate (%) with new location | Repeat rate $\geq$ 3 km | Average period between repeats (months) | Average distance between repeats (km) | Maximum distance travelled (km) |
|----------------------------------|----------------------|----------------|---------------|-----------------------|--------------------------|---------------------------|-----------------------------------|--------------------------------------|-------------------------|---|---------------------------------------|---------------------------------|
| Cape Sugarbird                   | 1950–2025 (75 years) | 12 461         | 1 257         | 10.1%                 | 8.8%                     | 281                       | 22.4%                             | 19.3%                                | 18.3%                   | 14                                      | 7.9                                   | 154.8<br>(68 months: 2019–2023) |
| Malachite Sunbird                | 1955–2024 (69 years) | 2 839          | 80            | 2.8%                  | 2.1%                     | 27                        | 33.8%                             | 16.3%                                | 23.8%                   | 28                                      | 24.4                                  | 160.0<br>(27 months: 1987–1989) |
| Orange-breasted Sunbird          | 1952–2024 (72 years) | 3 676          | 248           | 6.7%                  | 6.5%                     | 28                        | 11.3%                             | 10.1%                                | 4.4%                    | 15                                      | 3.9                                   | 37.8<br>(48 months: 2005–2009)  |
| Southern Double-collared Sunbird | 1953–2025 (72 years) | 7 815          | 376           | 4.8%                  | 4.2%                     | 61                        | 16.2%                             | 11.4%                                | 10.9%                   | 21                                      | 8.7                                   | 65.1<br>(16 months: 1992–1994)  |

and very large (> 5 000 ha) fires (Kraaij et al. 2025), as smaller fires were assumed to have limited effects, and inaccurate mapping of small fires might confound results. The data consisted of 11 large (1975–2017) and one very large fire (2015) in the Cape Peninsula and 385 large (1958–2025) and 137 very large fires (1948–2025) in Cape Nature managed conservation areas.

All sightings were mapped using QGIS 3.14 (QGIS Development Team 2024). The open-source South Africa 30-metre SRTM Digital Elevation Model layer obtained from the Regional Centre for Mapping of Resources for Development (RCMRD) (<https://rcmrd.africageoportal.com/>) was used for altitude. Individual maps were generated for each species, displaying their movement across years, within the same year (12-month period), and between breeding and non-breeding seasons.

### Data analysis

Bird movement data were not normally distributed (Shapiro–Wilk  $W = 0.502$ ,  $p < 0.001$ ). Therefore, to test for differences between species' movement, and for movement from one breeding to non-breeding season; a Kruskal–Wallis test was used. A  $t$ -test was used to compare distances travelled during the breeding and non-breeding seasons (6 months each). A post-hoc Dunn's test was used to identify differences between species. Fire was descriptively assessed by layering fire and bird movement data on QGIS to explore data overlaps pre- and post-fire. All statistical analyses were performed using R software (Version 4.2.7; R Core Team 2024).

## Results

### Repeat records

Total repeat rates in the southwestern Cape ranged from 2.8% for MS (Table 1,  $n = 80$ ) to 10.1% for CSb (Table 1,  $n = 1\ 257$ ). For all species, the largest proportion of repeats were recaptures, which ranged from 2.1% for MS (Table 1,  $n = 60$ ) to 8.8% for CSb (Table 1,  $n = 1\ 098$ ). CSb had the highest percentage of recaptures with a new location (Table 1, recapture rate = 19.3%,  $n = 242$ ), followed by MS (16.3%,  $n = 13$ ), SDcS (11.4%,  $n = 43$ ) and ObS (10.1%,  $n = 25$ ). Distances travelled by all four species rarely exceeded 3 km (range = 4.4% to 23.8% of repeat records). MS travelled the furthest distance (Table 1; 160.0 km) and had the highest overall average repeat record distance (Table 1; 24.4 km,  $n = 27$ ).

### Bird movement

All four species were most commonly ringed and sighted in areas within the urban zone of influence, with the majority located close to Cape Town, Pringle Bay and Hermanus (Figure 1). Movement distances differed significantly among species ( $\chi^2 = 27.894$ ,  $df = 3$ ,  $p < 0.001$ ), although SDcS did not differ from MS ( $Z = -0.59$ ;  $p = 0.277$ ) (Figure 2). Most records for all three species were movements from 0 to 5 km: CSb = 93.6% ( $n = 1\ 177$ ); MS = 80.0% ( $n = 64$ ); ObS = 99.2% ( $n = 246$ ); SDcS = 94.7% ( $n = 356$ ).

