

**THE BIOLOGY OF SUBURBAN OLIVE THRUSHES (*TURDUS  
OLIVACEUS OLIVACEUS*) IN THE EASTERN CAPE,  
SOUTH AFRICA**

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## ABSTRACT

This study investigated the biology of the Olive Thrush *Turdus olivaceus olivaceus* in Grahamstown, South Africa from 1998 to 2003. Behavioural differences between males and females, parent-young interactions, development of fledglings, and the role of song and moult in territorial behaviour were investigated. Comparisons of biometrics, moult and survival were made using Olive Thrush ringing data from other regions. There were no significant differences in mass, wing length or survival rate between the Eastern and Western Cape provinces, but primary wing moult started earlier in the Western Cape and coincided with the end of the main breeding periods in both provinces. Both males and females of breeding pairs remained in and defended their territories throughout the year, but there was some evidence that territorial defence was strongest during the breeding periods.

Roughly, every 100 eggs laid produce 50 fledglings. Out of these 20 to 30 reach the age of independence at approximately 50 days, and only five of these juvenile birds reach maturity. Adult survival was estimated at 80%, with a mean life expectancy of 4.5 years and a conservative estimate of maximum lifespan of 11 years.

Using ringing data and museum specimens, the Olive Thrush was compared with the Karoo Thrush *Turdus smithi*, a former race of the Olive Thrush. Olive Thrushes had shorter bills and wings, but were heavier than Karoo Thrushes from the Cradock district. There were also differences in bill and eye-ring colouration between these populations. No morphological differences were found between the sexes in either species.

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## 1 General introduction

Many birds today occupy urban habitats. While some species have been well studied in the temperate northern hemisphere, there have been fewer studies of such populations in temperate or sub-tropical southern regions. In South Africa common garden residents include the Olive Thrush *Turdus olivaceus*, for which only one previous study (Winterbottom 1966c) has examined “garden birds”. There have been no previous studies of individually marked Olive Thrushes using coloured rings. This offers an opportunity for comparison with studies of the European Blackbird *T. merula*, Song Thrush *T. philomelos*, Mistle Thrush *T. viscivorus* and the American Robin *T. migratorius*. Such comparisons may clarify common adaptations to this habitat, and differences between northern temperate and southern hemisphere birds, which have often been described as fundamentally different (Ghalambor and Martin 2001, Johnston *et al.* 1997, McCleery *et al.* 1998, Peach *et al.* 2001, Ricklefs 2000).

There is a monograph on thrushes of the world (Clement and Hathway 2000), and reviews of the biology (Urban *et al.* 1997) and taxonomy (Keith and Urban 1992) of African species. Recent phylogenetic studies have re-assessed both the familial relationships of the group, and the status of populations previously included within the Olive Thrush. These will be commented on where appropriate.

A former race *T. o. smithi* of the Olive Thrush has been raised to specific status (Bowie *et al.* 2003). In this thesis, the common name, Olive Thrush, may be used to refer to any race of *T. olivaceus*, and *T. o. smithi* will be referred to as the Karoo Thrush *T. smithi*. Where applicable and to avoid ambiguity, trinomial nomenclature has been used.

In many territorial species it is common for some individuals to be non-territorial and for young to pass through a pre-territorial phase (Smith and Arcese 1989).

Such individuals are often referred to as ‘floaters’ and the abundance of these, relative to breeders, is likely to affect some estimates, such as annual reproductive rate and territory size. Some studies (Smith 1978) have investigated the ratio of floaters to breeders for other species, but such data are lacking for Olive and Karoo Thrushes, and as pointed out by Verner (1985) the study of floaters is a neglected area of avian field biology. Oatley and Arnott (1998) suggested that the ratio of breeders to floaters would affect mist-net recapture rates and this was demonstrated by computer simulations (Bonnievie 2003). References to the subject of breeders and floaters are made where appropriate.

Many of the results of this thesis have been published (Bonnievie 2003, Bonnievie *et al.* 2003, Bonnievie *et al.* 2004, Bonnievie 2004), but in some cases additional data may have become available and some results may consequently differ slightly. Such differences are discussed in the relevant chapters. Where no improvements were possible, the text from the published work has been copied verbatim.

M.G. Winterbottom’s study of the Cape Thrush (Winterbottom 1966c) has been cited many times herein, and it is perhaps useful to point out that the other citations of “Winterbottom” reference the work of her husband, J.M. Winterbottom.

## 2 History, nomenclature and systematic notes

### 2.1 Introduction

The classification of thrushes in the genus *Turdus* Linnaeus (1758) has been subject to many changes, from family level down to specific and subspecific levels. Thrushes have generally been grouped with robins and chats in the large family Turdidae, a subfamily of the Muscicapidae. The “Basle sequence” of 1954 combined the Turdidae, Sylviidae (Old World warblers) and Muscicapidae into a single larger family, Muscicapidae (Clement and Hathway 2000). The phylogenetic classification by Sibley and Ahlquist (1990) suggested that the true thrushes (clade Turdinae) belong to the superfamily Muscicapoidea, and indeed were members of the same family as the flycatchers and chats, Muscicapidae. Voelker and Spellman (2004) re-assessed the superfamily Muscicapoidea and found that Turdinae were more closely related to the starlings Sturnidae and dippers Cinclidae, but that the clade was sufficiently distinct to be considered a family of true thrushes. This new Turdidae family differs from the pre-1990 one of the same name by the exclusion of chats Saxicolini (represented by the genera *Cercomela*, *Myrmecocichla*, *Namibornis*, *Oenanthe*, *Phoenicurus*, *Saxicola* and *Thamnolaea* in southern Africa).

Within the family the classification of thrushes is also under revision. Keith and Urban (1992) divided the *Turdus olivaceus* species complex into seven species, stating that the Olive Thrush was the most variable and difficult to categorise. This arrangement was adopted by Urban *et al.* (1997), but did not find universal acceptance (Clement and Hathway 2000: 37, 333). Within the classification of Turdinae the *Turdus* thrushes, as the most developed group, have usually been placed last (Clement and Hathway 2000).

Linnaeus first described *Turdus olivaceus* in 1766, from a type specimen from the Cape of Good Hope. Sclater (1930) listed eleven races of the Olive Thrush

from Sudan to the Cape Province, South Africa, including Cabanis'<sup>1</sup> Thrush *T. o. smithi*<sup>2</sup> Bonaparte 1850. These appeared in "A first guide to South African birds" (Gill 1936) as the Cape Thrush *T. o. olivaceus* and the up-country race *T. o. smithi*, which differed from the nominate race in having "a brownish tinge over the orange of the flanks and a completely yellow bill"; Gill also used the vernacular name, Cabanis's Thrush. Layard (1867) had referred to these taxa as "Turdus Olivaceus (sic), Cuv.; *T. Ochrogaster*, Sparm.; *Le Griverou*, Le Vail." and "Turdus Obscurus (sic), Smith; *T. Smithii*, Bp", respectively. Haagner and Ivy (1908) also recognised these taxa and commented: 'The best known species of Thrushes in this country [South Africa] are the Cape Thrush (*T. olivaceus*) and its "up-country" representative, the Orange-billed Thrush (*T. cabanisi*)'; they stated that the bill of *T. cabanisi* is wholly yellowish-orange, whereas the maxilla of *T. olivaceus* is a dusky olive-green.

Roberts (1940) also listed these two taxa as separate species, the Cape Thrush *Afrocichla olivacea olivacea* and the Namaqua Thrush *Afrocichla smithi*, and the bill and eye-ring colours were correctly illustrated by Norman Lighton in Roberts' "The Birds of South Africa". In the revised edition of "Roberts Birds of South Africa", McLachlan and Liversidge (1966) had lumped the two species together; they were listed as *T. o. olivaceus* and *T. o. smithi*, and the illustrations were still from the original plates.

In the Fifties and Sixties the vernacular names Olive Thrush and Cape Thrush were used interchangeably (Rowan 1964, Skead 1965, Winterbottom 1966c), as were Namaqua Thrush (Anon 1948) and Namaqua Olive Thrush (Brandt 1960). Cambell (1956), however, listed Olive Thrush, Cape Thrush and Namaqua Thrush separately in the same report of nest records, Olive Thrush referring to

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<sup>1</sup> Jean Louis Cabanis (1816 – 1906) collected and described many African birds. He worked at the Berlin Museum for 51 years, retiring as curator of birds (Mearns and Mearns 1998).

<sup>2</sup> Dr. Andrew Smith (1797 - 1872), its discoverer. The S.A.O.S. List Committee changed the type-locality of this race to Philippolis, Orange Free State (Clancey 1959), on the grounds of the route taken by Smith. The name antedates *T. cabanisi* Cabanis 1851, and replaced the pre-occupied *Merula obscura* Smith 1836.

races other than *T. o. olivaceus* and *T. o. smithi*. Winterbottom (1966c) published the first comprehensive study on *T. o. olivaceus*, and she used both of the English common names, Olive Thrush and Cape Thrush. The vernacular names Cabanis's Thrush and Namaqua Olive Thrush have been used exclusively for *T. o. smithi* in the literature, but Cape Thrush was used for any of the races in the Sixties and Seventies.

In 1967 the Vernacular Names Committee of the SAOS published the revised names that had been accepted by the SAOS council (Rose 1967), and the Cape Thrush became known as the Olive Thrush. Skead (1967) and Winterbottom (1967) adopted the new name the same year, but Pitman (1967), Uys and Macleod (1967) and Tree (1967) still referred to it as the Cape Thrush. From then on it was commonly known as the Olive Thrush, except for Elliott and Jarvis (1970, 1973). In the fourth edition of "Roberts" (McLachlan and Liversidge 1978) the plates had been touched up and *T. o. olivaceus* now erroneously had an orange eye-ring; the bill colours remained unchanged.

Five races were recognised in southern Africa by McLachlan and Liversidge (1978):

- a) "*T. o. olivaceus* Linnaeus, 1766: Cape of Good Hope. From the South Western Cape to about Grahamstown. Less buff-orange below, the flanks partly olive."
- b) "*T. o. pondoensis* Reichenow, 1917: Pondoland. (Transkei north to Natal and Swaziland). Yellow under-parts brighter and extending over flanks."
- c) "*T. o. transvaalensis* (Roberts), 1936: Woodbush, Transvaal. Differs from (b) only by its darker upper-parts and breast-band."
- d) "*T. o. swynnertoni* Bannerman, 1913: Chirinda Forest, Rhodesia."
- e) "*T. o. smithi* Bonaparte, 1850: S. Africa. (Little Namaqualand, central and northern Cape, Orange Free State, southern and western Transvaal). Very much less buff-orange below."

Clancey (1982) described a race *T. o. culminans* Clancey from montane forests in Zululand, which differed from *T. o. pondoensis* in lacking the olivaceous suffusion to the dorsum, wings and tail, and by being larger.

*T. o. smithi*, has now been raised to specific status as the Karoo Thrush *T. smithi* (Bowie *et al.* 2003), and this will be followed in the seventh edition of “Roberts”. It can be considered unfortunate that this easily recognisable taxon was not treated separately from the other Olive Thrush races for nearly 50 years, as the distributional, biometric and breeding data of these taxa from the potential regions of sympatry are now difficult or impossible to separate.

## 2.2 Results and conclusions

Phylogenetic studies suggest that the Turdinae clade of true thrushes is sufficiently distinct from the starlings and the flycatchers to warrant family status within the superfamily Muscicapoidea. The *Turdus olivaceus* species complex should accordingly be classified as follows:

Class: Aves

Order: Passeriformes

Superfamily: Muscicapoidea

Family: Turdidae

Genus: *Turdus*

Within the species complex, current evidence suggests that *T. o. smithi* warrants specific status. The common and scientific names of *T. o. olivaceus* and *T. smithi* have been subject to many changes (Table 2.1).

**Table 2.1:** Names used in the literature for *Turdus olivaceus olivaceus* and *Turdus smithi*. Names in other languages are given for completeness. Language abbreviations: A – Afrikaans, X – isiXhosa, Z – Zulu

<i>Turdus olivaceus olivaceus</i>	<i>Turdus smithi</i>
<i>T. olivaceus</i> Linnaeus, 1766	<i>Merula obscura</i> Smith, 1836
<i>T. ochrogaster</i> Sparm.	<i>T. smithii</i> Bonaparte, 1850
<i>Le Griverou</i> Le Vail.	<i>T. cabanisi</i> Cabanis, 1851
	<i>T. obscurus</i> Smith
<i>Afrocichla olivacea olivacea</i>	<i>Afrocichla smithi</i>
	<i>T. olivaceus smithi</i>
Cape Thrush	Orange-billed Thrush
	Cabanis's Thrush
	Cabanis' Thrush
	Namaqua Olive Thrush
	Namaqua Thrush
Olive Thrush	Olive Thrush
	Karoo Thrush
Kaapse Lyster (A)	Namakwalyster (A)
Olyf Lyster (A)	Olyf Lyster (A)
um-Swi (X)	um-Swi (X)
u-Muswi (Z)	u-Muswi (Z)

### 3 Materials and methods

#### 3.1 Study area, data and morphometrics

Five datasets of Olive and Karoo Thrushes were analysed:

- Ringing data from mist-netting by George Underhill in the south-western part of the Western Cape, mainly in Durbanville (33°50'S, 18°39'E), Betty's Bay (34°22'S, 18°56'E), Rondevlei (34°04'S, 18°30'E) and Klawersvlei (34°13'S, 18°26'E) [1972-1996].
- Ringing data from mist-netting by Chris Brown, Adrian Craig, Pat Hulley, and the author in the Eastern Cape, mainly in the Grahamstown (33°18'S, 26°31'E) and the Cradock (32°10'S, 25°36'E) districts [1984-2003]. Some of these were colour-ringed by the author.
- 1 340 South African ringing records [1957-2004] from the SAFRING database, including all recoveries and selected recaptures (those in electronic format).
- Ringing data from Grahamstown of birds caught in hand-nets, by hand or in drop-traps baited with fruit, by the author [1998-2003]. Some of these were colour-ringed. When possible, fledglings were caught and ringed or colour-ringed soon after leaving the nest.
- Specimens from the East London Museum were described and measured.

