

Site fidelity and recurrence of Barn Swallows *Hirundo rustica* in Zambia

Bennie van den Brink^a and Rob G. Bijlsma^b

Fidélité intra- et interannuelles d'Hirondelles rustiques *Hirundo rustica* à des sites d'hivernage en Zambie. Pendant les saisons d'hivernage de 2007/08 à 2010/11, 22.173 Hirondelles rustiques *Hirundo rustica* ont été capturées dans leurs dortoirs en Zambie centrale. Seize hirondelles avaient été baguées ou ont été recapturées en Europe (taux de reprise de 0,08%), dont 14 en Europe centrale et de l'Est (10–60°E) et deux en Europe de l'Ouest. La fidélité au site est élevée, avec deux à 38 reprises par site et par saison. Toutes les reprises provenaient des sites où les oiseaux avaient été bagués initialement, un à 75 jours après la première capture (moyenne de 22,7 ± 17,4 jours). Les reprises les années suivantes étaient fréquentes, toujours au dortoir où elles avaient été capturées pour la première fois. Les taux de retour étaient les plus élevés en 2008/09, et plus élevés pour les hirondelles baguées comme adultes (0,63%) que comme juvéniles (0,22%). Au cours de l'hivernage, les effectifs aux dortoirs en Zambie centrale diminuaient, surtout en janvier lorsque les oiseaux sont en pleine mue des rémiges, probablement à cause de la diminution des insectes disponibles pendant les pluies et de la migration progressive vers des dortoirs plus au sud (deux reprises dans la province du Gauteng, dans le nord de l'Afrique du Sud).

Summary. During the non-breeding seasons of 2007/08–2010/11 22,173 Barn Swallows *Hirundo rustica* were captured at roosts in central Zambia. Sixteen swallows had been ringed or were recaptured in Eurasia (recovery rate of 0.08%), of which 14 were from central and eastern Europe (10–60°E) and two from western Europe. Site fidelity was high, with 2–38 recaptures per site per season. All recaptures came from the sites where the birds had been ringed initially, 1–75 days after the first capture (mean 22.7 ± 17.4 days). Recaptures in subsequent years were frequent, always at the roost where first trapped. Return rates were highest in 2008/09, and greater for swallows ringed as adults (0.63%) than as juveniles (0.22%). During the course of the non-breeding season (mainly January, when the birds are in full moult of their flight feathers), numbers at central Zambian roosts declined, probably in response to the reduced availability of catchable insects in the rainy season and a redistribution to roosts further south (two recoveries in Gauteng, northern South Africa).

Ringing studies have revealed that many Palearctic migratory passerines exhibit site fidelity and recurrence within and between seasons in their African wintering grounds (Moreau 1969, Baillon *et al.* 1992, Sauvage *et al.* 1998, Salewski *et al.* 2000, King *et al.* 2001, Salewski *et al.* 2002). Site fidelity (i.e. return to a specific circumscribed site)—and to a lesser extent also recurrence (repeat presence in a more general area, *sensu* Sauvage *et al.* 1998)—of non-breeding Barn Swallows *Hirundo rustica* (hereafter swallows) have been described for the African wintering grounds, from Central Africa through Namibia, Botswana and South Africa (e.g. De Bont 1962, Becker 1974, Oatley 2000, van den Brink *et al.* 2000). The data obtained via geolocators and dataloggers appear to underscore, at least partly, the prevalence of site fidelity for a number of Palearctic migrants as originally revealed via use of metal rings (e.g. Hasselquist *et al.* 2017, Burman *et al.* 2019).

Swallows are also known for their high site fidelity on the breeding grounds (Cramp 1988). Data generated from the extensive ringing effort in Africa in past decades suggest a more or less similar strategy in the non-breeding season (Oatley 2000, Dowsett & Leonard 2001, Nuttall 2001, Roxburgh & Leonard 2007). Even during a severe drought in Botswana, in January 1995, when roosting swallows had dwindled to less than 1% of numbers in the previous year, and body masses of the remaining birds were close to starvation, four swallows were recaptured that had been ringed locally in previous years (van den Brink *et al.* 2000). Rainfall in the non-breeding season impacts survival and size of the breeding population of swallows (Robinson *et al.* 2008, Zwarts *et al.* 2009), but perhaps less so in seasonal habitats with recurring and predictable variations in rainfall. Migratory birds using such habitats may adapt to environmental stress by employing a more flexible migration strategy, wherein alternate