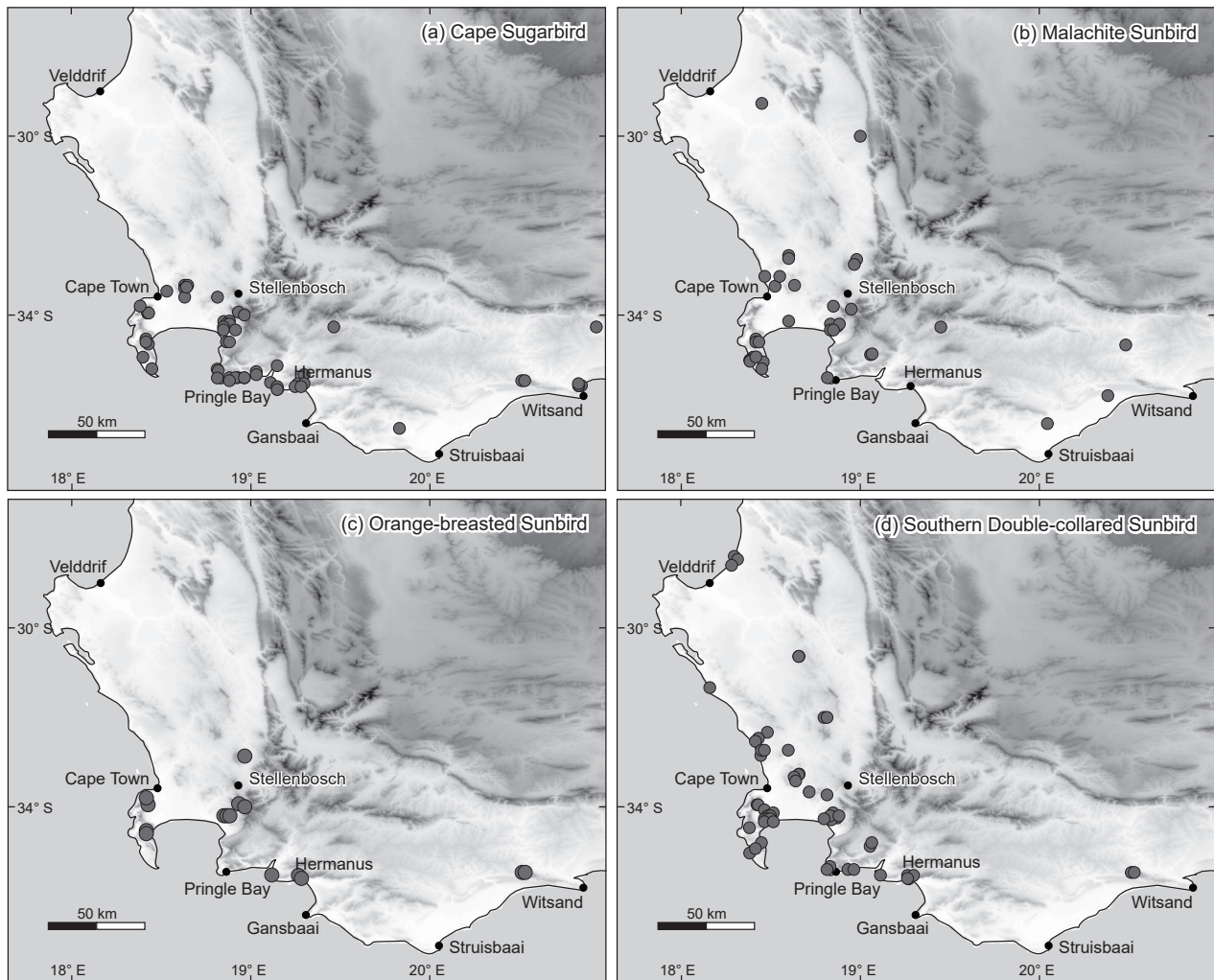
CSb produced the most movement records in the southwestern Cape, followed by SDcS, MS and ObS (Figure 3a–d). For all species, very few records were within