Wing, tail, culmen and tarsus lengths, and mass were measured using the methods of De Beer *et al.* (2000) for live birds. Wing, head, body and tail moult were recorded. Some females could be sexed by the presence of a brood patch. Age was determined where possible. Juvenile birds are identifiable by their spotted breasts and buffy edges to their wing coverts. Ringing data were used to compare biometrics of the two species and to investigate the growth of young Olive Thrushes.

Wing, culmen and tarsus lengths of museum specimens of Olive and Karoo Thrushes were measured and compared (**Chapter 7**).

Birds were colour-ringed using unique permutations, and were sexed by behaviour. Observations of colour-ringed birds (more than 350 hours) took place on Rhodes University campus, and in a few gardens, in Grahamstown from November 1997 to 2003. Nests were searched for and breeding birds were monitored during the nesting period even if they were not ringed. In the cases where only one member of a pair of adult birds was ringed, this was used, together with their association with their nest or ringed fledglings, to identify the individuals of the pair. The term “known adults” includes these as well as the colour-ringed adults. Colour-ringed birds were observed to provide information on the breeding biology (**Chapter 10**).

Every brood under observation was scored with status codes 1 to 7 (Harrison *et al.* 1997), once per day by direct observation or by inference. In nests where laying date or hatching date was not recorded, these were inferred using an incubation period of 14 days and a nestling period of 16 days.

The literature was reviewed for records of diet (**Chapter 11**) and interactions with other animals (**Chapter 12**).

Statistical tests follow Zar (1974) unless otherwise stated. All variables are in italics except for standard statistical symbols, such as *n*, *P*, *Z*, and *F*.

### **3.2 Distribution, habitat, movements and dispersal**

The distributions (**Chapter 4**) of Olive and Karoo Thrushes were mapped from museum and ringing records using ArcView 3.1 (ESRI 1996). SAFRING data of recoveries and selected recaptures, with additional recaptures from the Eastern and Western Cape datasets, were analysed for dispersal and movements

(**Chapter 4**). Observations of colour-ringed birds provided information on local movements and territorial presence.

### **3.3 Territories: size, occupancy and defence**

Territories were mapped from observations of territory holders and boundaries were identified when neighbours had territorial disputes. The size of a territory, where boundaries were known, was estimated from these mappings. Seven nests belonging to different pairs were discovered in adjacent territories, and the average territory size was estimated from the total area containing these nests.

Selected Grahamstown ringing data from 1986 to 2001 were used to investigate seasonal fluctuations in population density (**Chapter 5**). The number of adult Olive Thrushes captured per 100 hours of mist-netting was accumulated for each month of the year. The duration of each ringing session was taken as the time in hours from when the first bird (of any species) was ringed until the last bird was ringed; this estimate was used because the durations of the ringing sessions were not recorded. The total length of net was approximately 85m for each of these sessions.

### **3.4 Survival and life-history variables**

Annual adult survival rate (**Chapter 6**) of Olive and Karoo Thrushes combined for South Africa was estimated according to Haldane's method (Haldane 1952, Seber 1973: 247-249) using all SAFRING recoveries of birds ringed from 1957 to 1994, and using age classes from one to 11 years. This method assumes constant survival rates and recovery probabilities of all individuals. This maximum-likelihood estimate requires an iterative solution and a spreadsheet was used to perform the computations.

Adult survival rates (**Chapter 6**) for Olive Thrushes in the Eastern and Western Cape provinces were estimated according to the method of Ricklefs (1997), which assumes that the population size remains constant, and that the numbers of adult ( $A$ ) and juvenile birds ( $I$ ) were mist-netted in proportion to their abundance in the population. Assuming that juvenile birds are all recruits, the annual adult survival rate, by definition, may then be estimated by  $S = A/(A + I)$ , with an unbiased standard error of  $[(A * I)/(A + I)^3]^{1/2}$ . This estimate is unbiased if the collection probabilities and survival rates of all individuals are identical. Although some of the assumptions of this method may not be met, it is potentially useful because it can be applied to small data sets. Estimates using the Jolly-Seber method (Jolly 1965, Seber 1973) were not attempted because of the small sample sizes from the specific regions. Survival rates are given with standard errors where possible.

Mean life expectancy was calculated as  $E = -1/\ln(S)$ , where  $S$  is the survival rate (Seber 1973: 4).

The accumulated recovery rate from 1950 to 1995 was plotted and trends were explained using a mark-recapture simulation (Bonnievie 2003), extended to analyse mortality rates of marked individuals in addition to recapture rates.

For each nest the number of active days was calculated (Mayfield 1975) and the number of egg or nestling mortalities was recorded. Daily nest mortality rate ( $DMR$ ) and nesting success ( $NS$ ) were estimated according to Mayfield (1975):

$$DMR = M/D$$

$$NS = (1 - DMR)^P,$$

where  $M$  is the total number of nest mortalities,  $D$  is the total number of active days, and  $P$  is the sum of the incubation and nestling periods, i.e. 30 days. The laying period was not included as it is relatively short (2 to 3 days) and because it was difficult to determine mortalities during this period. Because nests were

monitored on a daily basis, it was not necessary to use “Mayfield logistic regression” to try to improve these estimates (Hazler 2004, Jehle *et al.* 2004).

It was not possible to monitor egg mortalities for every nest under observation, so the annual reproductive rate (the average number of eggs laid per individual per year) was estimated as half the average number of fledglings per pair per year, divided by the nesting success (*NS*). The number of fledglings per pair per year was estimated from one pair for two successive years, and one pair for one year. In all three cases, no breeding attempts were missed and all attempts, successful and unsuccessful, were included in the estimate.

The proportion of colour-ringed fledglings observed each week from fledging date until they were no longer observed in the area was plotted; as the fledglings were monitored closely, these are conservative estimates of the proportion that survived.

### **3.5 Breeding period and moult**

In Grahamstown, the breeding season was quantified by monthly sums of the product  $C_n D_{nm}$ , where  $C_n$  was the clutch size of nest  $n$ , and  $D_{nm}$  was the number of days nest  $n$  contained eggs or nestlings in month  $m$ . For other regions, the main breeding periods are from Vernon and Herremans (1997), Maclean (1993) and Winterbottom (1966c).

Primary wing moult (**Chapter 8**) was scored according to Ginn and Melville (1983) and converted to a percentage estimate of new feather mass grown (Underhill and Joubert 1995). The primary moult was analysed using the method of Underhill and Zucchini (1988), for type 2 data (moult not yet started, moult score, moult completed). The masses of individual primaries needed for the moult analyses were measured from road casualties ( $n = 2$ ); the relative sizes of full-grown primaries are sufficiently consistent that a small sample could be used

(Underhill and Joubert 1995). The timing and duration of moult between the Eastern Cape and the Western Cape were compared. An estimated 95% of the population start moult within about  $\pm 1.96$  standard deviations of the mean starting date.

Active moult was looked for in “known birds” in the field to try to ascertain differences in the timing of moult of males and females, and when juvenile birds moult into adult plumage.

### **3.6 Calls and song**

Song output (**Chapter 9**) was measured by counting the number of song phrases (“*tu-wheet, tu-wheet*” representing one phrase), up to a maximum of 15 phrases on a maximum of three occasions (morning, midday and evening) per day in the study area. Using this method, the maximum possible measure of song output per day is 45. These counts were accumulated for each month of the year in 2002.

The records of Olive Thrushes noted on Diaz Cross Bird Club outings, within a 50 km radius of Grahamstown, were totalled for each month of the year from December 1991 to February 2002, and then normalised on the number of outings for each month. This measure of the frequency of Olive Thrushes detected per outing per month was compared to the frequency of song data. These records were also compared to the reporting rates for Zone 8 (Vernon and Herremans 1997), in which the study area falls.

Calls and song were recorded with a Sennheiser directional microphone and a Sony TC-D5M tape recorder. From observations the contexts of calls were related to behaviour. Sonograms were produced with Avisoft-SASlab Light for Windows, version 3.74. The sounds were digitised at 44kHz and the sonograms were all produced with the same vertical and horizontal scales for easy

comparison, rather than being optimised for detail in each type of call. The urban environment was very noisy which sometimes made recording difficult; no attempts were made at filtering out background noises in the sonograms.

### **3.7 Breeding biology**

Since 1997 breeding pairs and their young have been observed at nests ( $n = 15$ ) and in their territories (**Chapter 10**). The five territories were labelled A to E, each nest was numbered with a territory label prefix, and each brood was assigned a unique code. Nests were inspected using a mirror mounted on a metal pole to determine laying and hatching dates. The length of time that the males and females stayed on the edge of the nest, after feeding the nestlings and before flying off again, was recorded during some observation periods; to compare the average difference between male and female times, records were excluded if the female settled to brood the nestlings. Parental cleaning of nests was monitored, but observations were difficult from below the nests and records were only kept when the eating of faecal sacs was seen. The monitoring of the fledglings included changes in plumage and bill colour, description of calls and observation of feeding skills. Three nests were collected for analysis of nesting material after the young had fledged and the female had built and laid eggs in a new nest (In retrospect this is insufficient information to ascertain that the female will not reuse the nest as it was later found that females may return to old nests after they had built and used other nests).

Average nest initiation dates with standard deviations were calculated for both breeding seasons. The average re-nesting interval for successful broods was calculated from the fledging dates to the laying dates of the following broods; there was only one re-nesting interval for failed broods, taken from the failure date to the next laying date (Mayfield 1975). Calculations of re-nesting intervals did not include records from the minor breeding season, and hence does not span the inactive period in the middle of winter.

## 4 Distribution, habitat, movements and dispersal

### 4.1 Introduction

Of the 65 world-wide *Turdus* species only 16 are migratory, and many of the African and Neo-tropical species are either very sedentary or confined to short-distance seasonal movements (Clement and Hathway 2000). All thrushes are chiefly forest dwellers, but within many species part of the population has adapted to gardens and suburbia; very few live in open habitats devoid of trees or bushes (Clement and Hathway 2000). The Olive Thrush is a common garden bird in most regions of South Africa (Vernon and Herremans 1997), and in mountainous regions they may show altitudinal migration (Urban *et al.* 1997).

The following citations from “Ostrich” give some references to the distribution and habitat of *T. o. olivaceus*:

- “Common around Cape Town” (Gill 1936).
- “Temperate Forests or thick streamside vegetation in the south-western Cape” (Winterbottom 1966c).
- "The Thrush is really a forest bird and its presence elsewhere is as a casual forager. Since forest patches are almost entirely on the mountains, its more frequent appearance in Macchia than in the other vegetation types is to be expected" (Winterbottom 1966a)
- “Possible in all districts but commonest in the better bushed and forested areas of the coastal belt” (Skead 1967).
- “Despite the apparent suitability of the riverine bush habitat which contains mainly umbrageous large trees, this species is exceedingly rare and was recorded only twice during the period”; Uys and Macleod (1967) in the De Hoop vlei region, 1957-1966.

Skead (1964a, 1964b, 1967) further described the habitat and habits of the Olive Thrush in parts of the Eastern Cape Province: it occurred in the forests, on the

forest edge into adjoining Macchia and in tall Macchia, especially “in kloofs and better riverside scrub; it was a common and abundant resident that was seldom seen but more often heard, mostly in the mornings and the evenings. During the day it spent most of the time on the forest floor, and at night in the canopy”. Winterbottom (1966a) reported it in 6% of lists from Macchia, 2% of lists from Coastal Macchia and absent in Coastal Renosterbosveld.

The following citations from “Ostrich” give some references to the distribution and habitat of *T. smithi*:

- “Very common bird along all water-ways, especially where trees are dense. Seen throughout the year” (Brandt 1960).
- “Essentially an inhabitant of thick, streamside cover. It's presence in 6% of the Karroid Broken Veld lists is surprising but reaches 15% in Central Upper Karoo” (Winterbottom 1966b).
- “Inland it occurs along the riverside bush and at farms where good gardens are kept. Also inhabits wattle plantations” (Skead 1967).
- “Seen daily in riverine bush at Viool’s Drift and once in similar terrain at Ai-Ais” (Winterbottom 1967).
- “Seen at Vredendal, Kakamas, Upington and Prieska. Probably in all townships and dorps where there are plenty of trees and scrubs” (Pitman 1967).
- “A widespread resident of riverside bush and gardens. Up to 15 birds counted together on *Cotoneaster* sp. berries in garden at Kapkop in the winter” (Collett 1982).

Winterbottom (1966b) additionally reported the Olive Thrush (from the distribution these records would pertain to *T. smithi*) in 1% of lists from Strandveld, and 1% from Succulent Karoo.

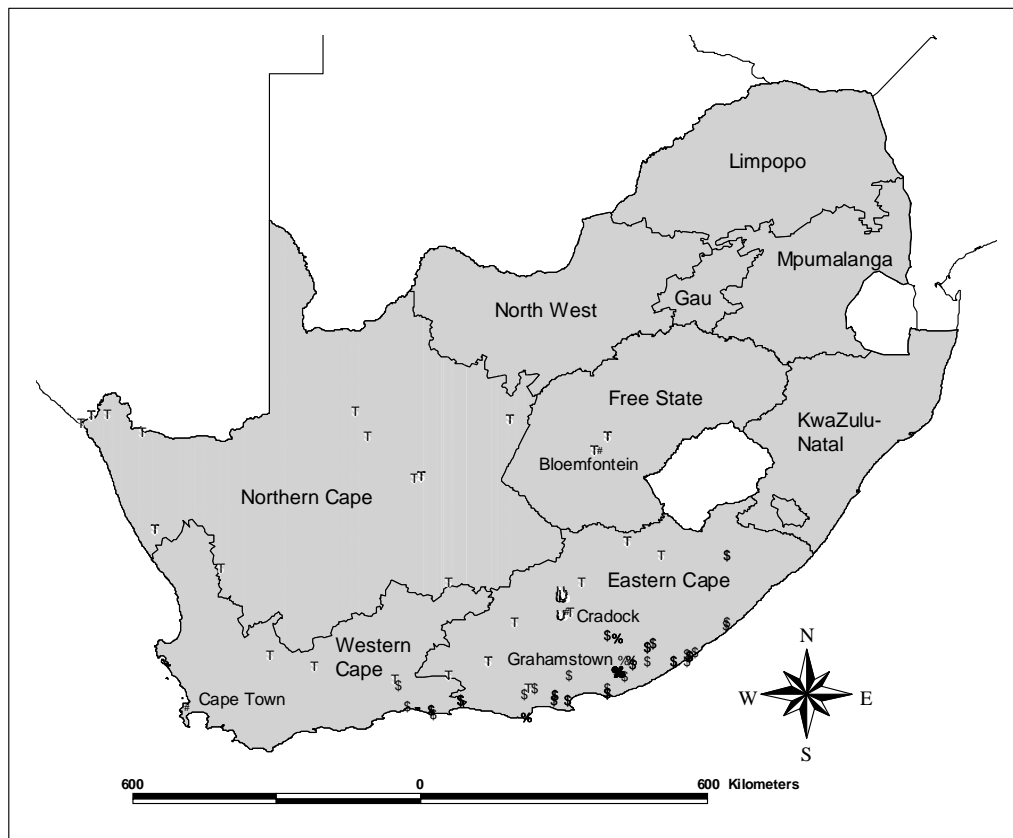
Published ringing records (McLachlan 1965, Oatley 1992, Oatley 1997, Oatley and Best 1997) suggest that movements are predominantly short-distance. One

of the most notable recoveries (Oschadleus 1999) is of an Olive Thrush (from the distribution this record would pertain to *T. smithi*) 482km from the place of ringing.