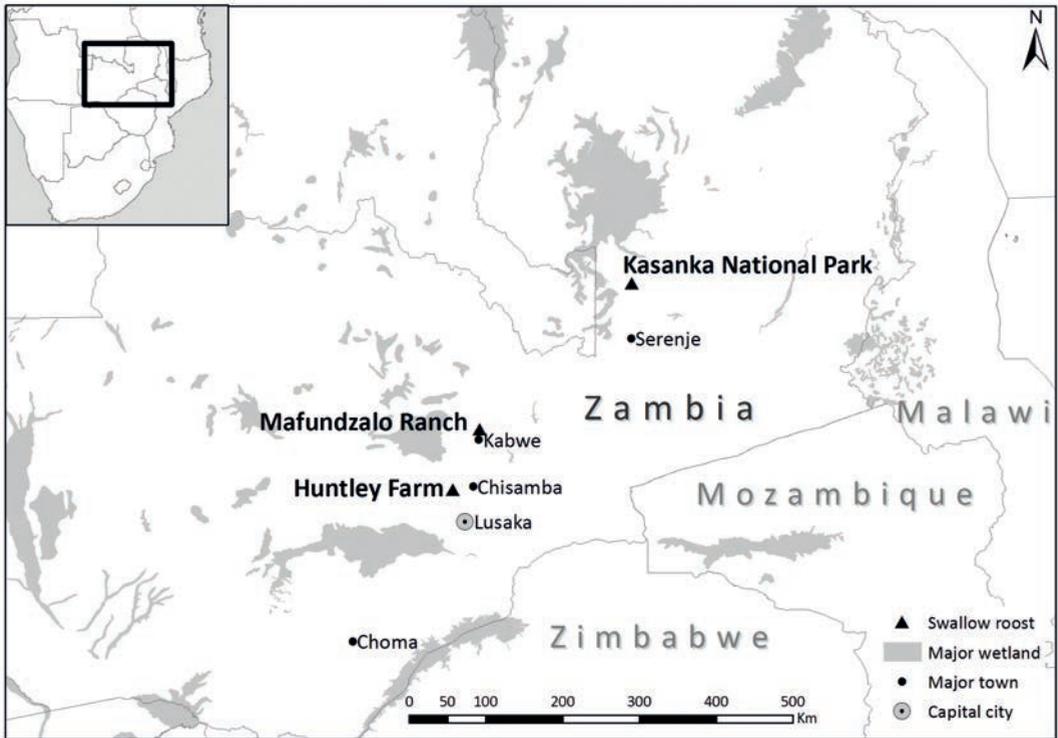


Figure 1. Map of Zambia with location of Barn Swallow *Hirundo rustica* roosts sampled in the present study. Carte de la Zambie avec les positions des dortoirs d'Hirondelles rustiques *Hirundo rustica* prospectés dans la présente étude.

sites are used and shifts in phenology may occur (Altwegg *et al.* 2012, Burman *et al.* 2018).

In Zambia, swallows are considered passage migrants and non-breeding visitors, with large roosts occurring in a few places on southbound passage (October–December); fewer, albeit still large, numbers may remain in Zambia during the rains, but significant roosts during northbound passage are decidedly few (Dowsett *et al.* 2008). We studied site fidelity and recurrence of swallows by alternate trapping at two to three roosts in central Zambia in the non-breeding seasons of 2007/08–2010/11. We were especially interested to learn if swallows were faithful to roosts having arrived at their non-breeding site, and whether movements from such sites to other regions in Africa could be detected.

Study sites and Methods

The Central African peneplain in Zambia lies predominantly between 900 and 1,400 m, and is intersected by large rivers and lakes flanked with permanent wetlands and seasonal swamps, typical

swallow habitat, with food (flying insects) and roosts (reedbeds) in profusion. Between Lusaka and Kasanka several wetlands along a north-east–south-west gradient were located where swallows used roosts during at least part of the non-breeding season (Fig. 1). The sites were chosen because of their general accessibility and position along a north–south axis, with two roosts in close proximity (75 km: Chisamba and Kabwe) and another further away (Kasanka: 300 km north-east of Kabwe). Several other sites were investigated for the presence of trappable swallows in 2007/08, notably at Itawa Dam near Ndola (12°58'18"S 28°39'59"E) and the Nkanga River Conservation Area near Choma (16°37'19"S 26°59'53"E); these sites proved to be dangerous (armed robbery) or unprofitable in terms of numbers of swallows. The north–south axis was employed to anticipate a continuation of swallow migration towards more southerly wintering areas during the course of the non-breeding season. The three main study sites were easily accessible by car, except Kasanka during periods with heavy rainfall.