the same year and between breeding and non-breeding seasons (Figure 3a–d). A juvenile MS (sex unknown) ringed in Olifantsbos in the Cape Peninsula had a repeat record 160.0 km north in Piketberg 27 months later (Table 1, 1987–1989; Figure 3b). Two additional MS moved farther than 95 km, one from Swellendam to Villiersdorp (95.9 km; 2004–2004; 1 month) and the other from Durbanville Nature Reserve to Porterville (98.5 km; 1991–1992; 10 months) (Figure 3b). Another individual travelled 41.1 km from Olifantsbos to Pringle Bay in three months in 1995 (Figure 3b). SDcS travelled only 8.7 km ( $n = 61$ ) placing second in average distance travelled (Table 1) with its farthest distance being 65.1 km from Betty's Bay to Durbanville Nature Reserve over 18 months (1992–1994) (Figure 3d). CSb travelled on average 7.9 km (Table 1;  $n = 281$ ), with the highest distance being by one adult male travelling 154.8 km over 58 months (2019–2023) from Witsand to Vermont (Figure 3a). One female CSb moved a total of 124 km in less than two months moving from Dewetsbaai, Betty's Bay to Durbanville Nature Reserve (1990; 63 km), and had a repeat record in Grootvlei, Betty's Bay just seven days later (1990; 61 km), being the individual travelling the farthest in the shortest period of time (Figure 3a). Several CSb also displayed regular movement within Betty's Bay ( $n = 133$ ; 7.7 km), and Fernkloof Nature Reserve ( $n = 26$ ; 14 km; and  $n = 24$ ; 3 km) (Figure 3a). Although ObS has the most restricted movement (Table 1; mean = 3.9 km,  $n = 28$ ), an adult male travelled 37.8 km from Paarl Bird Sanctuary to Helderberg Nature Reserve over 48 months in 2005–2009 (Table 1; Figure 3c). Distances travelled did not differ between males and females for SDcS and CSb; however, data were deficient for ObS and MS (Supplementary Figure S1 and Table S1).

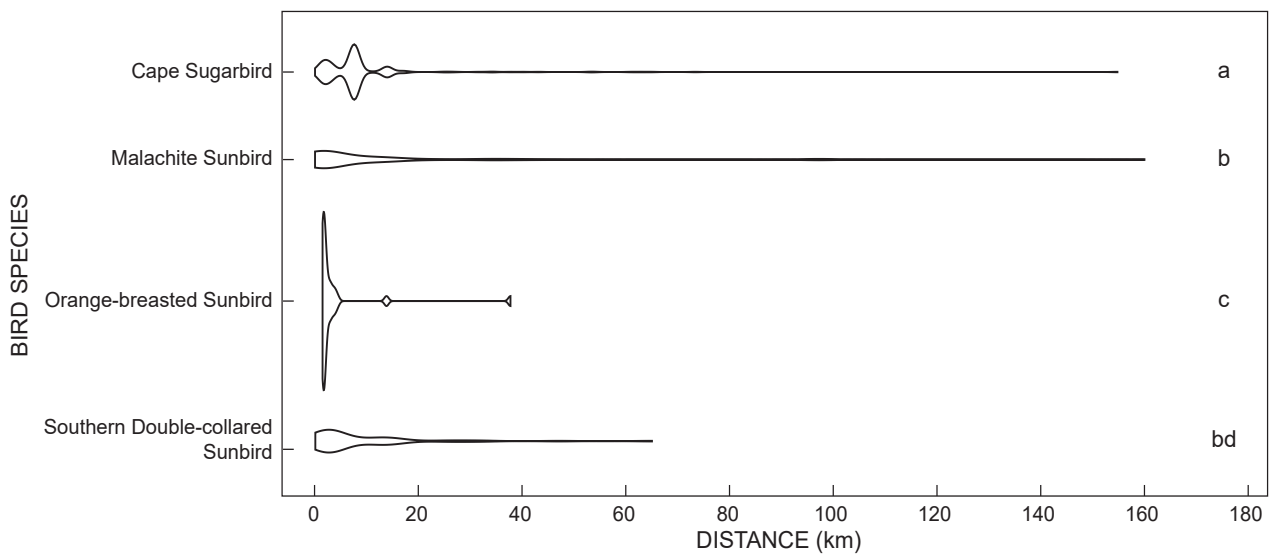
When comparing average movement between the breeding and non-breeding seasons (one movement within a 12-month period), ObS (1.8 km) and CSb (6.5 km) ( $Z = 1.49$ ;  $p = 0.068$ ), and SDcS (11.8 km) and MS (28.9 km) ( $Z = 0.45$ ;  $p = 0.326$ ) travelled similar distances. No difference was found in distances travelled within the breeding versus non-breeding seasons (6-month period each) for all species (CSb:  $T = -1.165$ ,  $p = 0.245$ ; MS:  $T = 0.334$ ,  $p = 0.744$ ; ObS:  $T = -0.143$ ,  $p = 0.887$ ; SDcS:  $T = -0.400$ ,  $p = 0.692$ ).