## 4.2 Results

### 4.2.1 Distribution and habitat

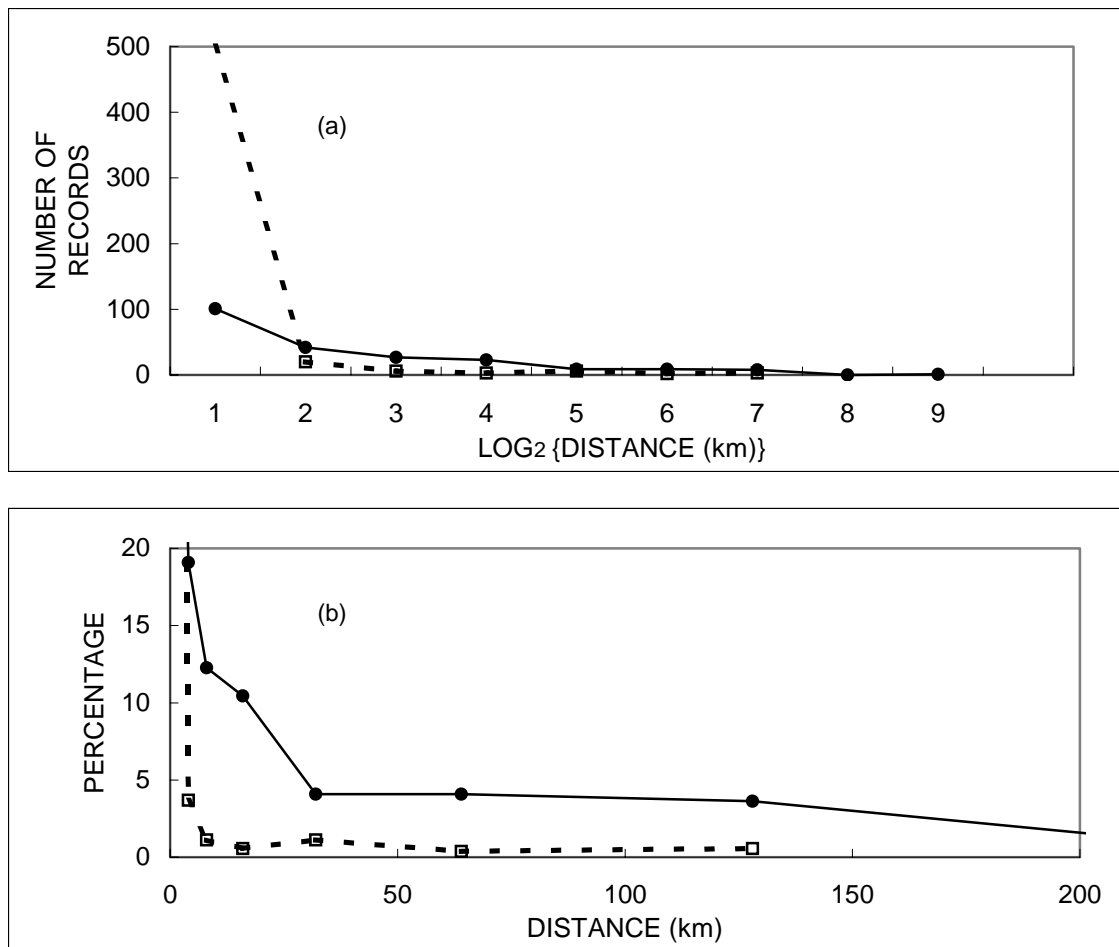
There was no overlap in the distributions of Olive and Karoo Thrushes from the East London museum collections and ringing data from the Eastern Cape (Figure 4.1).



**Figure 4.1:** Distribution of Olive Thrushes (black) and Karoo Thrushes (white). Data were obtained from museum specimens (triangles) and ringing records (squares). Gau – Gauteng

#### 4.2.2 Movements and dispersal

Of the 19 thrushes recaptured at the Eastern Cape sites, only two (one a juvenile) were away from the original ringing site, whereas recoveries were generally away from the ringing site. Analysis of SAFRING recaptures and recoveries produced a similar pattern (Figure 4.2).



**Figure 4.2:** Distances moved of recaptured (dotted) and recovered (solid) Olive and Karoo Thrushes. (a) There are nearly five times more recaptures than recoveries within 2km of place of ringing, but for all other distance classes there are more recoveries than recaptures. Log<sub>2</sub>(distance) is used to provide better resolution for smaller distance classes corresponding to 0, 2, 4, 8, 16, 32, 64, 128 and 256km. (b) Recaptures and recoveries as percentages of the total recaptures and recoveries provides better vertical resolution. 93% of recaptures were within 2km (not shown); 46% of recoveries were within 2km (not shown); there was one recovery at 482km (not shown)

### 4.3 Discussion

In his first letter to Barrington in 1769, Gilbert White noted three *Turdus* species as winter birds of passage in the south of England (White 1941). The Blackbird was not listed, possibly because of its very complex migration patterns both within Great Britain and Ireland and between there and continental Europe, combined with some birds over-wintering in England. It is also likely that suburban Blackbirds have a tendency to be more resident than rural birds (Hillstead 1945, Snow 1958).

Many of the *Turdus* thrushes in temperate latitudes, such as the Blackbird and the American Robin, flock and migrate together in the non-breeding season and may have communal roosts (Clement and Hathway 2000). Species at lower latitudes that are non-migratory seem less dependent on such social gatherings (Clement and Hathway 2000) and Olive Thrushes in Grahamstown are good examples of such populations. In these suburban Olive Thrushes, paired birds roost together with their young, but they do not tolerate other conspecifics in their territory, which is defended throughout the year (**see Chapter 5**). Recaptured Olive Thrushes were almost always near the original site of ringing, and most often at the same site; it is likely that these individuals are mostly resident breeders. Recoveries were more often away from the original ringing site, which may suggest that birds are more vulnerable away from the area with which they are familiar; these are most likely non-breeders or floaters. This fits a model where the mortality rate of dispersing independent fledglings and non-territory holders, is much higher than that of dependent fledglings and adults (**see Chapter 6**).

## **5 Territories: size, occupancy and defence**

### **5.1 Introduction**

In Oxford Botanical Gardens, Blackbirds are strongly territorial and mated pairs usually stay in their territories throughout the year. The sizes of their territories range from 1370m<sup>2</sup> to 2000m<sup>2</sup> (Snow 1958). Winterbottom (1966c) suggested that mated pairs of Olive Thrushes stay in their territories throughout the year in the Cape Town Public Gardens, but acknowledged that this could not be demonstrated without colour-ringing. She estimated an average territory size of 1500m<sup>2</sup> (0.4 acres in original), and she observed parties of up to 12 birds in the non-breeding season.

Winterbottom (1966c) made the following comments on the role of males and females in territorial defence: "except in one case, I only saw one bird defending at a time", "males defended as they were seen to fly to a branch and sing" and "both birds chased off an intruder and the male returned to the neighbourhood of the nest and sang". Winterbottom (1966c) seems to have been aware that some birds did not sing and reasonably assumed those to be females, but at the time it was not known that female Olive Thrushes do not sing.

### **5.2 Results**

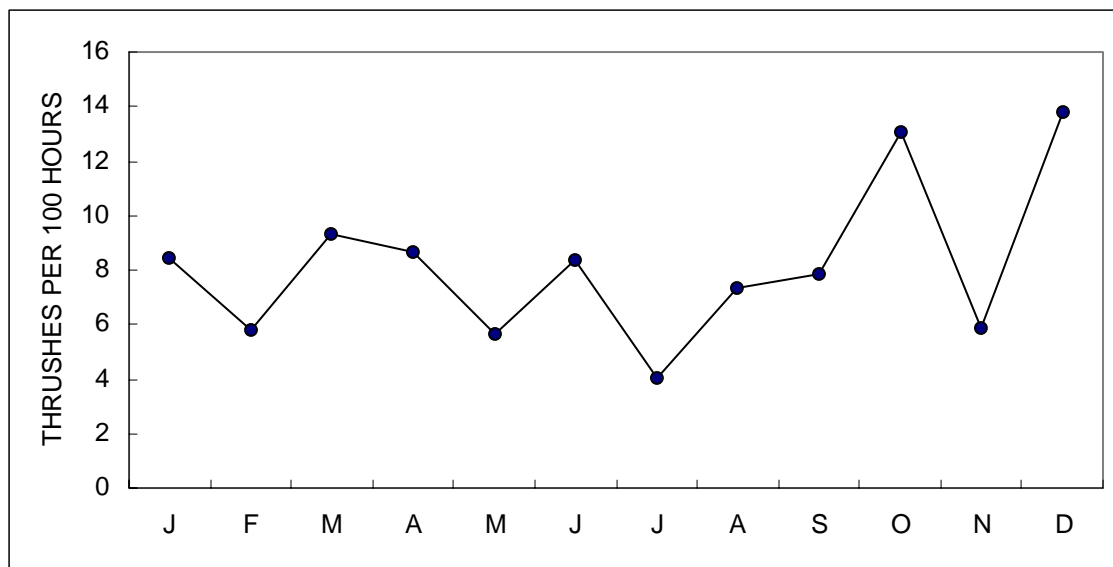
#### **5.2.1 Territory size and population density**

There was no obvious seasonal variation in population density. From 1 100 hours of mist-netting, the monthly capture rates of adult Olive Thrushes varied from 4-14 per 100 hours (Figure 5.1), and this variation could be caused by a seasonal variation in the density of floaters.

The size of territory B was estimated from boundary mappings and was approximately 10 000m<sup>2</sup>. From seven active nests in adjoining territories in a total area of 90 000m<sup>2</sup>, the average territory size was approximately 13 000m<sup>2</sup>.

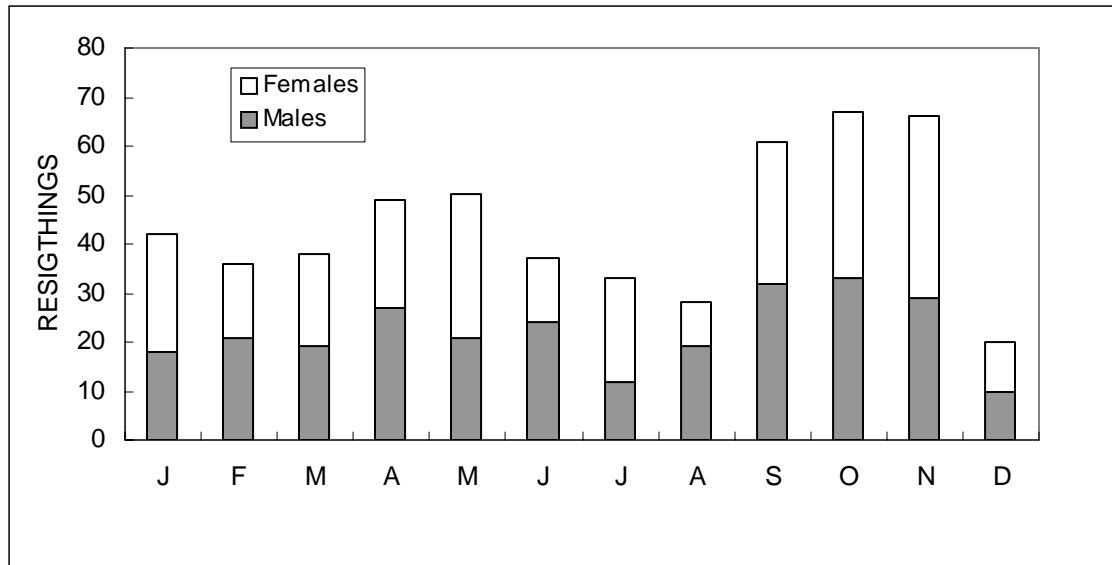
### 5.2.2 Territorial occupancy

One pair of Olive Thrushes bred four times in 2002 and five times in 2003 (Table 10.1). The male (4A13185) and the female (4A13188) of this pair were both ringed after the first colour-ringed brood had fledged. More than half of the re-sightings of colour-ringed thrushes were of this pair.



**Figure 5.1:** Monthly variation in capture rates of adult Olive Thrushes (number of thrushes captured per 100 hours of mist-netting) from 1986 to 2001

Adult thrushes were re-sighted in their territories in every month of the year (Figure 5.2). No colour-ringed adults or dependent fledglings were re-sighted outside of their territories or those of their nearest neighbours.