Figure 2. View of Kasanka roost, 7 March 2008 (Bennie van den Brink)

Vue sur le dortoir d'hirondelles de Kasanka, 7 mars 2008 (Bennie van den Brink)



Figure 3. View of Kabwe roost with Barn Swallows *Hirundo rustica* gathering, evening of 11 December 2009 (Bennie van den Brink)

Vue sur le dortoir de Kabwe, avec les Hirondelles rustiques *Hirundo rustica* se rassemblant au dessus du site, le soir du 11 décembre 2009 (Bennie van den Brink)



Figure 4. View of Chisamba roost in the background, 13 December 2008 (Bennie van den Brink)

Vue sur le dortoir de Chisamba, à l'arrière-plan, 13 décembre 2008 (Bennie van den Brink)

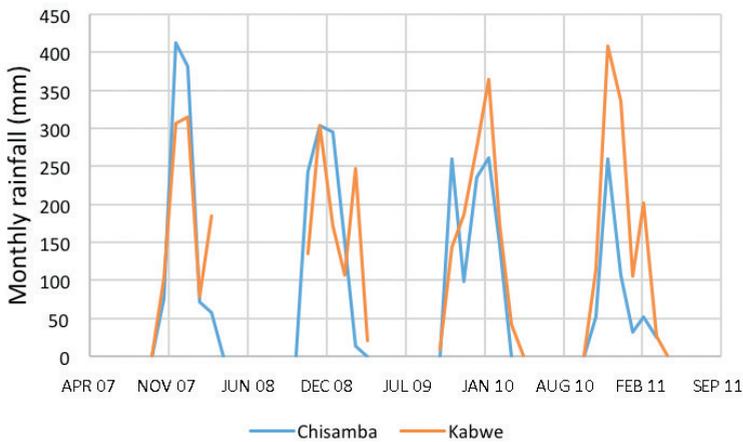


Figure 5. Monthly rainfall in mm for October–April 2007–11 for two Barn Swallow *Hirundo rustica* roosts in Zambia (data: Zambeef for Chisamba; D. Burton for Kabwe).

Variations de la pluviométrie mensuelle en mm en octobre–avril 2007–11 à deux dortoirs d’Hirondelles rustiques *Hirundo rustica* en Zambie (données : Zambeef pour Chisamba ; D. Burton pour Kabwe).

Kasanka National Park (12°35'19"S 30°14'37"E): a natural wetland along the Musola River near its confluence with the Kasanka River, one of the areas in the park with extensive reedbeds (Fig. 2). It forms part of the Greater Bangweulu Ecosystem. A large swallow roost was sampled in 2007/08 and 2010/11. Roosting numbers varied greatly, between hundreds and >100,000.

Mafundzalo Ranch, Kabwe (14°18'42"S 28°27'70"E): an artificial lake, with a small reedbed (*Phragmites*) used for roosting by swallows, and for roosting and nesting by Village Weavers *Ploceus cuculatus*, the latter sometimes interfering with swallow trapping, with sometimes large numbers of weavers becoming ensnared in the nets (Fig. 3). Rising water levels during the rains sometimes necessitated a shift of mist-nets to higher ground closer to the trees surrounding the dam. This roost usually held hundreds to thousands of swallows, occasionally tens of thousands.

Huntley Farm (Zambeef), Chisamba (15°01'27"S 28°08'89"E): an artificial lake, fringed with a mixture of *Typha* and *Phragmites* (Fig. 4). During the rainy season, the water level of the lake rises considerably, preventing trapping along the shoreline. Mist-nets were accordingly relocated to higher ground, increasing the distance between the nets and roost site, and adversely impacting trapping results. Roost size varied between years, from thousands to tens of thousands.