### Bird movement in response to fire

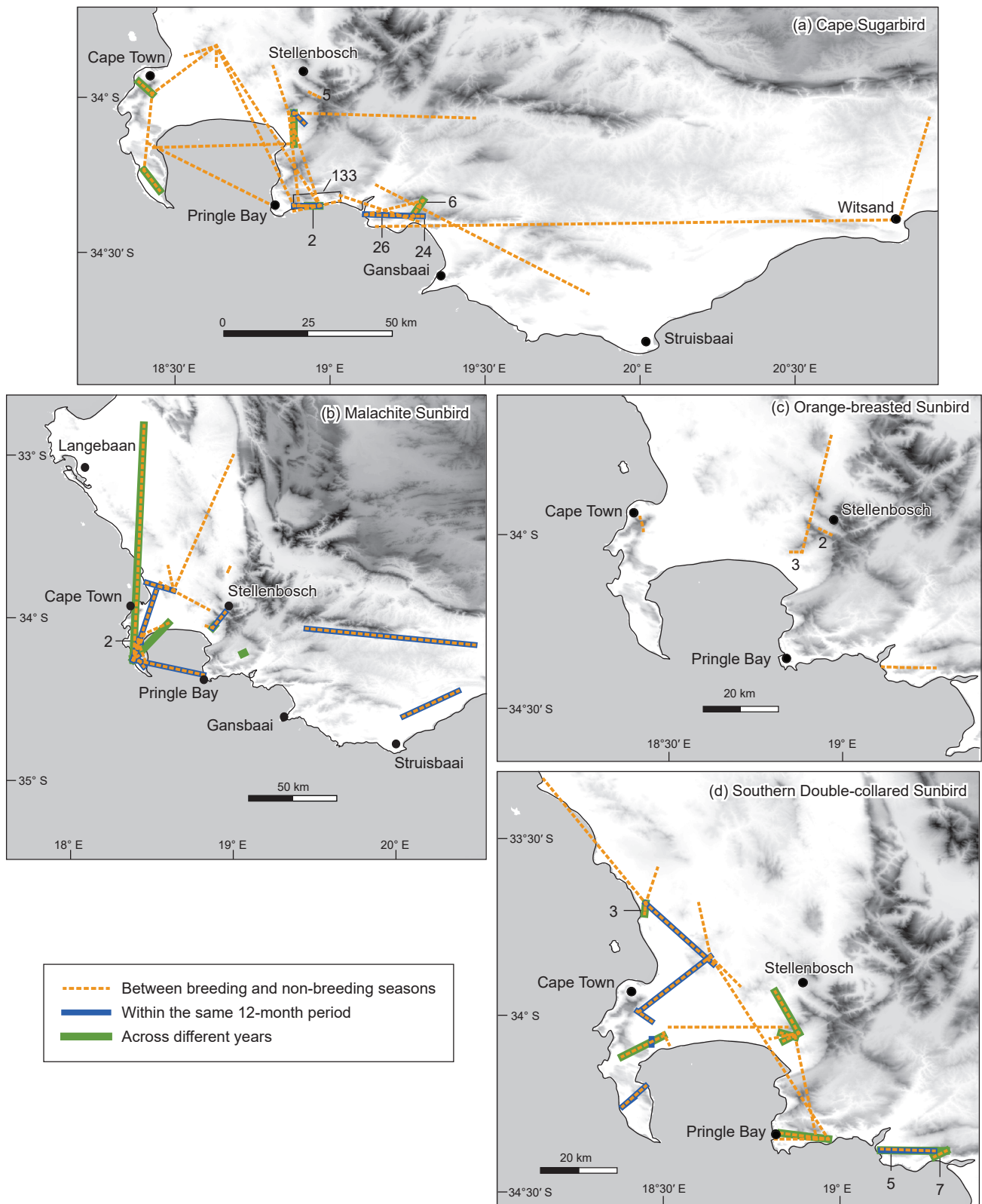
Bird movements in response to fire were variable and did not show a consistent directional pattern away, from, or towards, burnt areas. At Kogelberg Nature Reserve, nine CSb and two SDcS were present within 1–3 years following a very large wildfire (10 130.5 ha) (1991) suggesting little or no movement from the site. Similarly, on the Cape Peninsula, two SDcS were present 1–14 months after two large fires (1 089.7 ha and 1 948.4 ha). Most bird records recorded within a period in which there was a fire (3 090 ha) were at Olifantsbos, TMNP in 1986. Two CSb ringed one year before the fire (1985) showed contrasting responses: one had a repeat record 27 km north in Kirstenbosch Botanical Gardens two months post-fire, and one had a repeat record 8 km south at Bordjiesrif in 1987. Seven MS were also ringed at Olifantsbos one year before the fire, four had repeat records 4–48.5 km from the burnt area