**Figure 5.2:** Number of days known adult male ( $n = 4$ ) and female ( $n = 5$ ) Olive Thrushes were re-sighted in their territories for each month of the year from 1998 to 2003 (stacked columns)

### 5.2.3 Territorial defence

Both males and females in this study defended their nest and territory. Known females chased intruders on eight occasions, known males on 17 occasions, and pairs chased intruders together on four occasions. The main intruders were other Olive Thrushes, which were chased from anywhere in a territory. Fork-tailed Drongos *Dicrurus adsimilis* ( $n = 2$ ) and Red-winged Starlings *Onychognathus morio* ( $n = 2$ ) were chased when close to nests. Black-headed Orioles *Oriolus larvatus* were sometimes chased ( $n = 2$ ) when close to nests, other times not ( $n = 1$ ). Cape White-eyes *Zosterops capensis* ( $n = 5$ ) were not chased when very close to nests, even on two occasions when the females were incubating. Nests were defended only after eggs were laid. During the moulting season, January to March in the study area (**see Chapter 8**), pairs remained in their territories. During this time birds were more secretive and more tolerant of intruders. A moulting resident ignored an intruder in one instance, and on other occasions moulting residents would hop towards intruders without giving serious chase. On

one occasion a pair of moulting residents was involved in a vicious fight, which included pecking and clawing, with an intruding Olive Thrush that eventually was chased off.

### 5.3 Discussion

Breeding Olive Thrushes in this study were resident in their territories throughout the year. The monthly differences in the number of re-sightings (Figure 5.2) were influenced by many factors, e.g. the birds are easier to find when nesting, and these data do not represent seasonal variation in population density.

Olive Thrushes in the region of this study moult mainly from January to March (**see Chapter 8**), at which time they are more secretive than usual. Some evidence was found for the “hawk-dove-bourgeois” game-theory strategy (Maynard Smith 1978): during the breeding period owners of a territory always won territorial disputes in their own territory; during the moulting period, when territorial defence was the weakest, disputes were sometimes the most vicious, possibly because intruders had opportunities to settle temporarily in already occupied territories.

The mapped territory size of 10 000m<sup>2</sup> (n = 1) and the estimated average size of 13 000m<sup>2</sup> (n = 7) on Rhodes University campus are considerably larger than the average (1 500m<sup>2</sup>) in the Cape Town Public Gardens (Winterbottom 1966c). If buildings and roads are excluded, the suitable feeding areas of the Rhodes University territories were approximately 5 000m<sup>2</sup>. A possible explanation for this difference is that the Cape Town Gardens were more productive. In Malawi the size of territories range from 5 000m<sup>2</sup> to 60 000m<sup>2</sup> (Keith *et al.* 1992). The territory size of the Olive Thrush in the Cape Town Public Gardens is similar to that of the Blackbird in Oxford Botanical Gardens.

Earlé and Oatley (1983) suggested that at least some mated pairs of Orange Thrushes *Zoothera gurneyi* also remain in their territories throughout the year and estimated the size of their territories in forests at approximately 11 000m<sup>2</sup>.

Knowing that breeding male Olive Thrushes were resident in their territories throughout the year, the seasonal variation in song output (**see Chapter 9**) can be mostly attributed to breeding and territorial behaviour, rather than seasonal migration which is known to occur in other parts of the range of the Olive Thrush (Urban *et al.* 1997).

## 6 Survival and life-history variables

### 6.1 Introduction

Bird ringing started in the late Forties in South Africa and the first rings were used on 1 August 1948. The first Olive Thrush was ringed in the 1950/51 ringing year. By the late Fifties, bird ringing had taken off in South Africa and in 1957 the first Olive Thrush was recovered. Rowan (1964) analysed the records of a ringing station (1954-1961) and reported on lapse rates and mortality. During this time 32 adult and 15 nestling Olive Thrushes were ringed and there were 10 recaptures (recaptured a total of 28 times) and 10 recoveries. Early ringing reports (Ashton 1950, Ashton 1952, Ashton 1954a, Ashton 1954b, Ashton 1956, Ashton 1957, Elliott 1974, Elliott and Jarvis 1970, Elliott and Jarvis 1972, Elliott and Jarvis 1973, McLachlan 1961, McLachlan 1962, McLachlan 1963, McLachlan 1964, McLachlan 1965, McLachlan 1967, McLachlan 1969) were published in *Ostrich* and these included yearly ring and recovery totals for the Olive Thrush. Recapture and recovery rates for the period 1981-1992 were 1.2% and 1.6% respectively (Oatley 1992). Survival rates have been estimated for some South African Ploceidae (Craig 1982, Craig and Manson 1979) and the Cape Sparrow *Passer melanurus* (Dean 1978), and here such an analysis has been carried out on the Olive Thrush. Estimates of adult survival rates are compared between the Eastern Cape and Western Cape, and reproductive rate, nesting success and juvenile survival rates are estimated.

Ricklefs (1997) compared demographic characteristics amongst New World thrushes, and Kemp (1985) discussed the importance of understanding the scaling relationships of life-history traits and pointed out that there is a lack of good comparative data for the African avifauna.

## 6.2 Results

From the proportion of adults and juveniles in mist-net samples, annual adult survival rates were estimated: In the Eastern Cape 86 adult birds and 21 juvenile birds gave an estimate of  $0.80 \pm 0.05$ ; in the Western Cape the estimate was  $0.78 \pm 0.03$  from 124 adult and 36 juvenile birds, which is not significantly different from the Eastern Cape ( $Z = 0.34$ ,  $P = 0.37$ ). Observations confirmed that Olive Thrushes obtain adult plumage in their second year, or near the end of their first year (**see Chapter 8**). No data on the age of first breeding are available.

Haldane's method provided an annual survival rate estimate of  $0.72 \pm 0.03$  for South Africa from 1957 to 1994 (Table 6.1). This is likely to be an under-estimate as birds were not all ringed in their first year.

**Table 6.1:** Application of Haldane's method.  $D_j$  is the number of birds recovered at age  $j$ . Although Haldane's method allows for future recoveries, recoveries of birds ringed after 1994 have been excluded in this analysis

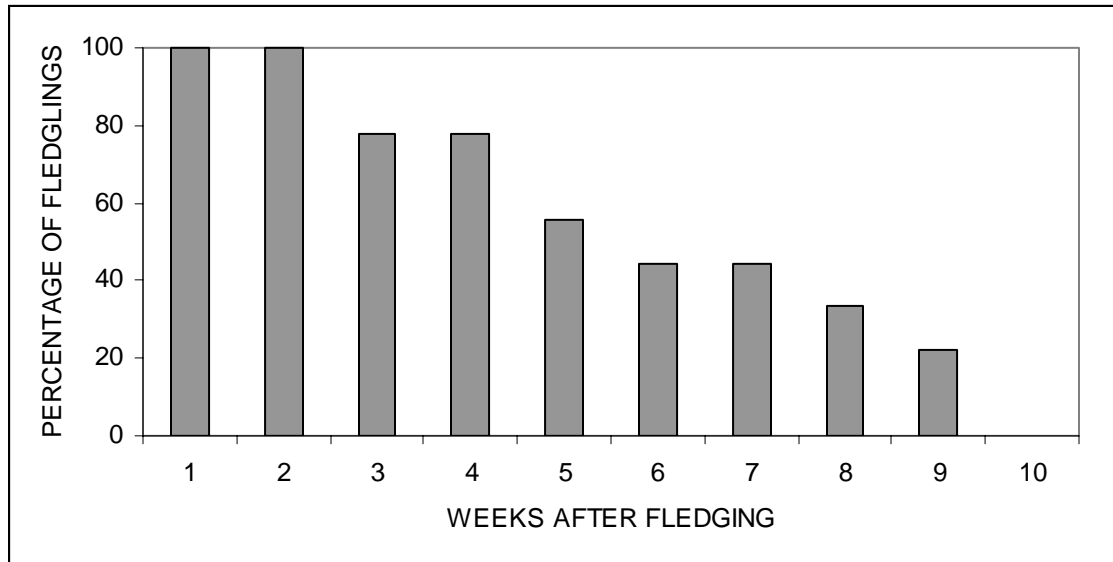
Year Ringed	$i$	Age on recovery ( $j$ )										$r_i$	$t - i + 1$	$r_i * (t - i + 1)$	
		1	2	3	4	5	6	7	8	9	10				11
1957	1	0	1		1								2	38	76
1958	2	0			3			1					4	37	148
1959	3	2			1								3	36	108
1960	4	0											0	35	0
1961	5	0		1									1	34	34
1962	6	1	1	1									3	33	99
1963	7	1	1							1			3	32	96
1964	8	3						1					4	31	124
1965	9	1	1		1								3	30	90
1966	10	1	2	1									4	29	116
1967	11	1			1						1		3	28	84
1968	12	1			1								2	27	54

Year Ringed	<i>i</i>	Age on recovery ( <i>j</i> )										<i>r<sub>i</sub></i>	<i>t - i + 1</i>	<i>r<sub>i</sub></i> * ( <i>t - i + 1</i> )
		1	2	3	4	5	6	7	8	9	10			
1969	13	3	2								1	6	26	156
1970	14	2				1						3	25	75
1971	15	2			1		1					4	24	96
1972	16	3	1									4	23	92
1973	17	1		1								2	22	44
1974	18	0	1	1								2	21	42
1975	19	1	2									3	20	60
1976	20	0						1				1	19	19
1977	21	1										1	18	18
1978	22	1		1								2	17	34
1979	23	0		1								1	16	16
1980	24	0										0	15	0
1981	25	0	2									2	14	28
1982	26	0	1									1	13	13
1983	27	4	2	1								7	12	84
1984	28	2		1								3	11	33
1985	29	4			1							5	10	50
1986	30	1			1						1	3	9	27
1987	31	3	1					2				6	8	48
1988	32	2	4		1	1						8	7	56
1989	33	6		1	2		1			1		11	6	66
1990	34	3		2								5	5	25
1991	35	4	1		1	2		1	1			10	4	40
1992	36	1	2	1					1		1	6	3	18
1993	37	3	3	1	1		1	1				10	2	20
1994	38	2	3	4	1		1	1				12	1	12
1995	39	1	2	1	1	1								
1996	40	7	3	1	1	3								

Year Ringed	<i>i</i>	Age on recovery ( <i>j</i> )										<i>r<sub>i</sub></i>	<i>t - i + 1</i>	<i>r<sub>i</sub></i> * ( <i>t - i + 1</i> )		
		1	2	3	4	5	6	7	8	9	10				11	
1997	41	2	4	2		2										
1998	42	3	1	1												
1999	43	3	2		2	2										
2000	44	1	3	1												
2001	45	1	5	1												
2002	46	5														
2003	47	8														
2004	48	1														
Totals	<i>D<sub>j</sub></i>	60	31	18	17	4	4	5	5	2	1	3	150	741		2201
	<i>jD<sub>j</sub></i>	60	62	54	68	20	24	35	40	18	10	33	424			

Using a range of survival rate from 0.72 to 0.80 the respective mean life expectancies are 3 to 4.5 years. Because the former is expected to be an underestimate, it seems reasonable to use  $S = 0.80$  from the Eastern Cape for the estimation of life-history parameters for this province. Three birds were recovered in their 11<sup>th</sup> year after ringing (Table 6.1), one of which was ringed as an adult; this makes 11 years a conservative estimate of maximum lifespan.

The survival rate of dependent fledglings ( $S_f$ ) and the age of independence were estimated from closely monitored fledglings (Figure 6.1). A minimum estimate of the proportion surviving to independence was 56%, using an age of independence of 50 days (5 weeks after fledging). The age of independence was based on observations of fledglings, mostly of their feeding skills and their associations with their parents. No colour-ringed fledglings were recovered.



**Figure 6.1:** Percentage of closely monitored fledglings ( $n = 9$ ) still present in their natal territories each week from fledging date until they disappeared

There were six nest mortalities during 299 active nest days, giving a daily nest mortality rate of 2% and a nesting success of 55%. The average number of fledglings per pair ( $n = 3$ ) per year was  $6.3 \pm 2.1$ . Using a nesting success of 55% for all nests, the number of eggs laid per breeding adult per year, or annual reproductive rate for breeders,

$$\beta_b = \frac{6.3}{2 \times 0.55} = 5.7$$

The ratio of breeders to floaters is unknown for Olive Thrushes, so for the sake of life-history estimations I shall use a ratio of 1:1, giving a reproductive rate,

$$\beta = 2.9 \quad (\text{i.e. half of the above})$$

In a stable population, annual recruitment rate ( $R$ ) must equal adult mortality rate ( $M$ ) (Ricklefs 1997),

$$R = M = 1 - S$$

Recruitment rate is the product of juvenile survival rate ( $S_j$ ) and reproductive rate (Ricklefs 1997),

$$R = \beta \times NS \times S_j$$

Therefore,

$$S_j = \frac{1 - S}{\beta \times NS} = 0.13 = 13 \%$$

The juvenile survival rate ( $S_j$ ) is also the product of the survival rates of dependent fledglings ( $S_f$ ) and independent fledglings ( $S_i$ ),

$$S_j = S_f \times S_i$$

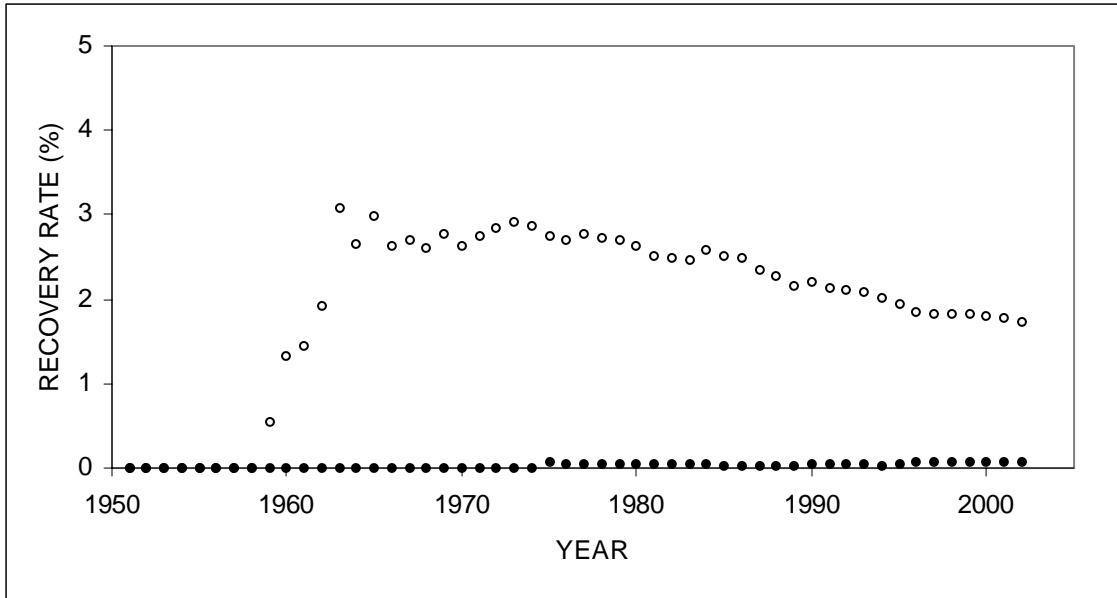
Taking the  $S_f = 0.56$  from above, the survival rate of independent fledglings is then,