The presence of swallows in Zambia coincides with the rainy season from late October to March/April, when temperatures range between 20 and 35°C. Mean annual rainfall is highest in the north, with up to 400 mm/month (Dowsett *et*

al. 2008). Marked variations between years are typical, and during our study in 2007/08 through 2010/11 rainfall in October–April varied between 532 and 1,504 mm, depending on year and site (Fig. 5). In 2007/08–2009/10 rainfall anomalies within the investigated region (between Chisamba and Kabwe) were above the long-term average (1980–2016), but below average in 2010–11 at Chisamba (Makondo & Thomas 2020).

Aerial insect abundance was recorded by means of a butterfly net with a diameter of 40 cm mounted atop the front bumper of the car (Fig. 6). A straight stretch of road (1 km long) was chosen in the vicinity of the roost sites to drive the car at a speed of 60–80 km/h, prior to swallow-trapping efforts in the evening (usually between 13.00 and 16.00 hrs). Insects were collected from the net after the stop, but the strongest flyers may have escaped before the net could be effectively closed. As a consequence, mostly tiny insects were collected ($n = 2,863$), with some larger flies ($n = 52$), beetles ($n = 9$), grasshoppers ($n = 2$) and spiders ($n = 2$) (Table 1). During heavy rainfall few flying insects were active. The Chisamba site was located near a large slaughterhouse (Zambeef) where insects abounded and many swallows were seen foraging during the daytime.

Swallows were captured following a strict protocol. One hour before sunset, we erected up to 36 m of mist-nets in reedbeds (up to 51 m at Kasanka in 2010/11). Nets were placed in one or two lanes perpendicular to the edge of the reedbed. Swallows were attracted by broadcasting their song. On evenings with heavy rain we used fewer nets or elected not to trap. Swallows that



Figure 6. Monitoring insects by car-mounted net, Chisamba, 5 February 2008 (Bennie van den Brink)

Suivis d'insectes avec un filet à papillon monté sur la voiture, Chisamba, 5 février 2008 (Bennie van den Brink)

Table 1. Average number of aerial insects captured by car-mounted butterfly net on 1-km stretches of road near three Barn Swallow *Hirundo rustica* roosts in Zambia during the 2007/08 season, averaged per month and per transect, with monthly means for humidity and temperature.

Tableau 1. Nombre moyen par mois et par transect d'insectes aériens capturés avec un filet à papillon monté sur la voiture sur un trajet de 1 km près de trois dortoirs d'Hirondelles rustiques *Hirundo rustica* en Zambie pendant la saison de 2007/08, avec les moyennes mensuelles d'humidité et de température.

Month	November	December	January	February	March
Chisamba					
Insects (\bar{x})	5	21	71	88	34
Transects (n)	3	7	5	4	4
Humidity (%)	55	61	76	56	51
Temperature (°C)	28.0	26.8	24.0	28.6	28.9
Kabwe					
Insects (\bar{x})	40	28	42	56	51
Transects (n)	6	4	3	7	5
Humidity (%)	49	77	56	62	72
Temperature (°C)	29.9	24.3	24.9	27.4	25.1
Kasanka					
Insects (\bar{x})	20	21	34	42	40
Transects (n)	1	4	9	4	2
Humidity (%)	48	67	74	64	68
Temperature (°C)	28.8	24.6	24.3	26.0	28.0

were trapped were ringed, aged and released on the spot. Whenever possible, a random sample of ten adult and ten juvenile swallows was used to record biometrics and moult; these were released the next morning. All recaptures were fully processed for biometrics and moult (van den Brink 2008). In addition, moult was recorded in a much larger

sample (1,686 birds) in 2007/08. Moult was scored following the six-point scale (0–5, from old to new) as depicted in Ginn & Melville (1983).

At each roost we trapped on 3–13 successive evenings, before switching to the next roost. During periods with large numbers we prolonged trapping sessions at the same roost, except during

Table 2. Catching periods, number of trapping days, number of trapping sessions, max. number present on a single day and total number of Barn Swallows *Hirundo rustica* present for all trapping days combined at three sites in Zambia in four consecutive non-breeding seasons.

Tableau 2. Périodes de capture, nombre de jours et de séances de baguage, et nombre d'Hirondelles rustiques *Hirundo rustica* présentes (maximum journalier et nombre additionné pour tous les jours de baguage) à trois sites en Zambie sur quatre saisons d'hivernage consécutives.