**Figure 1:** Ringing and repeat locations of the Cape Sugarbird (a), Malachite Sunbird (b), Orange-breasted Sunbird (c), and Southern Double-collared Sunbird (d) in the southwestern Cape, South Africa



**Figure 2:** Distribution of distances exceeding 3 km travelled by four nectar-feeding bird species in the southwestern Cape, South Africa. Species sharing letters are not significantly different



**Figure 3:** Movement pathways of the Cape Sugarbird (a), Malachite Sunbird (b), Orange-breasted Sunbird (c), and Southern Double-collared Sunbird (d) between breeding and non-breeding seasons (dashed orange), within the same year (i.e. 12-month period) (blue), and across different years (green) within the southwestern Cape, South Africa. Numbers indicate the number of individual birds using the same pathway, whereas unnumbered pathways indicate a single individual

within 6–8 months, and one repeat record in the burnt area one month after the fire. Three of these seven birds were immature. Another MS was ringed in the burnt area one year post-fire and moved 160 km north by 1989. A SDcS ringed one month after the fire gave a repeat record along the burnt area boundary at one and seven months post-fire.

## Discussion

Our analysis of 75 years of ringing data revealed four key findings about nectar-feeding bird movement in the southwestern Cape. First, the furthest national distances recorded for three nectar-feeding bird species (MS, ObS and SDcS) were recorded within the southwestern Cape. Second, the habitat-generalist MS and SDcS travelled further than the fynbos-dependent CSb and ObS. Third, the birds showed spatial shifts associated with breeding, with MS found an average of 29 km from their breeding-season locations when having a repeat record in the non-breeding season. Fourth, despite adequate repeat rates (2.8–10.1%), the spatial bias in ringing sites toward the urban zone of influence limited our ability to assess movement through fragmented landscapes. Together, these findings demonstrate that while ringing data can quantify the spatial scale of nectarivore movements, understanding how these species deal with and move through human-modified landscapes requires more targeted sampling.

### Repeat records

Since most studies differentiate between recapture, recoveries and resightings, we will discuss and compare our recapture rates with the literature for more appropriate comparisons. The total recapture rates for MS (2.1%) and SDcS (4.2%) were lower than those of a previous study in the Eastern Cape (6.6% and 10.6% respectively; Bonnevie et al. 2023) and KwaZulu-Natal (MS = 4.6%; Symes et al. 2001). However, CSb recapture rate (8.8%) was similar to that of Altwegg and Underhill (2006), which ranged from 6.1 to 17.1% (Betty's Bay), and 7.1% to 14.4% (Helderberg Nature Reserve) for females and males respectively. Fraser et al. (1989) had much lower recovery rates (MS: 1.25%; ObS: 0.65%; CSb: 0.60%, SDcS: 0.58%) for six years of data than we report here. While a larger geographic area, as in our study, increases the chances of recapturing very mobile fledglings (Lebreton 2001), it may also reduce overall repeats due to the larger sample size. A good example illustrating this is the repeat rate of Rufous Hummingbirds *Selasphorus rufus* (0.2%) on a continental scale (Rousseau et al. 2020) compared to that of Ruby-throated Hummingbirds *Archilochus colubris* (9.2%) in home gardens in Illinois (Hutcheson 2012). However, for CSb, despite our larger study area, we found a comparable recapture rate to the smaller scale studies in Betty's Bay and Helderberg Nature Reserve (Altwegg and Underhill 2006) despite the latter's data being incorporated into this study via the SAFRING database.

