

Apparent survival rates of Cape Sugarbirds *Promerops cafer* at a breeding and a non-breeding site

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Reliable estimates of survival rates of southern African bird species are still rare. Yet precise information on life history traits of birds from this southern Mediterranean-type climate would help in evaluating the generality of global patterns of avian life history. We estimated annual survival of Cape Sugarbirds *Promerops cafer* at a breeding site and a non-breeding site, using capture-mark-recapture methods. Consistent between the two sites, annual survival was 0.54 for females and 0.64 for males, with an average of 0.62 at the breeding site. These estimates are close to estimates for more tropical African species, but at the upper range of estimates for northern-temperate passerines. With their small clutches, Cape Sugarbirds thus have a life history that is more similar to tropical passerines than to northern-temperate passerines. We found a high proportion of transient individuals at the non-breeding site, but not at the breeding site. This suggests that Cape Sugarbirds employ two strategies to cope with the spatially variable food supply during the non-breeding season. About half of the individuals appear to visit the same set of sites every year, whereas the others are more opportunistic and tend to visit different sites in different years.

Introduction

The two species of sugarbirds, the Cape Sugarbird *Promerops cafer* and Gurney's Sugarbird *P. gurneyi*, form the monogeneric family Promeropidae, endemic to southern Africa. Recent research has demonstrated that, in terms of Sibley and Ahlquist's (1990) phylogeny, the sugarbirds are basal to the Passeroidae, a large superfamily that contains five families — Nectariniidae (169 species), Melanocharitidae (10), Paramythiidae (2), Passeridae (386) and Fringillidae (993) — with c. 15% of the extant bird species of the world (Del Hoyo *et al.* 1992, Barker *et al.* 2004, Beresford *et al.* 2005). Given the basal position of the sugarbirds, information on the life history of the sugarbirds is of particular value to phylogenetic research. Apart from a survival rate estimate based on non-standard methods by Yom-Tov *et al.* (1994), this paper presents the first of such information on the Cape Sugarbird. De Swardt and Peach (2001) presented survival rates for the other taxon in the family, Gurney's Sugarbird.

Passerine birds of the humid tropics have higher survival rates than similar species living in northern temperate regions (Johnston *et al.* 1997, Peach *et al.* 2001, Ghalambor and Martin 2001, but see Karr *et al.* 1990 even though that study did not correct for the effect of transients). This pattern is generally explained by climatic differences favouring different life histories (Murray 1985, Skutch 1985, Martin 1996). There are few data on survival of afrotemperate passerines to evaluate if the same rule holds true on the Southern hemisphere. In particular, there are few data available on survival rates of southern African passerines, and the only other analyses which make use of statistically-sound estimation methods are those of de Swardt and Peach (2001), for Gurney's Sugarbird, and estimates for one population of Sociable Weavers *Philetairus socius*

(Brown *et al.* 2003, Covas *et al.* 2004). Peach *et al.* (2001) reported survival for passerines at a more tropical location in Malawi (16°S).

Cape Sugarbirds occur in the fynbos biome and are mainly restricted to sites that have stands of nectar-producing Proteaceae. Among the visited plant species are the sugarbush *Protea*, the Pincushion *Protea Leucospermum* and Pagodas *Mimetes*, or nectar-producing alien plants, such as the gum tree *Eucalyptus* spp., sisal plants *Agave americana*, and the New Zealand Christmas Tree *Metrosideros excelsa*. Sugarbirds use these flowers both for their nectar and to eat the insects that are attracted to such flowers (Tjørve *et al.* 2005). At most sites, a limited range of nectar-producing species occurs and these are occupied by sugarbirds during the period in which nectar is being produced. Consequently, many sugarbirds are nomadic, moving between patches of nectar-producing plants. We know little about the extent, scale and regularity (on an annual basis) of these annual movement patterns (Broekhuysen 1959, Hockey *et al.* 2005).