Site/Winter	2007/08	2008/09	2009/10	2010/11
Chisamba				
Periods	29 Nov–22 Mar	6 Dec–19 Jan	8 Nov–26 Jan	20 Nov–11 Jan
Days	24	21	33	26
Sessions	6	4	6	4
Max.	5,000	9,000	10,000	100,000
Totals	17,685	19,675	46,280	712,070
Kabwe				
Periods	24 Nov–19 Mar	8 Dec–7 Feb	10 Nov–3 Feb	16 Nov–7 Jan
Days	24	30	38	20
Sessions	6	4	6	5
Max.	50,000	4,000	30,000	35,000
Totals	319,325	36,250	268,935	81,175
Kasanka				
Periods	4 Dec–22 Mar	–	–	29 Nov–16 Dec
Days	24	–	–	8
Sessions	6	–	–	2
Max.	10,000	–	–	150,000
Totals	38,950	–	–	370,000

the first season when we visited the roosts via a fixed rotating schedule. Each roost was visited between two and six times per season. Trapping was performed from November onwards, for 0.5–4.0 months per winter (Table 2).

Results

During the four non-breeding seasons of 2007/08–2010/11 a total of 22,173 swallows was captured, generating 22 foreign recoveries (recovery rate 0.099%). When recoveries from the Eurasian breeding range alone are considered, the recovery rate drops to 0.08% (16 recoveries). Only two swallows originated in western Europe (west of 10°E), 14 came from central and eastern Europe (from Hungary through Belarus, Ukraine and Russia), and none from the East Palearctic (east of 60°E).

Arrival, numbers and length of stay

Numbers of Barn Swallows encountered at Zambian roosts during the first half of November remained low, but increased dramatically in the

second half of November when substantial rain fronts were developing (Fig. 7). In general, a north–south passage was registered, with largest numbers first at Kasanka (12°S) around late November/early December, then successively at Kabwe (14°S) in mid December and at Chisamba (15°S) in late December/early January. Annual variations in timing were marked, however, with later peaks in years with (far) fewer roosting swallows (e.g. 2008/09).

Roosts rarely exceeded 50,000 swallows. Numbers may have been somewhat inflated given that our use of a recorder attracted birds which otherwise might have roosted elsewhere. Swallow numbers dropped steeply after early January and typically remained low thereafter. In early February a resurgence in numbers was recorded at Kabwe, but not at Chisamba or Kasanka. Only in one of the four seasons did the observation period include all of February and most of March, hence the poor coverage of the return migration towards the breeding grounds (Fig. 7). The large number

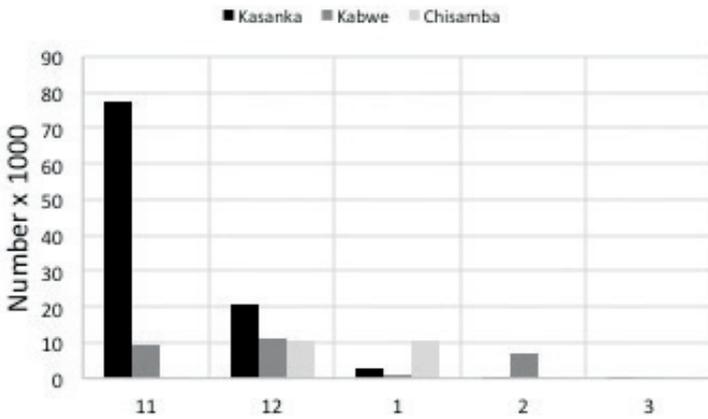


Figure 7. Seasonal evolution of Barn Swallow *Hirundo rustica* numbers at three sites in Zambia, averaged for November–March 2007/08–2010/11 (for Kasanka only 2007/08 and 2010/11).

Évolution saisonnière du nombre d'Hirondelles rustiques *Hirundo rustica* à trois sites en Zambie pour la période de novembre à mars de 2007/08 à 2010/11 (Kasanka : seulement 2007/08 et 2010/11).