### Bird movement

All four species were most common in areas within the urban zone of influence, with the most records close to Cape Town, Pringle Bay and Hermanus (Figure 1). This

could be due to biases in ringing site selection, but also the distribution of people, and socio-economic and political factors (Thorup et al. 2014). In the southwestern Cape, most large towns are coastal (Figure 1), thus potentially impacting bird recapture rates and recoveries.

Contrary to the hypothesis that the habitat-generalist MS and SDcS would travel less than the fynbos-dependent CSb, MS and SDcS were found to travel the furthest. This could be due to nectar availability. If nectar-feeding birds have sufficient nectar sources available year round, they may have no incentive to move far from the site (Calf et al. 2003; Altwegg and Underhill 2006). They may instead increase visitation to individual habitat patches (Garrison and Gass 1999). Furthermore, Cloete (2023) found that protea nectar availability per unit area, and thus CSb presence, increases with patch size. Therefore, CSb may not have moved far, because they had access to sufficient nectar, and most of their movement pathways were located in fairly natural areas (Figure 3A) instead of in the highly urbanised lowlands of Cape Town where resource availability is reduced (Mnisi et al. 2021). This contrasts with ObS, which, as expected, had the most limited movement due to its relatively restricted range (Williams 1993), high specialisation, sensitivity (Pauw and Louw 2012; Cloete 2023), and preference for fynbos vegetation (Fraser et al. 1989). However, since ringing only indicates the distance between two capture locations (Thomas et al. 2015), the distances reported here are likely underestimates. For example, the furthest record for CSb across its range is a recovery of 365 km (Darroll et al. 2024), which supports its highly specialised feeding habitat. Furthermore, ringing records only represent endpoints, but movement in between and the potential importance of urban greenspaces and nature reserves as stepping stones remain unknown.

The national maximum distances for all species (Darroll et al. 2024), except for CSb, were recorded in this study. However, since our study used more precise locations, i.e. coordinates including seconds, there were minor decimal differences. These maximum distances, however, far exceed those recorded for all species, except MS, almost four decades ago by Fraser et al. (1989). With the benefit of a much larger dataset and a much longer timeframe, here we found that CSb could travel as far as 154.8 km, ObS 37.8 km and SDcS 65.1 km, as opposed to the respective 60 km, 7 km and 34 km recorded in Fraser et al. (1989). While the data used by Fraser et al. (1989) are a subset of data used in this study, it shows how ongoing ringing efforts can improve our understanding of bird movements over time. MS also had the highest overall average distance travelled (24.4 km), which corresponds with Fraser et al. (1989) who found that MS moved the farthest, primarily in the post-fledgling stage. This finding highlights the potential value of repeat data in monitoring post-fledgling dispersal, particularly since it is largely unexplored in the literature (Jones et al. 2026). Although MS travelled the farthest overall, one CSb travelled a total of 124 km in less than two months, with almost half the distance travelled in just seven days (61 km). This pays testament to its highly mobile nature whilst seeking out nectar sources, as highlighted in other studies (Cloete 2023). Rebelo et al. (1984) highlighted the potential

altitudinal migration of ObS while tracking nectar resources; however, there was no clear evidence from the ringing data to support this pattern. Besides one record of an individual moving from the higher elevation Olifantsbos to the coastal Pringle Bay (Figure 3B), there was no evidence to suggest MS being an altitudinal migrant in the Cape region, despite this behaviour being found along the east coast of South Africa (Symes et al. 2001; Bonnevie et al. 2023).