Breeding occurs in the austral winter, coinciding with the flowering season of the most widespread and abundant *Protea* species, such as the Common Sugarbush *Protea repens* and the bearded and spoon-bract sugARBUSHES (e.g. the Narrow-leaf SugARBUSH *P. neriifolia*: Rebelo 1995). Egg laying peaks in April and May, but can occur at any time of the year if nectar resources are sufficient (Hockey *et al.* 2005). The breeding cycle, from initiation of nest building to fledging, takes c. 10 weeks (Broekhuysen 1959).

Cape Sugarbirds are sexually dimorphic, with males being 19% heavier than females (Seiler and Fraser 1985). The tails of males (mean 259mm, maximum 360mm) are more than twice as long as those of females (mean 125mm,

maximum 188mm); males retain their long tails throughout the year, not only in the breeding season (Seiler and Fraser 1985). The male performs an elaborate display, which includes whipping the long tail over its back and under its belly and flapping its wings in such a way that the large bulge on the sixth primary produces a distinct vibratory sound (Skead 1967). The female builds the nest and incubates the eggs (most frequent clutch size is two eggs); the male assists with bringing food to the nestlings, doing about one quarter of the feeding visits (Broekhuysen 1959, Skead 1967). Given the large differences between the male and the female, both in their behavioural roles and in size and shape, we would anticipate substantial differences in attributes such as survival and catchability between the sexes.

Methods

Study sites and fieldwork

This analysis is based on capture-recapture fieldwork undertaken at two sites in the Western Cape Province: Betty's Bay (34°21'S, 18°55'E) between 1986 and 1996, and the Helderberg Nature Reserve (34°04'S, 18°52'E), between 1997 and 2000.

The site at Betty's Bay has an area of about 5ha zoned as public open space, immediately west of Jock's Bay. The sugarbirds are attracted to the Green Tree Pincushion *Leucospermum conocarpodendron* subsp. *viridum*, which flowers and produces nectar from September–December. In addition, there are a few New Zealand Christmas Trees on plots in the area, and these have a similar flowering period and are visited by the sugarbirds for their nectar. For the remainder of the year, sugarbirds occur in this area as transients. At Betty's Bay, all data were collected during the non-breeding season, between the end of October and end of January.

The Helderberg Nature Reserve lies on the south-facing slope of the Helderberg Mountains, near Somerset West. The cultivated section of the Reserve has an area of 26ha. Because many trees had been planted, the diversity and density of *Protea* trees was greater than that found naturally in the Western Cape. The Shuttlecock Sugarbush *P. aurea* (peak flowering time January–June) and the Forest Sugarbush *P. mundii* (flowers mainly from February to September; Rebelo 1995) were the most abundant species. Further descriptions of this study site are contained in Calf *et al.* (2003a, b, c). At the Helderberg reserve, birds were captured throughout the year, from June 1997–June 2000. Taking account of the breeding phenology of these birds, we estimated survival for the period from March–February of the following year.

At both the Helderberg Nature Reserve and Betty's Bay, sugarbirds were captured in mist-nets and SAFRING rings were used for individual identification. Birds in their first year were recognised by the retained gape, short tails and pale plumage characteristics, as described by Seiler and Fraser (1985). All other birds were classified as adults. Diagnostic features of adult male Cape Sugarbirds are tails longer than 200mm and a distinct bulge on the sixth primary; they also have longer wing lengths than females (male range 86–101mm; females 77–87mm: Seiler and Fraser 1985). Birds were released at the site of their capture.

Statistical analyses

We used standard capture-mark-recapture (CMR) methods to estimate survival and related parameters (Lebreton *et al.* 1992). These methods separate survival from recapture rates, where the recapture rate is the probability of capturing an individual, given that it is alive and trappable at that time.