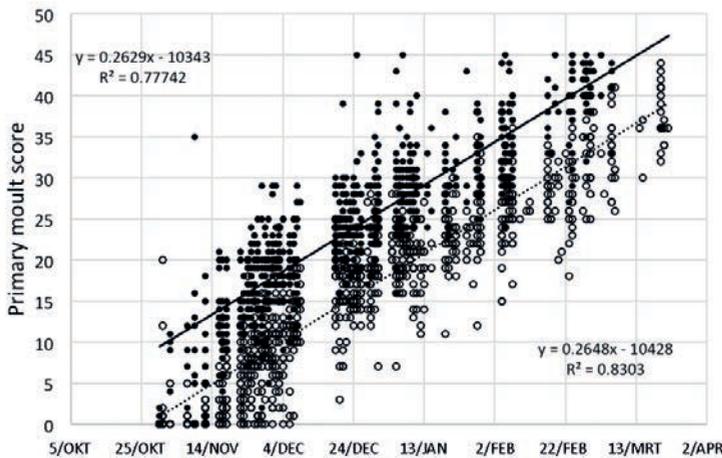


Figure 8. Primary moult score of 757 adult (black circles) and 929 juvenile (open circles) Barn Swallows *Hirundo rustica* captured in Zambia in 2007/08.

Phénologie et durée de la mue des rémiges primaires d'Hirondelles rustiques *Hirundo rustica* adultes ($n = 757$; cercles noirs) et juvéniles ($n = 929$; cercles ouverts) capturées en Zambie pendant la saison d'hivernage de 2007/08.

of swallows in the first part of the non-breeding season (November–December) counter-intuitively coincided with the smallest number of flying insects captured on nearby car transects (Table 1).

Swallows using northern roosts probably stayed longer than those frequenting roosts further south. At Kasanka (12°S), the time elapsed between capture and recapture was on average 38.8 ± 24.6 days ($n = 6$, range 4–62 days), at Kabwe (14°S) 24.1 ± 17.4 days ($n = 66$, range 1–75 days) and at Chisamba (16°S) $18.1 \text{ days} \pm 12.7$ ($n = 25$, range 1–51 days).

Moult

In the first half of November most adults had already started moulting, steadily progressing towards late February/early March, when primary moult was almost completed. Juveniles moulted

at the same speed, but with a delay of eight days compared to adults (Fig. 8).

Site fidelity

In most years and sites, 2–38 swallows were recaptured 1–75 days after the initial capture at the same site (mean 22.7 ± 17.4 days). In only two cases, Chisamba in 2007/08 and Kabwe in 2010/11, within-season captures were absent (but relatively small numbers were trapped; Table 3). A single swallow was recaptured at another roost within the same season, i.e. a juvenile ringed on 10 November 2007 at the Itawa Dam near Ndola, northern Zambia (12°58'18"S 28°39'59"E) and recaptured on 29 November 2007 at the roost near Chisamba, c.145 km to the south. Of 167 recaptured swallows, 66 were recaptured at the same roost up to three years later (Table 4). Except for the above-mentioned swallow from Ndola, all

Table 3. Rainfall in October–April (in mm), number of Barn Swallows *Hirundo rustica* captured, number recaptured within the same season, and mean number of days that elapsed between capture and recapture (range) for Chisamba and Kabwe over four consecutive seasons.

Tableau 3. Pluviométrie en octobre–avril (mm), nombre d'Hirondelles rustiques *Hirundo rustica* capturées et recapturées par saison, et nombre moyen de jours écoulés entre le baguage et la reprise à Chisamba et Kabwe pendant quatre saisons consécutives.

Season	2007/08	2008/09	2009/10	2010/11
Chisamba				
Rainfall	1,002	1,010	1,006	532
Captured	1,014	1,477	2,228	3,495
Recaptured	0	2	2	22
\bar{x} days (range)	–	23 (12–34)	35 (31–38)	16 (1–51)
Kabwe				
Rainfall	984	982	1,190	1,188
Captured	2,278	2,312	3,255	1,108
Recaptured	2	37	30	0
\bar{x} days (range)	60 (45–75)	18 (1–60)	27 (1–52)	–

Table 4. Number of juvenile and adult Barn Swallows *Hirundo rustica* captured at roosts in Zambia in 2007/08 through 2010/11, and numbers recaptured in later years. Year 0 = year of first capture.

Tableau 4. Nombre d'Hirondelles rustiques *Hirundo rustica* juvéniles et adultes capturées à des dortoirs en Zambie entre 2007/08 et 2010/11, et nombre de reprises les années suivantes. Année 0 = année de la première capture.

Age at capture	Captured	Year of recapture			
		0	1	2	3
1 year	16,189	80	31	4	1
>1 year	4,787	21	21	7	2

Table 5. Recaptures of Barn Swallows *Hirundo rustica* at roosts in Zambia in successive non-breeding seasons; year 0 = year of capture.