$$S_i = \frac{S_j}{S_f} = 0.23 = 23\%$$

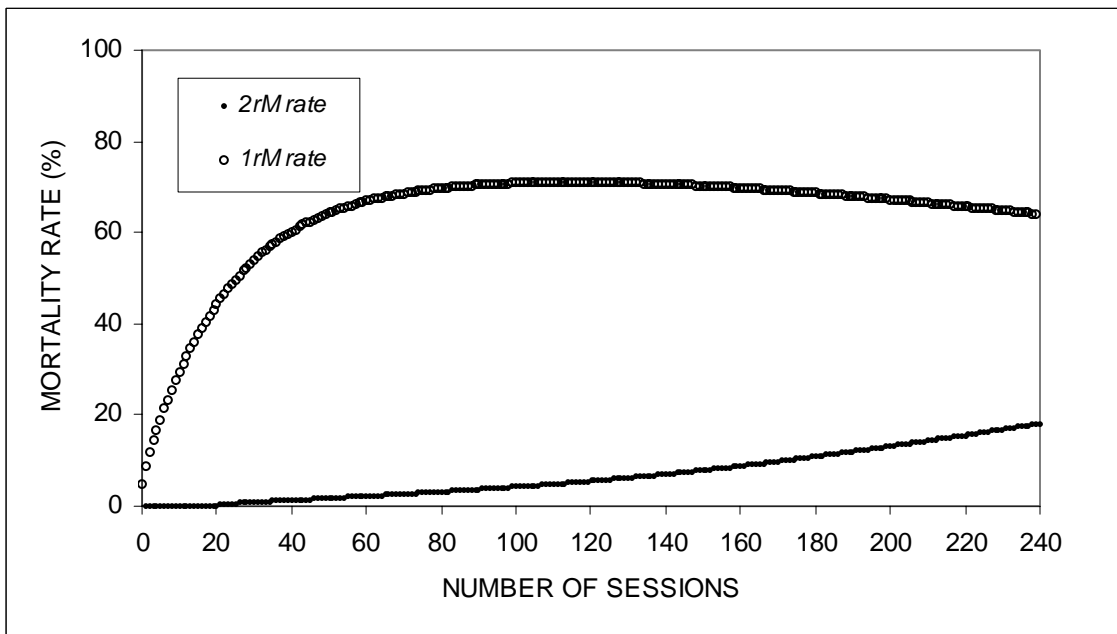
The accumulated recovery rate (Figure 6.2) shows a gradual decrease from 3.1% in 1962 to 1.9% in 1995. This can be explained by a steady increase in ringing effort, which was simulated with a capture-recapture and recovery model<sup>3</sup> (Figure 6.3). For a long-term national dataset, a steady increase in effort would be expected as the number of ringers increase gradually with time.

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<sup>3</sup> This simulation model allows the user to investigate the effect on accumulated recapture and recovery rates (plotted against session number) with varying survival rates and probability of capture (effort) of unmarked, ringed and recaptured birds. Intuitively, it would perhaps be expected that the recovery rate would approach a fixed value asymptotically with time.



**Figure 6.2:** Accumulated recovery rate from 1950 to 1995 (open dots: recovery rate of birds that were not previously recaptured, solid dots: recovery rate of birds that were previously recaptured); for each year the recovery rate is the ratio of all birds recovered up to that year to all birds ringed up to that year



**Figure 6.3:** Simulated mortality rate of ringed birds not previously recaptured (*1rM*: open dots) and birds recaptured (*2rM*: solid dots). The simulation was run with one session per month and an annual survival rate of 80%

### 6.3 Discussion

The estimation of adult survival rate (Ricklefs 1997) uses the following assumptions:

- The population density is constant.
- The collection method is unbiased.
- The survival rate of all individuals is the same.

The second assumption may not be valid with mist-netting: Very young fledglings do not fly around as much as older birds and are therefore not as prone to capture; older fledglings, not as familiar with the territory as the adults, may be more prone to capture. If the proportion of juvenile birds mist-netted is less than their proportion in the population, then the adult survival rate will be an over-estimate. The third assumption at first seems invalidated by the survival rates of dependent fledglings (56%) and independent fledglings (23%). However, it is the survival rates of individuals *subsequent* to mist-netting that are assumed to be the same, so the above estimates do not apply to the juvenile birds sampled for this analysis. Furthermore, if the mortality rate of juvenile birds is higher than that of adults, then not all the juvenile birds mist-netted become new recruits; this would make the adult survival rate by this method an under-estimate. Because the adult survival estimate is annual, seasonal variation in the proportion of adult and juvenile birds in the population should not introduce a bias (provided all months of the year are sampled sufficiently). This method may be useful for other species where, as in the genus *Turdus*, first-year birds can be distinguished from adults, and sample sizes are small.

The estimated daily survival rate of Olive Thrush fledglings was almost constant at 0.98 from the third to the ninth week after leaving the nest. This compares with 0.965 and 0.967 for the Song Thrush and the Blackbird, respectively, both over the first 35 days after fledging (Bradbury *et al.* 2000).

Lack (1946) estimated the survival rate of the Blackbird at 60% and that of the Song Thrush at 55%, with further life expectancies of 1.9 and 1.6 years, respectively (calculated from first January 1 of life). This agrees with the generalisation that adult survival rates for insectivorous passerines are lower in the northern hemisphere than in the southern hemisphere (Peach *et al.* 2001).

Densities and survival rates of Blackbirds are higher in urban than in rural habitats (Snow 1958). One reason for the higher survival rates in urban environments may be because of an expected lower ectoparasite load; in France, 74% of rural Blackbirds carried *Ixodes* ticks, compared to 3% of urban birds (Gregoire *et al.* 2002).

The gradual decrease in recovery rate can be explained by a corresponding increase in ringing effort with time. When ringing effort increases over time, as the number of ringers increase, the *accumulated mortality rate of marked individuals that have previously been recaptured decreases*. It is assumed that the recovery rate is proportional to the mortality rate of marked individuals. This suggests that accumulated recovery rates should be interpreted cautiously when ringing effort is not constant. This result is not intuitive and is difficult to explain, but the use of a simulation to test the result provides one possible interpretation. It is also interesting to note that this possible explanation is extrinsic to the species' biology and is a result of the data collection method.

## 7 Biometrics and morphology

### 7.1 Introduction

Biometrics of *T. o. olivaceus* and *T. o. smithi* were treated separately by McLachlan and Liversidge (1978), but were lumped by Maclean (1993). With the reclassification of *T. o. smithi* (Bowie *et al.* 2003) it is necessary to re-assess the biometrics of these taxa. The biometrics of Olive Thrushes from the Eastern Cape and the Western Cape were not significantly different from each other, but Olive Thrushes from the Grahamstown district were significantly different from those of the Karoo Thrush from the nearby Cradock district (Bonnievie *et al.* 2004). The description “Olive Thrush has reddish orange bill and bright orange eye-ring” of Urban *et al.* (1997) must pertain to the Karoo Thrush as a former race *T. o. smithi* of the Olive Thrush.

### 7.2 Results

#### 7.2.1 Wing length

In the Eastern Cape, nestlings at 7 and 14 days old had wing lengths of 37mm and 72mm, respectively. When the young birds fledge at 16 days old their estimated wing length is  $82.3 \pm 4.2$ mm (n = 6) approximately 40mm shorter than the adult wing length. There was no significant difference in the wing length of adult Olive Thrushes (Table 7.1) between the Eastern Cape and the Western Cape.

**Table 7.1:** Regional comparison of wing length (mm) of Olive Thrushes (mean  $\pm$  standard deviation, maximum and minimum)

Region	Mean	Max	Min	Sample size	Z	P
Eastern Cape	$123.4 \pm 4.9$	133.0	103.0	164	0.4	0.7
Western Cape	$122.8 \pm 4.7$	135.0	112.0	134		

### 7.2.2 Mass

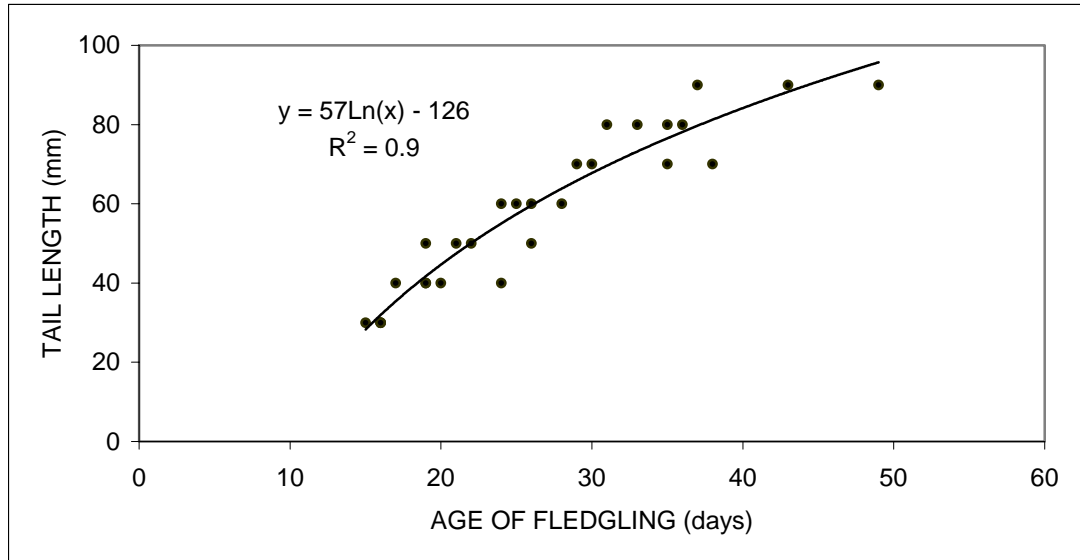
A nestling that fell out of the nest at 7 days old had a mass of 49.5g. When the young fledge they have an estimated mass of  $63.6 \pm 3.9\text{g}$  ( $n = 6$ ). There was no significant difference in the mean mass of adult Olive Thrushes between the Eastern Cape and the Western Cape (Table 7.2). Of 19 adult Olive Thrushes recaptured in the Eastern Cape, 7 had gained mass, 10 had lost mass and two had not changed. Between ringing and recapture, there was an average decrease in mass of less than 1% per bird. Daily fluctuations in mass were not taken into consideration. Two juvenile birds had increased in mass by 15g and 27g since time of ringing.

**Table 7.2:** Regional comparison of the mass (g) of Olive Thrushes (mean  $\pm$  standard deviation, maximum and minimum)

Region	Mean	Max	Min	Sample size	Z	P
Eastern Cape	$82.6 \pm 6.4$	100.0	65.0	161	1.7	0.09
Western Cape	$81.4 \pm 5.6$	96.0	61.5	133		

### 7.2.3 Tail length

The rectrices start growing after the remiges, and at 7 days old nestlings still do not have tail feathers. Nine days later, when the young fledge, their tail length was estimated at  $27.0 \pm 2.9\text{mm}$  ( $n = 7$ ); the estimated tail length of adult Olive Thrushes in the Eastern Cape was  $98.5 \pm 12.0\text{mm}$  ( $n = 4$ ); tail length can be used to estimate the age of fledglings to the age of 40 days (Figure 7.1).



**Figure 7.1:** Tail lengths of young Olive Thrushes increase logarithmically and may be useful in estimating the age of young fledglings (Eastern Cape data)

#### 7.2.4 Culmen length and bill colour

The culmen length of a nestling at 7 days old was 12.4mm. At fledging age the culmen length was estimated at  $15.0 \pm 0.4$ mm ( $n = 5$ ). The bills of young Olive Thrushes in the Eastern Cape are dusky-brown with the mandible turning yellow with age and the maxilla turning yellow at the tip and lower margin. The adult culmen length was  $21.6 \pm 1.1$ mm ( $n = 4$ ). The maxilla of the adult Olive Thrush in the Eastern Cape is dusky-brown with a yellow tip and lower margin, and the mandible is yellow.

#### 7.2.5 Tarsus length

The tarsus length of a nestling at 7 days old was 25.5mm. At 16-18 days old the tarsi were fully grown, and there was no significant difference between the tarsus lengths of adults and young fledglings (Table 7.3).

**Table 7.3:** Tarsus lengths of adult and fledgling Olive Thrushes in the Eastern Cape (mean  $\pm$  standard deviation, maximum and minimum)

Age	Mean	Max	Min	n	Z	P
16-18 days	35.5 $\pm$ 1.0	37.0	34.2	6	1.8	0.7
Adult	33.0 $\pm$ 1.0	34.0	32.0	3		

### 7.2.6 Comparison with the Karoo Thrush

From an unsexed sample of live birds, the Karoo Thrush ( $n = 30$ ) was longer-winged than the Olive Thrush ( $n = 144$ ),  $F_{1,172} = 11.4$ ,  $P < 0.001$ ). Olive Thrushes in the Grahamstown district were heavier (Table 7.4) than Karoo Thrushes in the Cradock district ( $F_{1,165} = 19.5$ ,  $P < 0.001$ ). From sexed museum specimens there were no significant differences in wing length, culmen length or tarsus length between males and females of either species.