CMR methods assume that all individuals have the same survival and recapture probabilities. We tested these assumptions by goodness-of-fit tests in the program U-CARE (Choquet *et al.* 2001). Neither data set violated the assumptions significantly (Helderberg: $\chi^2 = 5.4$, $df = 8$, $p = 0.71$; Betty's Bay: $\chi^2 = 37.7$, $df = 49$, $p = 0.88$). However, the data from Betty's Bay contained transients (one-sided test for transience, $p = 0.01$). Such a mixture of transients and residents causes survival to be underestimated (Pradel *et al.* 1997) during the first time interval after initial capture. We therefore accounted for lower apparent survival during the first year after marking, and only report survival rates for residents (see Pradel *et al.* 1997 for details). During the first year of the study, residents could not be separated from transients, and we therefore also did not report survival for the year 1986/1987.

In both data sets, we examined the effect of time and sex on survival and recapture rates. For the data from the Helderberg reserve, we further examined differences between one-year-old birds and older ones. We were unable to estimate juvenile survival because of insufficient data. For the data from Betty's Bay, we also investigated whether the proportion of transients varied over the years and between the sexes. There was no evidence for a significant proportion of transients in the Helderberg reserve (see goodness-of-fit test, previous paragraph) and we did not further examine this point. We fitted all statistical models using the program MARK (White and Burnham 1999), and based model selection on the sample size-adjusted Akaike's Information Criterion (AICc, Burnham and Anderson 2002).

Results

At Betty's Bay, 774 females and 645 males were ringed, of which 47 and 110 were recaptured at least once in a year subsequent to the year of ringing. At the Helderberg reserve, 425 females and 374 males were ringed, of which 30 and 54 were recaptured at least once. We did not observe any individuals moving from one location to the other and there were no recaptures of previously-ringed birds. Model selection favoured a model with constant survival and sex- and time-dependent recapture rates for the Helderberg reserve (Model 1, Table 1). This model was twice as well supported by the data as the next-best model, allowing for a sex effect on survival (Model 2; ratio of Akaike weights 0.57/0.26). The best model for Betty's Bay contained interactive effects of sex and time on survival, and sex- and time-dependent recapture rates (Table 2).

Both data sets yielded similar survival rates. According to the best model, annual sugarbird survival at the Helderberg reserve was 0.62 ± 0.10 (mean \pm SE). The second-best model estimated female survival at 0.53 ± 0.15 and male survival at 0.66 ± 0.12 . At Betty's Bay, survival varied over time (Figure 1), and the average was 0.54 ± 0.08 for females

Table 1: Summary of model selection for Cape Sugarbird survival at the Helderberg Nature Reserve from 1997–2000. We evaluated the effects of age, sex and time on survival, and the effects of sex and time on recapture rates. The columns headed 'Survival' and 'Recapture' show the effects contained in a particular model. A plus sign (+) indicates additive effects, and an asterisk (*) indicates effects plus their interaction. Model selection was based on Akaike's Information Criterion (AICc), where a lower value indicates a better model. Δ AICc shows the difference in AICc between the current model and the best one. Akaike weights measure the relative support each model has, compared to the other models in the set. K is the number of parameters, and the 'Deviance' column is the difference in $-2 \log$ Likelihood between the current model and the saturated model, the saturated model being the one with the number of parameters equal to the sample size

	Survival	Recapture	AICc	Δ AICc	Akaike weights	K	Deviance
(1)	Constant	Sex + time	583.25	0.00	0.572	5	35.68
(2)	Sex	Sex + time	584.84	1.59	0.258	6	35.24
(3)	Time	Sex + time	587.18	3.93	0.080	7	35.54
(4)	Age + sex	Sex + time	587.65	4.40	0.063	8	33.97
(5)	Age + sex + time	Sex + time	589.67	6.42	0.023	9	33.94
(6)	Age + sex + time	Sex * time	593.55	10.30	0.003	12	31.66
(7)	Age * sex * time	Sex * time	605.32	22.07	0.000	19	28.85

Table 2: Summary of model selection for Cape Sugarbird survival at Betty's Bay from 1986–1996. All models accounted for the effect of transients. See legend of Table 1 for further details