Tableau 5. Reprises d'Hirondelles rustiques *Hirundo rustica* aux dortoirs en Zambie pendant quatre saisons d'hivernage. Année 0 = année de baguage.

Capture/recapture	Year 0	Year 1	Year 2	Year 3	Total captured
2007/08	8	12	8	3	4,995
2008/09	39	26	3		3,789
2009/10	32	14			5,483
2010/11	22				6,727

recaptures in later years were from roosts where the swallows had been ringed.

Return rate

The chance of being recaptured in a later year was three times higher for swallows that had been adult when trapped for the first time than for juveniles (Table 5). The lower return rate of first-year swallows was consistent with a declining percentage of juveniles over the course of the non-breeding season from October through March, i.e. respectively 84%, 80%, 80%, 72%, 75% and 75% (based on respectively 32, 5,245, 10,051, 5,754, 1,017 and 32 age-identified captures, combined for 2007/08 through 2010/11). That is, under the presumption that catchability of adults and juveniles did not change over time, the return rate in successive years was variable between years. Of swallows captured in 2008/09, 0.68% was recaptured the next year, almost three times greater than re-traps in 2007/08 and 2009/10 (0.24–0.26%, Table 5).

Discussion

Zambia is an important staging area for European swallows. Dowsett *et al.* (2008) reported roosts of 2–3 million birds during southbound migration, but far fewer on northward passage. The large majority of these birds originate from central and eastern Europe (10–60°E), as suggested by 14 of 16 European recoveries resulting from our ringing 22,173 Swallows over four consecutive non-breeding-seasons (the remaining two west of 10°E). A similar provenance of Zambian Swallows was also apparent from extensive ringing near Choma (16°38'N 27°00'E) in 1971–74, which generated 30 recoveries in Europe: one in the west, 27 in the central states and two in the east (as tabulated in Dowsett & Leonard 2001: 27–28).

The 22,173 ringed swallows yielded a recovery rate of 0.08% for birds ringed or recovered in Europe. This low recovery rate is similar to that calculated in southern Africa for swallows ringed since 1987 (0.08%) and is consistent with the decline in recovery rate noted in South Africa since at least the 1950s. Swallows ringed in South Africa before 1987 had a recovery rate of 0.38% (Burman *et al.* 2018), whereas Dowsett (2009) obtained 33 foreign recoveries from 13,991 Swallows ringed in Zambia in four years between 1970 and 1974 (recovery rate of 0.24%). Declining reporting

rates for ringed birds have been known for decades (Bezzel 1995, Schlenker 1995) and are probably associated with a change in behaviour among the public (Robinson *et al.* 2008).

At roosts in central Zambia we recorded the highest numbers in the first two months after swallow arrival in November and a relative paucity after early January. These data suggest that many swallows depart Zambia in the second part of the non-breeding season, presumably in favour of regions further south (Altwegg *et al.* 2012), although a redistribution within Zambia cannot be eliminated. A ring analysis of swallows captured in various parts of South Africa showed that 81% of ringed swallows encountered in the Gauteng region originated from central and eastern Europe (10–60°E) and 19% from western Europe (west of 10°E). This preponderance of East European swallows accords well with the ratio encountered in Zambia, but contrasts with swallows from other parts of southern Africa where more equal mixtures of western, central and eastern populations in various combinations were recorded (Burman *et al.* 2018). The Gauteng region in northern South Africa lies directly south of central Zambia, c.1,200 km from where our effort was conducted. In fact, the only two recoveries of our Zambian-ringed swallows in South Africa came from Gauteng; an adult ringed near Kabwe on 14 January 2009 and recovered at Roodepoort on 30 October 2010, and a juvenile ringed on 13 December 2010 at Kasanka and recovered in Morelatakloof on 3 February 2015.