**Table 7.4:** Morphological data of *T. o. olivaceus* and *T. smithi*. Mass and wing length are from living birds. Culmen and tarsus lengths are from museum specimens

		Mass (g)	Wing length (mm)	Culmen (mm)	Tarsus (mm)
<i>olivaceus</i>	n	137	144	43	40
	Range	65.0-101.5	103-133	17.5-24.5	30.0-35.0
	Mean	84.2	122.4	20.8	32.5
	SD	6.7	5.0	1.4	1.2
<i>smithi</i>	n	30	30	35	34
	Range	72.0-86.0	117-131	20.0-24.0	30.0-34.5
	Mean	78.2	124.6	22.2	32.3
	SD	4.1	3.6	1.1	1.2

The maxilla of the adult Olive Thrush is dusky-brown with a yellow tip and lower margin, and the mandible is yellow. The bill of the Karoo Thrush is completely

yellow. The Olive Thrush has a brown eye-ring, whereas the Karoo Thrush has an orange eye-ring. Data on the bill colour and size of young Karoo Thrushes are lacking. From museum specimens the culmen length of *T. smithi* was significantly longer (Table 7.4) than that of *T. o. olivaceus* ( $F_{1,76} = 23.5$ ,  $P < 0.001$ ), but that there was no significant difference in tarsus length between the taxa ( $F_{1,72} = 0.7$ ,  $P = 0.4$ ).

### 7.3 Discussion

For warm-blooded vertebrates, Bergman's rule predicts that races from cooler climates should be larger than those from warmer climates, and Allan's rule predicts that their protruding body parts should be shorter in cooler climates (Mayr 1963). In Grahamstown (which is about 200km south of Cradock) *T. o. olivaceus* should accordingly be heavier and have shorter bills than *T. smithi* in Cradock, and significant differences in mass, wing and culmen lengths between *T. o. olivaceus* and *T. smithi* were indeed found and were in agreement with these generalisations. The longer wings and bills, coloration of eye-ring and bill of *T. smithi*, add morphological differences to the molecular findings of Bowie *et al.* (2003). Geographical variation in mass, and size of protruding body parts, of *T. o. olivaceus* was not significant between the Eastern Cape and the Western Cape (approximately 1 000km apart). Both Grahamstown and Cradock in the Eastern Cape fall into a predominantly summer rainfall climatic zone, whereas the Western Cape is in a winter rainfall zone. It appears that the mountain chain (Winterberg, Amatola, Drakensberg) separates the two populations, and may have served as a geographical barrier prior to differentiation and speciation. However, the detailed distribution and possible sympatry of the two taxa has yet to be investigated.

## 8 Breeding periods and moult

### 8.1 Introduction

Post-nuptial moult is common in many passerine species (Craig 1983, Payne 1972), and there have been comparative studies on some species in southern Africa (Craig *et al.* 2001, Oschadleus *et al.* 2000). According to Clement and Hathway (2000) adults of all thrush species have two moult periods every year; a complete or full pre-basic moult following the breeding season (post-nuptial) and a partial pre-alternate moult before breeding. They, however, acknowledge that little is known about moult in tropical species.

Major and minor breeding periods have been documented for the Olive Thrush in the Western Cape (Winterbottom 1966c), and the main breeding period is similar throughout the Southern African region, except in the Western Cape where it is about a month earlier (Vernon and Herremans 1997). The timing of pre-basic moult of Olive Thrushes was related to their breeding seasons in two different climatic regions, the Eastern and Western Cape provinces of South Africa

### 8.2 Results

The minor and major breeding periods in the Western Cape were earlier than those in the Eastern Cape (Table 8.2).

The relative masses of primaries were estimated from two recoveries (Table 8.1).

**Table 8.1:** Mean mass (mg) of individual primaries P1 to P10 (descendant) for the Olive Thrush (n = 2)

P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
34.1	34.3	37.0	41.7	48.1	50.0	48.8	47.2	40.2	4.4

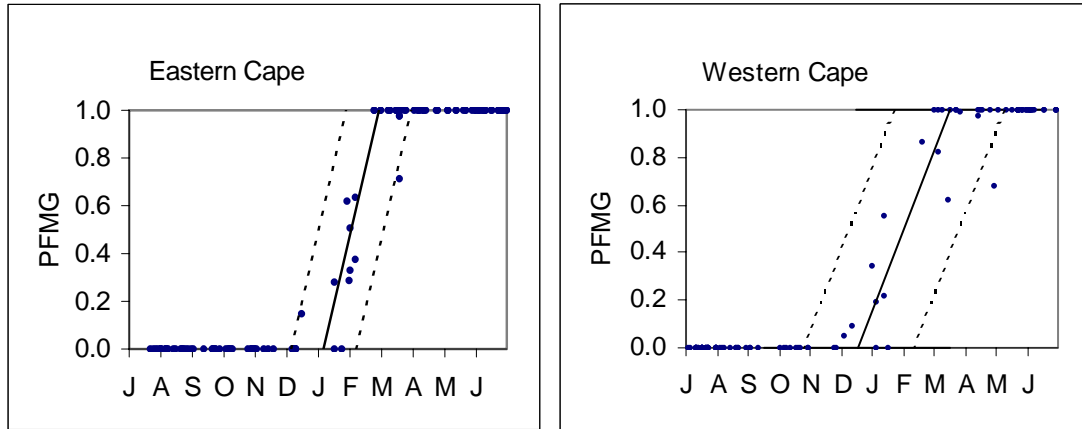
**Table 8.2:** Breeding periods, <sup>1</sup>McLachlan and Liversidge (1978), <sup>2</sup>Winterbottom (1966c), <sup>3</sup>Collett (1982), <sup>4</sup>Maclean (1993)

Region	Peak	Main	Minor	Remarks
South Africa <sup>1</sup>	Sep-Oct		Feb	
Eastern Cape	Sep-Nov	Aug-Dec	Mar-Apr	(Figure 8.2)
Western Cape <sup>2</sup>	Sep-Oct	Aug-Nov	Feb-Apr	All months
Katkop <sup>3</sup> (Eastern Cape)		Oct-Dec		
Natal <sup>4</sup>	Nov	Sep-Jan		
Transvaal <sup>4</sup>	Sep-Dec	Aug-Mar		
Zimbabwe <sup>4</sup>		Sep-Jan		

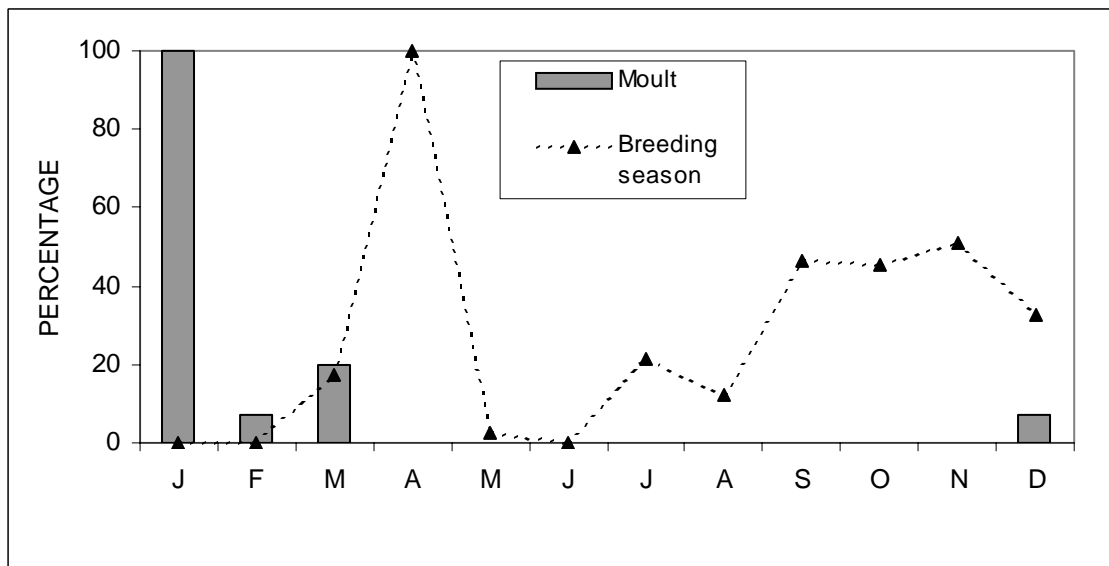
Moult started earlier in the Western Cape than in the Eastern Cape (Table 8.3, Figure 8.1), but the difference between the two provinces was not significant ( $Z = 1.8$ ,  $P < 0.07$ ). The start of moult, however, did coincide with the end of the breeding season in both regions. The duration of primary wing-moult was significantly shorter ( $Z = 2.4$ ,  $P < 0.02$ ) in the Eastern Cape (53 days) than in the Western Cape (89 days), and the moult completion dates were 23 Feb and 10 March, respectively.

**Table 8.3:** Regional comparison of primary moult estimates  $\pm$  standard errors, and main breeding period ( $n =$  before moult + in moult + moult completed)

Region	Duration (days)	Mean starting date, MSD	Standard deviation of MSD (days)	n
Eastern Cape	53 $\pm$ 8	1 Jan $\pm$ 6	16 $\pm$ 3	56 + 11 + 78
Western Cape	89 $\pm$ 13	11 Dec $\pm$ 10	27 $\pm$ 4	61 + 12 + 60



**Figure 8.1:** Percentage feather mass grown (PFMG) for the Olive Thrush in the Eastern Cape (left) and the Western Cape (right). The solid lines estimate the progression of moult and the dotted lines indicate the 95% confidence limits



**Figure 8.2:** Annual cycle of the Olive Thrush in the Eastern Cape. Breeding period (dotted line) is expressed as a percentage of the maximum (egg-days per month); moulting period (columns) is the normalised number of birds in active moult for each month

One juvenile bird (4A13183) from the minor breeding period in April/May was re-sighted near its parent's territory in March the following year, and by this time it had moulted into adult plumage.

### 8.3 Discussion

Primary wing moult in South African Olive Thrushes started at the end of the breeding season, supporting previous findings of post-breeding moult (e.g. Craig *et al.* 2001, Oschadleus *et al.* 2000) in many African passerines. Although the difference in Mean Starting Date of moult was not significant between the Eastern and western Cape, it is likely to be biologically important as such regional differences have been found in other species (Craig *et al.* 2001); perhaps the failure to show a significant difference was because of the small sample size of birds in active moult. The difference in moult duration between the Eastern Cape and the Western Cape could also be an artefact of the small proportion of birds in active wing moult; there seems to be no good biological explanation for such a difference.

One juvenile bird (4A13183), of less than one year old, was re-sighted in March, and by this time it had moulted into adult plumage; presumably during the same period from January to March that adults normally moult in this region. Young birds from the end of the major breeding season did not moult into adult plumage during the normal adult moult period. This suggests that nestlings from the minor breeding period moult into adult plumage in their first year, whereas nestlings from the major breeding period would only moult into adult plumage in their second year.

The Orange Thrush in Natal and Mpumalanga moults from January to April/May (Earlé and Oatley 1983). The duration of moult for the Olive Thrush (Table 8.3) compares with that of the Blackbird of 70 to 90 days in Europe (Kasperek 1981).

## 9 Calls and song

### 9.1 Introduction

Muscicapidae is a large family, and many species therein, particularly robins, are some of our best-known songsters. Gilbert White (1941, in his second letter to Barrington, 1769) recorded seasonality in the songs of the Blackbird and the Song Thrush.

For a thrush, the Olive Thrush is a humble songster (Gill 1936). The song has been described in different ways: “weety weef” or “weety, weety, weet” (Gill 1936), “wheety wheety wheety” in full force just before and through the nesting period (Winterbottom 1966c), and a short but melodious “wheety-wheety wheet” (McLachlan and Liversidge 1981). Calls include a loud “chink” or “tschuck” (McLachlan and Liversidge 1981), but few studies have attempted to provide descriptions or detailed contexts of calls. Two alarm notes have been described: “chook chook chook”, (Winterbottom 1966c) and a thin “tseep” (Maclean 1993).

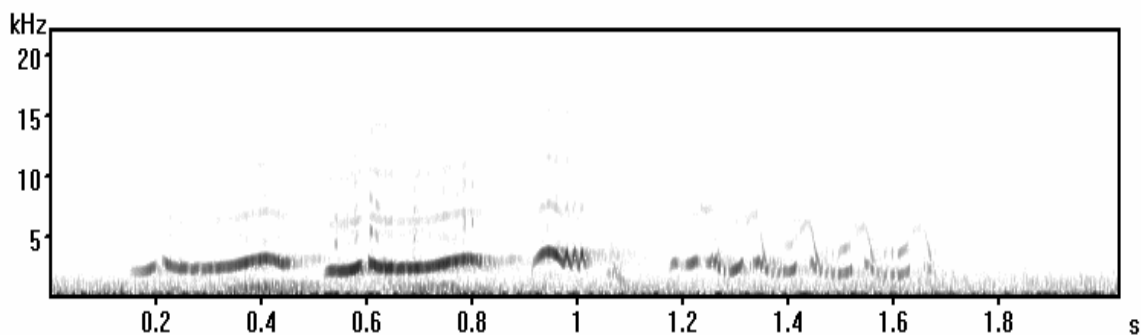
The Olive Thrush is an excellent mimic (McLachlan and Liversidge 1981), and sometimes includes a few vocal imitations in its song (Vernon 1973). It starts singing before dawn and alarm notes may attract many conspecifics (Skead 1964a, 1964b).

The only other published study of song in African thrushes is by Pomeroy (1993), who investigated seasonal variation in the song output of the African Thrush *T. pelios* in Uganda.

## 9.2 Results

### 9.2.1 Song

Only males sang; known males were observed on 265 occasions and sang on 119 of those; known females were observed on 262 occasions, but were never seen singing. Males only sang in their territories. A typical song phrase lasted for about 0.8s, and often had a jumble of notes at the end.