	Survival	Recapture	AICc	Δ AICc	Akaike weights	K	Deviance
(1)	Sex * time	Sex + time	1 445.74	0.00	0.994	32	145.11
(2)	Sex * time	Time	1 457.11	11.38	0.003	31	158.58
(3)	Sex * time	Sex	1 457.99	12.26	0.002	23	176.05
(4)	Constant	Sex + time	1 484.21	38.48	0.000	13	222.77
(5)	Sex	Sex + time	1 484.60	38.86	0.000	14	221.12
(6)	Sex + time	Time	1 485.37	39.63	0.000	22	205.49
(7)	Sex	Time	1 494.58	48.84	0.000	13	233.14

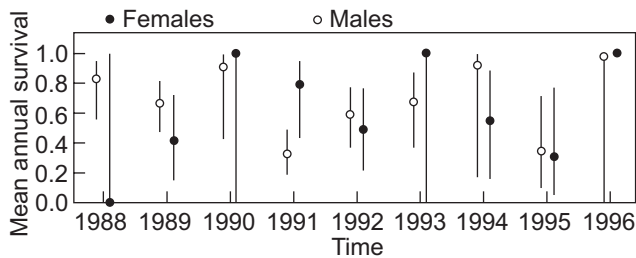


Figure 1: Estimated survival rates of female and male Cape Sugarbirds at Betty's Bay. The vertical lines show 95% confidence intervals. The estimates are from Model 1, Table 2. Those estimates which are at the border (0 or 1), or for which the confidence interval ranges from zero to one, were not included when calculating average survival

and 0.64 ± 0.07 for males. We obtained these mean estimates by treating time as a random effect (Burnham and White 2002). This method allows decomposing the variance into a component caused by biological processes and another component due to sampling variance. The temporal process variance was 0.03 for males. For females, this method did not yield a reliable estimate because female survival could reliably be estimated for too few years (Figure 1). The estimated proportion of transients at Betty's Bay was 53%.

The recapture rates varied over the years at both sites and were, on average, 0.12 ± 0.03 for females and 0.25 ± 0.05 for males in the Helderberg reserve. At Betty's Bay, the recap-

ture rates averaged 0.06 ± 0.01 for females and 0.24 ± 0.03 for males.

Discussion

We estimated survival of Cape Sugarbirds at a breeding and a non-breeding site for two different populations. Consistent between the two sites, annual survival was 0.54 for females and 0.64 for males, with an average of 0.62 at the breeding site. In contrast, de Swardt and Peach (2001) estimated survival of Gurney's Sugarbirds at 0.81 and found no differences between the sexes. In both studies, females had lower recapture rates than males. This demonstrates the importance of accounting for recapture probabilities, to get unbiased survival estimates for both sexes. De Swardt and Peach (2001) attributed the lower recapture rate for female Gurney's Sugarbirds to their lower aggressiveness and less territorial behaviour, compared to the males. However, our study showed similar differences in recapture rates at the non-breeding and the breeding site, even though — contrary to Broekhuysen (1959) — both male and female Cape Sugarbirds defend feeding territories outside of the breeding season (Collins 1983, Rebelo, pers. comm.). Alternatively, the lower recapture rate for females may be related to differences between the sexes in movement or activity radius. Yom-Tov *et al.* (1994) reported survival rates for Cape Sugarbirds that are lower than our estimate, but their estimate is biased towards low values because they did not account for recapture probabilities.