The recaptures of swallows at Zambia roosts indicate some site fidelity, with re-traps of birds up to 75 days after initial capture. Of 101 swallows recaptured in Zambia within the same season, the mean duration of stay amounted to 22.7 ± 17.4 days (but see trapping periods, Table 2, which did not always cover the entire non-breeding season), substantially shorter than calculated for adults and juveniles trapped at Katanga, DR Congo, in 1955/56 and 1956/57, i.e. 48 and 44 days, respectively (De Bont 1962). The shorter stay at Zambian roosts, perhaps related to rainfall-induced shifts to roosts further south in the latter part of the non-breeding season, implies that moult of flight feathers may commence at widely separated locations (see Gauteng recoveries above). Duration of primary moult is variously estimated at 120–195 days (De Bont 1962, Francis 1980,

van den Brink *et al.* 2000), with adverse local conditions leading to a substantially longer moult period (van den Brink *et al.* 2000). The large-scale departure of swallows from Zambia in January commences when the birds are in full wing and tail moult, with adults just past the midpoint of primary moult and juveniles lagging behind by on average eight days (Fig. 8). As aerial feeders, swallows usually moult one primary (sometimes two, when one of the flight feathers is almost full grown) simultaneously (van den Brink *et al.* 2000), whereas their pointed wings possess a high aspect ratio and hence low flight costs (Jenni & Winkler 2020). A within-season 'hop' of >1,000 km whilst moulting is therefore not likely an energetically costly affair, even when excluding the possibility of suspended moult.

Site fidelity of swallows at roosts in Zambia was frequent. All 66 controls in subsequent years were from the same roost as where birds had been initially ringed. High site fidelity was also recorded in DR Congo in the mid 1950s, where 17 juveniles and 13 adults from a total of 1,596 ringed were recaptured at the same site the following year (De Bont 1962). Ringing at various localities in South Africa revealed that 68 of 120 recaptures in subsequent years were at the same roosts (Oatley 2000). A much lower recurrence was found in northern Botswana: just five adults of 15,820 ringed in two preceding years in the early 1990s; however, the enormous size of this roost, with >2 million birds in the second year of the study, may have reduced the chances of recapture (van den Brink *et al.* 1997, Zwarts *et al.* 2009). For Zambian swallows, the meagre evidence suggests that birds use successive roosts far apart (central Zambia and the Gauteng region in northern South Africa), as reported for two of our catches in subsequent years, and mentioned for two more swallows ringed in the early 1970s near Choma, and recovered in subsequent years in Free State and Transvaal (Dowsett 1977; R. J. Dowsett *in litt.* 2021). When Zambian roosts are used repeatedly between years, why not those used by the same birds in the same year further south as well? The strategy of using multiple 'wintering' sites and stopovers, sometimes repeatedly between years, has been observed in several other passerines on both sides of the Atlantic (Palearctic–African and American), such as Great Reed Warbler *Acrocephalus arundinaceus* (Hasselquist *et al.*

2017), Marsh Warbler *A. palustris* (Pearson *et al.* 2014), Garden Warbler *Sylvia borin* (Iwajomo *et al.* 2011), Wood Thrush *Hylocichla mustelina* (Stanley *et al.* 2012) and Swainson's Thrush *Catharus ustulatus* (Cormier *et al.* 2013), as well as Common Swift *Apus apus* (Wellbrock *et al.* 2017). Two of six tagged swallows from Lithuania switched 'wintering site' in southern Africa in 2012/13: a female arrived in the non-breeding area in south-eastern South Africa, and after 55 days moved to another non-breeding area in the same region (duration of movement two days), whereas a male arrived in eastern DR Congo on 7 October 2012, then transferred to a site in south-western South Africa after 47 days, taking 21 days to reach the second destination (Briedis *et al.* 2018). And five of 22 Dutch swallows equipped with geolocators used two or three successive sites in 2012/13 within Central and southern Africa, the other birds just one (Stichting Hirundo 2021). Switching between sites during the non-breeding season may be a common strategy for birds using seasonal habitats (Underhill 2007). Continued or excessive rainfall, with declining catchability of flying insects (but not necessarily fewer insects; see Table 1), may well be the trigger for swallows roosting in Zambia to redistribute their wintering quarters southwards in the second half of the non-breeding season. Termite activity in high rainfall regions (>750 mm rainfall per year, as in Zambia), for example, is highest in the transitional season, i.e. with neither high nor low rainfall, but lower during heavy rainfall (Davies *et al.* 2015).

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- ^a *Hirundo Foundation, Bovenstraatweg 17, 8096 PC Oldebroek, Netherlands. E-mail: zwaluwbrink@hotmail.com*
- ^b *Doldersummerweg 1, 7983 LD Wapse, Netherlands. E-mail: rob.bijlsma@planet.nl*

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