Comparison of movement between the breeding and non-breeding seasons (one movement in a 12-month period) indicated that MS travelled the farthest on average (28.9 km) with ObS moving the least (1.8 km). Once again, the fynbos-dependent ObS and CSb, and the habitat-generalist MS and SDcS travelled different distances, with the habitat-generalists travelling the furthest on average. The reason for CSb travelling less than the generalists could be due to some individuals defending territories even outside the breeding season (Altwegg and Underhill 2006). However, bird movement was found to be similar within the breeding season compared to the non-breeding season (six months respectively). This was not expected because nectar-feeding bird movement is influenced by seasonal food availability (Bonnevie et al. 2023), often resulting in birds leaving their territories in the non-breeding seasons to find food elsewhere (Calf et al. 2003). Although the low sample size likely impacted the results, this pattern could be explained by nectar-feeding birds having no incentive to move regardless of the season if sufficient nectar sources are available year-round (Calf et al. 2003; Altwegg and Underhill 2006).

### ***Bird movement in response to fire***

Since fire is known to impact bird movement (Sandberg et al. 2016), with nectarivorous bird densities decreasing in post-fire vegetation (Fraser et al. 1989) and birds switching to alternative habitats (Fraser and McMahon 1992; Sandberg et al. 2016), historic fire records were assessed, but there were insufficient repeats after large and very large fires; therefore, no clear pattern was discernible. Although three MS moved concurrently with the fire, they were immature; therefore, their movement may simply be due to post-fledgling dispersal and not in response to the fire. It is also important to note that these birds move regardless of fire (Craig and Hulley 1994). Furthermore, even if there are many nectar-feeding birds in an area before a fire, only a small proportion are ringed and few are recaptured. Although spatial data from the Southern African Bird Atlas Project 2 could not be used to compare the reporting rates for nectar-feeding bird species before and after the occurrence of fires in large natural areas, the coarse scale of the data limits the value in transformed landscapes. Citizen science applications, such as iNaturalist (<https://www.inaturalist.org/>) and Bindo (<https://www.bindo.app/>) may, however, provide additional insight into nectarivore abundance and potential movement patterns in transformed habitats because they have more precise locations. Although some studies have considered nectarivorous bird ringing rates and body condition in areas before and after fires (Lee and Barnard 2014; Lee 2019), and visitation to flowering plant species in burnt patches (Geerts et al. 2012; Mantintsilili et al. 2026), understanding where they move after a fire is imperative, particularly in

fragmented landscapes with isolated patches of natural habitat remaining.

Seventy-five years of bird ringing by ornithologists and citizen scientists across the southwestern Cape has provided a valuable dataset revealing that some nectar-feeding birds travel their furthest distances within the southwestern Cape and show distinct seasonal movement patterns linked to breeding. This long-term ringing effort contributes to critical baseline knowledge about how these pollinators navigate landscapes, which can help in predicting their responses to ongoing habitat transformation. However, the spatial concentration of ringing efforts in protected areas means we cannot determine whether birds exhibit similar movement patterns across urban matrices or whether they avoid crossing developed landscapes altogether. Since most repeats were located in more natural areas, the data could not infer movement across fragmented landscapes, highlighting the need for more ringing within urban nature reserves and parks. Historical bird movement (pre-1990s) could not be compared to modern records (post-1990s) to determine the impact of urbanisation on bird movement due to the lack of comparable data. Therefore, whether bird movement differs between urban and natural areas remains inconclusive. One solution is to undertake frequent ringing at multiple sites to target nectarivores, as was done via ringing and colour ringing by Oschadleus and Fraser (1988). A similar study was conducted with weavers on the Cape Peninsula, in this case showing how they used wetlands as stepping stones to move through the urban matrix (Calder et al. 2015).

### **Conclusion**

Our findings demonstrate the value of sustained ringing programmes for revealing movement patterns at scales relevant to landscape-level conservation, but future work combining targeted ringing across urban gradients with modern tracking technology, such as radio-tracking or miniaturised Global Positioning System (GPS) devices, will be essential for understanding which sites they select for breeding, how their movement is influenced by fire and the availability of specific plant species, and whether these mobile pollinators can maintain connectivity across increasingly fragmented fynbos landscapes.

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