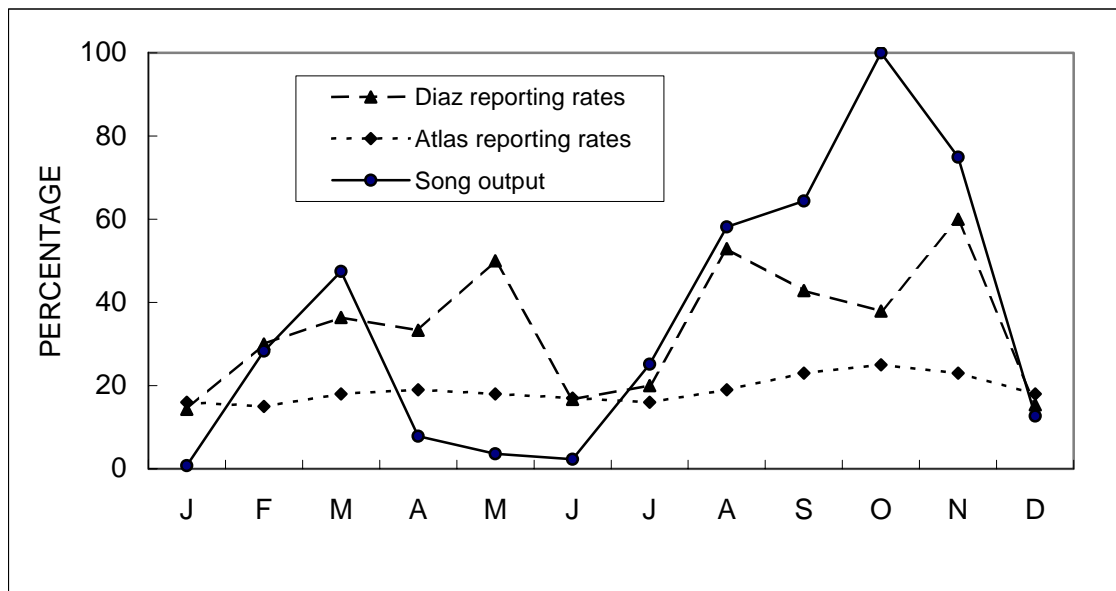


**Figure 9.1:** Olive Thrush song. The typical musical phrase at the beginning lasted for about 0.8s

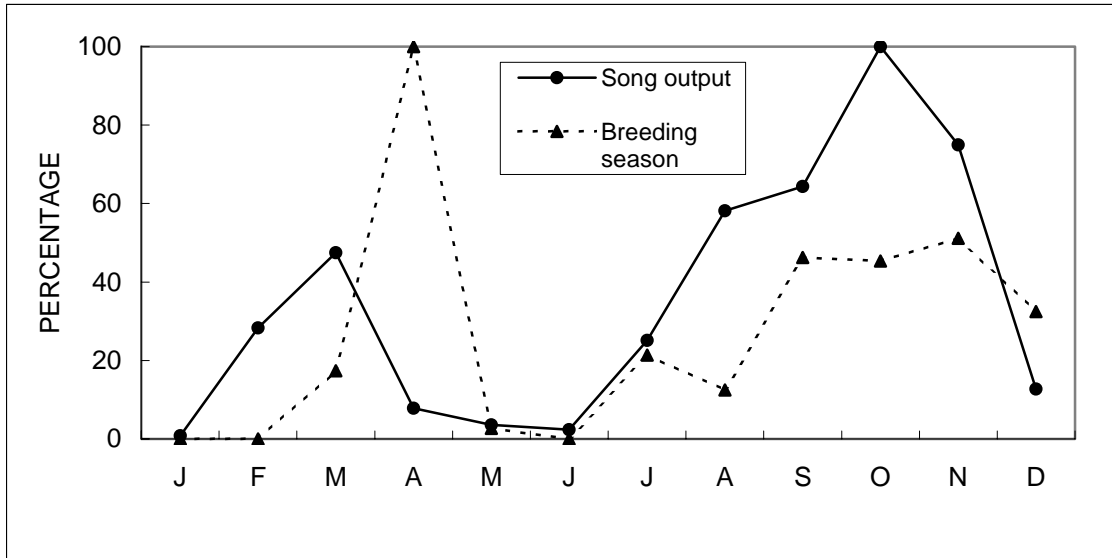
The song output of the Olive Thrush varied seasonally in this study area (Figure 9.2 and Figure 9.3), and correlated positively with the breeding seasons (cross-correlation coefficient  $r_{sb} = 0.6$ , s.e. = 0.3, lag = 1 month). Males started singing in late January/early February and again in July. When males started to sing, they appeared to do so across town from approximately the same date (A. Craig and P. Hulley, personal communications).

The volume of the songs varied, with this being loudest before incubation commenced, and songs could be heard from a distance greater than 100m. During the nesting period males often sang away from the nest, but they also sometimes sang close to the nest, particularly when the females were away. The males often sang a few phrases softly close to the nest while holding food for the nestlings in their bills.

Vernon and Herremans (1997) suggested that the seasonal variation in reporting rates of the Olive Thrush (reproduced in Figure 9.2 for completeness) may be attributed to increased conspicuousness when birds are singing. These reporting rates correlated ( $r = 0.8$ ) with song output in this study. The Diaz Cross Bird Club reporting rates of the Olive Thrush, from the vicinity of Grahamstown, had peaks in May, August and November and these also correlated ( $r = 0.6$ ) with song output.



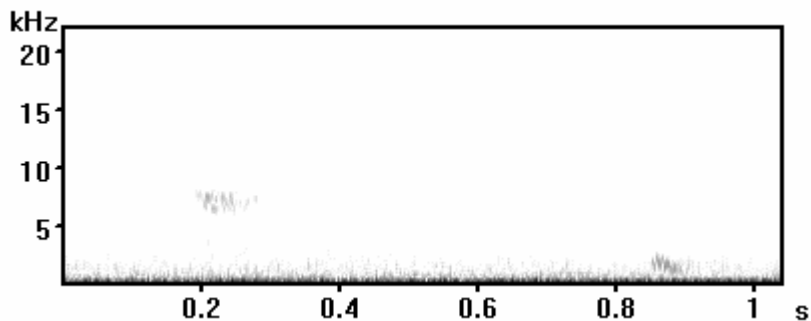
**Figure 9.2:** Comparison of reporting rates for Olive Thrushes for Zone 8 (adapted from Vernon and Herremans 1997: 155), Diaz Cross Bird Club reporting rates, and song output



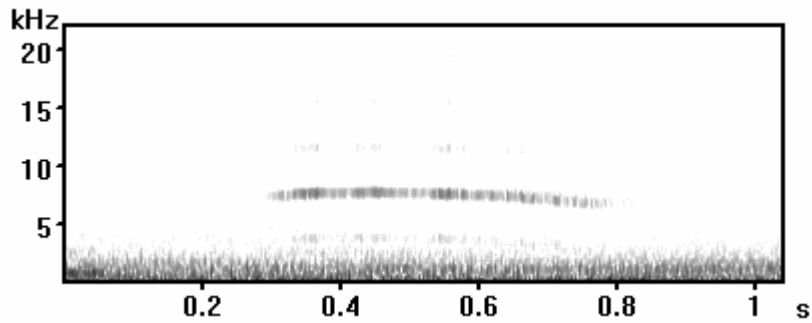
**Figure 9.3:** Accumulated monthly song output compared to breeding season. Monthly values are expressed as a percentage of the maximum

### 9.2.2 Alarm calls

Three alarm calls were identified. Firstly, a low “Chook” (Figure 9.4) repeated a few times in response to the presence of cats, or humans at close range. Secondly, a high pitched and drawn out “Teeeeeee” (Figure 9.5) when raptors had been seen. This call was repeated many times at 4-5s intervals, possibly until the danger had passed, and then repeated less and less often at the end.

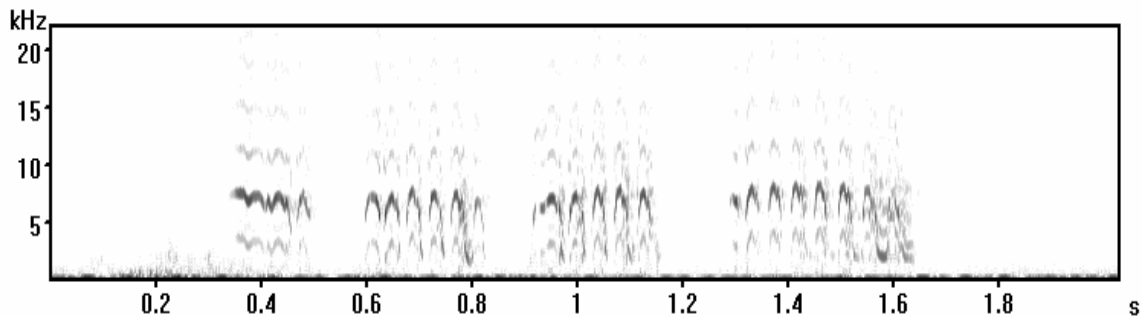


**Figure 9.4:** Alarm call for ground dangers such as cats. The typical “tsik” at 0.2s seemed to be an early warning to be alert, followed by the low frequency “chook” (about 2kHz) at 0.84s



**Figure 9.5:** The Alarm call for aerial danger lasted for about 0.5s and was repeated at 4-5s intervals until the danger had passed. The low frequency noise band (< 2.5kHz) is from a background air-conditioner

Thirdly, a trilling “Trrr-trrr-trrr-trrr” (Figure 9.6) when birds were handled or when nests were inspected. A parent would use this call when fledglings were handled and this would immediately summon the mate to the scene and it would then also call. Adults also used this trill to warn off intruding Olive Thrushes and during defensive chases.

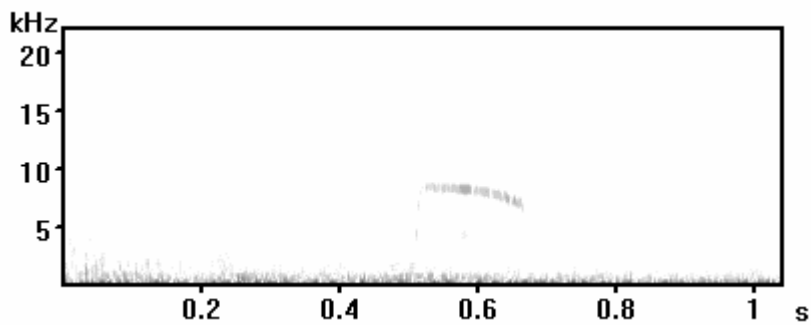


**Figure 9.6:** Trilling alarm call that was used for immediate danger. This call was from a Karoo Thrush, which is similar to that of the Olive Thrush

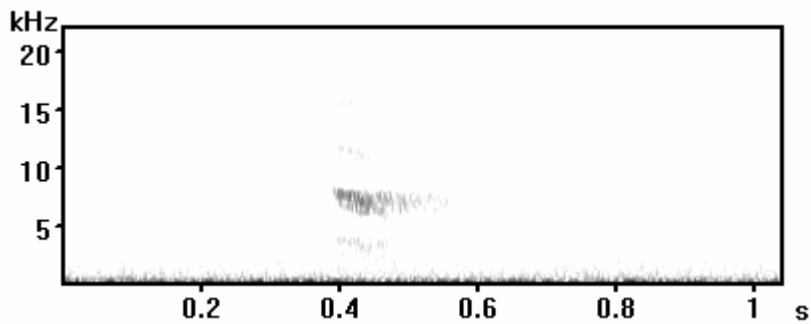
### 9.2.3 Contact calls

The adults made a sharp “tsik” call (Figure 9.7), often as they flew from a perch or the nest, but also while sitting still. In the latter case it may be a “non-critical” alarm call to a mate, prompting it to be alert. It was also used during territorial disputes. The call often elicited a “tsik” response from the mate. When they had

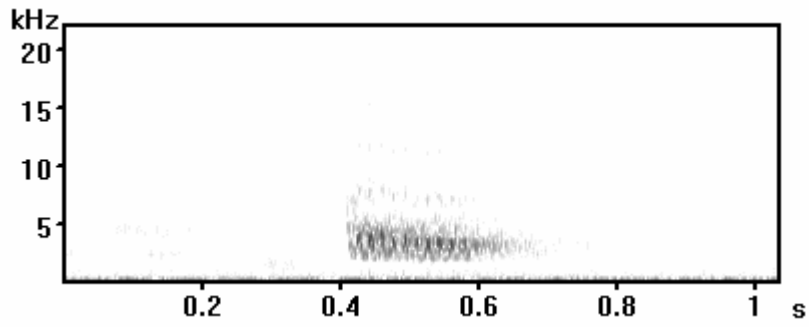
young these responded with a similar but lower pitched “tuik” (Figure 9.8), and vice versa. During the first few days out of the nest the chicks sometimes produced a nasal “krrrrr” (Figure 9.9) at about 5s intervals, speeding up as the parents approached. When the adults approached the fledglings with food, the young typically called a soft “ti-ti-ti-ti” (Figure 9.10) prior to being fed. A loud “tak-tak-tak” (Figure 9.11) was often used in flight, and by family members when they gathered to roost in the evenings. Females on occasion also used this call while on the nest, and the male then often responded with a few song phrases or a “tsik” from a nearby perch.