According to recent phylogenetic evidence, sugarbirds

form the basal group of the large superfamily Passeroidea, and are closely related to sunbirds (family Nectariniidae) (Barker *et al.* 2004, Beresford *et al.* 2005). There are still few reliable estimates of survival for African passerines. Our survival estimate for the Cape Sugarbird is within the range of the estimates for five sunbird species in Malawi (0.55–0.90), albeit somewhat lower than their mean (0.71, Peach *et al.* 2001). Our estimate is close to the mean of all 28 passerine species for which Peach *et al.* (2001) estimated survival in Malawi (0.64), and the estimates for Sociable Weavers near Kimberley, South Africa (0.66, Brown *et al.* 2003, Covas *et al.* 2004). It is near the upper limit of the range of survival estimates for northern-temperate passerines (Johnston *et al.* 1997). Sugarbirds thus exhibited the life history of a typical tropical bird with low clutch size (1–2 eggs: Hockey *et al.* 2005) and relatively high adult survival. This finding does not support the notion that annual variability in climate determines life history (Ricklefs 1980), because Cape Sugarbirds are endemic to the southern tip of South Africa, with its temperate Mediterranean-type climate. On the other hand, Cape Sugarbirds are exposed to high rates of nest predation (Broekhuysen 1959, Calf *et al.* 2003b). Higher nest predation in the tropics compared to northern-temperate regions is one proposed explanation for the life history differences among birds living in these two regions (Skutch 1985), even though the generality of this pattern has been questioned (Martin 1996).

The Helderberg Nature Reserve is a breeding site, and although sugarbirds move out of it during the non-breeding season, there are always sugarbirds present. This is because many nectar-producing plants have been planted in the reserve, and there is always at least one species providing some nectar (Calf *et al.* 2003a).

In contrast, the site at Betty's Bay is exclusively a non-breeding site for sugarbirds. The models suggested that about half of the birds recorded at this site were transients — birds that visited the site only in one of the years of our study, but not during the other years. For the remaining birds, this site was part of a regular annual itinerary. The survival rates for both males and females of the non-transient component of the sugarbird population at Betty's Bay were essentially identical to those of the breeding population in the Helderberg Nature Reserve. Because we cannot distinguish between mortality and permanent emigration, this result implies that for half of the sugarbird population, site faithfulness to non-breeding sites is the same as to breeding sites.

Our results suggest that sugarbirds have two strategies for finding the scattered patches of nectar-producing plants during the non-breeding season. Some part of the population (about 50% at Betty's Bay) adopts an 'itinerant' strategy of visiting the same sites every year on a regular itinerary, and the other part of the population adopts an 'explorer' strategy, finding a new set of nectar-producing sites each year.

The advantage of the 'itinerant' strategy is that it would reduce the need to search for a new feeding site when a site seasonally stops producing adequate nectar. The strategy can be visualised as a chain of several (perhaps four or five) sites visited in sequence throughout the year. The disadvantage is that if a site is destroyed between the

annual visits (either due to natural occurrences such as fire or to anthropogenic events such as clearance for agriculture or housing development), the chain of sites is broken and the bird may be forced to adopt an 'explorer' strategy or might not survive.

The 'explorer' strategy will work successfully when successive seasonal feeding sites are unpredictable or harder to find. Birds that adopt the 'explorer' strategy would require a longer search time, but are likely to reach relatively rich new sites.

The implications of our results on sugarbird movement patterns need to be confirmed by observing the movement of individual birds in more detail, e.g. through radio-tracking. However, the movement patterns of Cape Sugarbirds are likely to affect the dynamics of plant populations, because the birds are important (but not exclusive: Rebelo 1995) pollinators for many Proteaceae species. For example, Collins (1983) and Wright *et al.* (1991) found greatly reduced seed-set in *Mimetes hirtus* and *Protea laurifolia*, after excluding birds from the inflorescences. Other *Protea* species, however, were effectively pollinated by insects alone (Coetzee and Giliomee 1985, Wright *et al.* 1991). Understanding what factors affect the movement strategies and how fast individual sugarbirds can adapt their strategy may matter for predicting how the plant communities change in response to changed climate or human land use. For example, if the frequency of bush fires increases, a flexible movement strategy may become more advantageous for sugarbirds. Conversely, those birds adopting the flexible strategy may enhance the ability of the proteas to cope with the imposed shorter growth period.

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