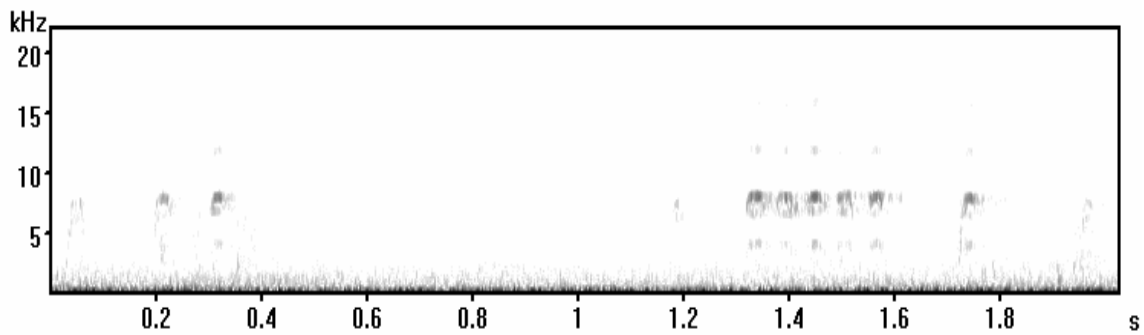
**Figure 9.7:** An example of the short “tsik” call, but it was variable in duration and shape



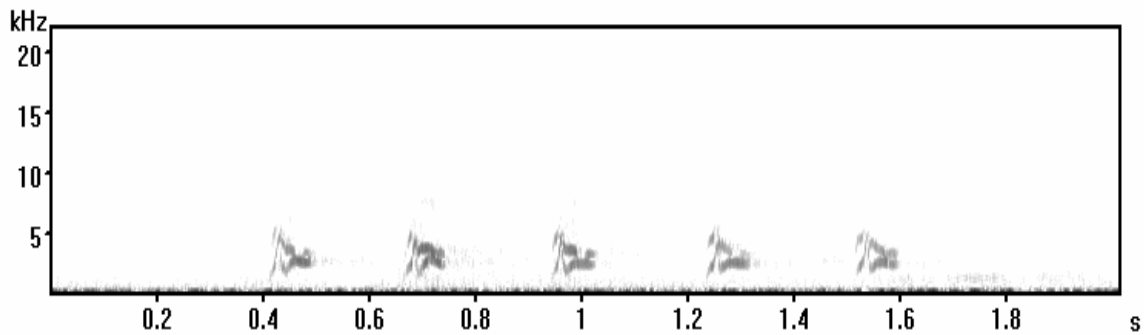
**Figure 9.8:** The “tuik” of dependent fledglings seemed to be the equivalent of the adult “tsik”



**Figure 9.9:** Very young fledglings produced a nasal “krrrrr”



**Figure 9.10:** A begging call of very rapid short “ti” notes. The chick received the food at 1.8s



**Figure 9.11:** “Tak-tak-tak” call used in flight and when birds gathered in the evenings

### 9.3 Discussion

Males only were recorded singing during this study. Shore-Baily (1924) reported a female Olive Thrush that sang in captivity in the presence of a male with which it bred, but made no mention of the origin of his captive birds, so that their taxonomic status is unknown. A female Blackbird in Europe sang simple and monotonous phrases after losing its mate (Snow 1958); female Blackbirds do not usually sing, but losing her mate could have induced hormonal changes, stimulating her to sing. At least two explanations thus exist for the singing behaviour of Shore-Baily's captive female. Firstly, it is possible that the singing female did not belong to the race *T. o. olivaceus*. This explanation is unlikely, as there is no evidence to suggest such variation within closely related taxa. Secondly, it is possible that keeping the female captive could have induced hormonal changes, stimulating her to sing.

In temperate regions many songbirds, including the Blackbird, do not sing throughout the year, but only during periods in summer related to their breeding. Some *Turdus* species may sing after a quiet period in autumn, and in England during winter, Song Thrushes sang for short periods mainly during dawn and dusk (Snow 2003). Pomeroy (1993) found that the African Thrush in Uganda sings throughout the year and has a pronounced peak at dawn, and suggested that these different patterns in seasonality of song between temperate and tropical songbirds are common. Song of the African Thrush correlated positively with rain and breeding in Uganda, with a main peak from February to April and a minor peak in November. Song output of the Olive Thrush in this study area also correlated positively with breeding season.

Seasonal variation in song could affect reporting rates during censuses. Apart from song, other calls (e.g. contact calls between adults and young) may be seasonal and could, therefore, also affect reporting rates. The peaks in reporting rates in April [Vernon and Herremans (1997)] and May (Diaz Cross Bird Club)

could also be attributed to increased conspicuousness resulting from increased activity when adults are feeding young.

## 10 Breeding biology

### 10.1 Introduction

The nesting habits of thrushes are very diverse and are poorly known for many of the species. Most of them build an open, cup-shaped nest, but in some species the nest has a domed roof; in southern Africa the *Turdus* thrushes generally strengthen their nests with mud, whereas the *Zoothera* thrushes do not (Tarboton 2001). Comments on the use of mud in nest building by the Olive Thrush vary, from “re-enforced with mud” (Gill 1936), “rarely bound with mud” (McLachlan and Liversidge 1981), “lined with mud and grass” (Maclean 1993), to “often uses mud” (Chittenden 1989). These discrepancies may result from regional variation and could possibly vary between races, or some references may have pertained to the Karoo Thrush, which inhabits drier regions. Winterbottom (1966c) summarised nest heights and mentioned that plastic was sometimes used in the nest construction.

The incubation period (14 days) and nestling period (16 days) are documented for other regions (McLachlan and Liversidge 1981, Urban *et al.* 1997) and for captive birds (Shore-Baily 1924), but there are no records of incubation or nestling periods for this species in South Africa. Clutch sizes vary from one to four eggs, with an average of 2.0 (Winterbottom 1966c). The egg colour is usually greenish-blue, boldly dotted and blotched with brownish slate and chestnut brown; rarely with ground colour cream tinged greenish or pinkish, and measure 29.3mm x 21.6mm (McLachlan and Liversidge 1981). Other data, such as post-fledgling parental care, and the development of fledglings, are lacking or incomplete.

Urban *et al.* (1997) mentioned that the male may brood the nestlings in the afternoon; this was however not observed for known males in this study. Winterbottom (1966c) observed a male standing on the edge of the nest for four

minutes and commented that on high nests such visits could give the impression that he was brooding. She also estimated that feeding intervals were normal for passerines.

## **10.2 Results**

### **10.2.1 Breeding season**

Five active nests were found in the minor breeding season when eggs were laid from the middle of March to the beginning of April; an average nest initiation date of 27 March  $\pm$  6 days. The minor breeding season was thus well synchronised (Figure 9.3). In this period it was more obvious that the males became quieter once the incubation had started. In the well-studied territories the Olive Thrushes all bred in the minor breeding period, one pair in two successive years. Four broods were ascertained to be the first breeding attempts of the major breeding season, with an average nest initiation date of 29 July  $\pm$  22 days. The major breeding season peaked from August to November.

### **10.2.2 Nests**

Only females built nests. Female 4H14901 started building nest E2 on 24 October 2001, but abandoned this attempt (the material kept falling down) and started building a new nest on the other side of the same tree at dawn on 7 November 2001. Female 4A13188 started building nest B4 on 13 July 2002, but only completed lining the nest on 16 August 2002; rain repeatedly washed the mud lining out of the nest structure. The main unlined structures of these nests were completed in half a day, but at two other nests the building was spread over a few days. One female started the construction with soft paper in the fork of two branches; small branches and leaf petioles were then dropped on top of the paper, which appeared to hold the building material in place. Once the nest structure was about half the height of the completed nest, it was shaped with new

material that was brought to the nest. During the next few days, or weeks, the females bound the structures with mud and leaves often collected from roof gutters. The females inserted the mud and leaves into the nest structures with their bills, and then climbed into the nests and pressed their bodies against the sides of the nests, presumably forming comfortable and well-fitting cups. During this process, the upper breast feathers sometimes became heavily soiled. The examination of three nests from this study area suggests that they were all constructed in the same way, with mud and leaves binding and sealing the nest. The females were not seen at their completed nests until they came back to lay eggs a week or two later. Nests were built at heights varying between 2m and 9m (Table 10.1).

Three of 15 nests studied were used for two consecutive broods, and one of these was re-used again, seven months later, after the female had built, and successfully bred in, two other nests (Table 10.1). The female relined this old nest with mud and leaves over a two-day period and then laid eggs 17 days later. A female completely destroyed a nest of the previous territory owners before building her own nest in exactly the same place (C. Charteris, personal communication), so perhaps females will only use their own nests?

### **10.2.3 Egg laying and incubation**

Only the female incubated. It was not possible to determine the laying dates by visual inspection of the nest, except in one case. Females were easily agitated during this time and there was concern that an observer's presence close to the nest could cause desertion. As a result, no data on the causes of egg or nestling mortalities were collected. For brood RU01C where the laying date was recorded, the female started incubation as soon as the first and only egg was laid. The single egg hatched 14 days later, but the nestling was dead on

inspection. For broods RU02B and RU03A the incubation periods were taken from the day the female started sitting until the day she started feeding; this gave

**Table 10.1:** Details of nests, broods and fledglings of Olive Thrushes. Each nest in territories A to E is numbered. The percentage of male and female feeds (n = 162) refer to observed feedings of the different fledglings, e.g. for brood RU03A one fledgling was fed 72% by the male and 28% by the female, while the other was fed 3% by the male and 97% by the female. Ring codes (colour-ringed birds): A = 4A13153, B = 4H14901, C = 4A13185, D = 4A13188, E = 4A22507, M = metal only

Nest	Height of nest (m)	Brood	Male ring code	Female ring code	Laying date	Eggs	Nestlings	Fledglings	Fledglings ringed	Fledglings Split	Male % feeds	Female % feeds
A1	8	HO98A	A	M	25/09/1998		1	0	N			
B1	4	RU01A		M	07/07/2001		2	2	N			
B1	4	RU01B		M	22/09/2001		3	3	N	Y	33;93	67;7
B2	9	RU01D		M	--/11/2001			0	N			
B3	6	RU02A	C		17/03/2002		2	2	Y	N	20	80
B4	7	RU02B	C	D	23/08/2002		2	2	Y	Y	19;75	81;25
B4	7	RU02D	C	D	20/10/2002	2	2	2	Y	N	33	67
B5	7	RU02E	C	D	27/11/2002		1	1	Y		3	97
B6	7	RU03A	C	D	01/04/2003		2	2	Y	Y	72;3	28;97
B4	7	RU03E	C	D	15/07/2003		1	0	N			
B7	7	RU03G	C	D	28/08/2003			2	N	N		
B4	7	RU03H	C	D	10/10/2003		2	2	Y	Y	100;0	0;100
B8	5	RU03L	C	D	01/12/2003		2	2	Y	N		
C1	4	RU03B			29/03/2003		1	1	N			
D1	3	RU03C			30/03/2003		2	2	Y			
E1	6	RU99A		M	15/11/1999		2	0	N			
E2	5	RU01C		B	13/11/2001	1	1	0	N			
E3	5	RU02C			09/09/2002	2	2	0	N			
E4	5	RU03D			30/03/2003		2	2	Y	N		
E5	2	RU03F		E	12/08/2003	2						
E5	2	RU03J		E	13/10/2003	2	2	2	Y			

incubation periods of 14 days. The female sat higher on the nest after the eggs had hatched and this, together with signs of feeding, may be useful in estimating the hatching date for inaccessible nests.

#### **10.2.4 Care of nestlings**

On the day that the eggs hatched only the female offered food to the nestlings. The male sometimes passed food to the incubating or brooding female on the nest, which the female then either fed to the nestlings or ate herself. The male also dropped food into the nest, which the female picked up and fed to the nestlings. After the first couple of days both parents fed the nestlings. Olive Thrush nestlings lie quietly in the nest until a parent arrives at the nest with food; when the parents lower their heads into the nest, the nestlings raise their heads up towards the parent. The nestlings also raised their heads when the parents lowered theirs to clean the nest. Observations during this study suggest that the female distributes the food more evenly between the nestlings than does the male. After feeding the nestlings, the female typically stayed on the edge of the nest for longer ( $60 \pm 48$ s,  $n = 15$ ) than the male ( $28 \pm 30$ s,  $n = 28$ ). Both males and females removed faecal sacs from the nest with females seemingly doing it after every feed ( $n = 14$  observations), whereas the male did it less frequently ( $n = 3$  observations). One male was also observed removing part of an eggshell from the nest. Normally the female flew directly to the nest when bringing food to the nestlings, whereas the male usually perched in a nearby tree, sometimes singing softly with food in his bill, before flying to the nest. The female may or may not stay on the nest when the male brings food.

When adults gather food for their young, they may drop the food already in their bills before probing for more, and then pick up the dropped food again together with newly found food. On one occasion a male was mobbed by Red-winged Starlings while gathering food for its nestlings, and it managed to pick up the food

already dropped before taking evasive action. On another occasion, when adult Olive Thrushes were carrying food to the nest, Cape White-eyes followed them closely, seemingly begging for the food.

Nestlings were preening at 10 days old and exercising their wings when 13 days old. When fledglings leave the nest they can barely fly, and those ringed were easily caught by hand or with a hand-net. The primary and secondary feathers of a nestling that fell out of a nest at 7 days were starting to emerge from pin.

The re-nesting interval for successful broods was  $26 \pm 15$  days ( $n = 5$ ), compared to 14 days for failed broods ( $n = 1$ ).

### **10.2.5 Care and development of fledglings**

Fledglings from nine broods were colour-ringed and one fledgling from another brood was ringed (Table 10.1); these young birds were recaptured and measured when possible. When the young fledge (16 days old), their bills are dark horn with a paler tip, their breasts are spotted, they have the characteristic buffy tips to the secondary coverts typical of the genus *Turdus*, and they still have greyish down on their heads. At 30 days old the mandible is paler with the tip turning yellow, and the fledglings are then feeding themselves, as well as being fed by the adults; one fledgling was still being fed at 48 days old. At 60 days old the bill is yellow except for the dorsal ridge of the maxilla, which is brown from the base, turning yellow at the tip. At this age young birds may also have a pale eyebrow. The fledglings typically reach independence 5 weeks after fledging (i.e. at approximately 50 days old) and may remain in the territory for at least 2 months. When the juvenile birds leave the territory they still have spotted breasts and buffy edges to the secondary coverts.

From the first day out of the nest, the young birds were guided by calls from the parents and were often lured with food to hedges and dense vegetation. The fledglings were sometimes separated spatially and parental duties divided between specific fledglings (Table 10.1). This was first observed with brood RU01B, where feeding of two of the fledglings was done predominantly by the female (67%) in one area, while the male fed the third fledgling (93% of feeds) in another area. The fledglings of this brood were not colour-ringed, but on this occasion the single fledgling was about 100m from the other two. Such “splitting” of the broods happened in the first few days after fledging. The fledglings were sometimes brought together again, and the specific fledgling-parent association was then generally maintained, although some “cross-feeding” would occasionally take place. When such broods were “split” again a subsequent time the original fledgling-parent associations were restored.

The fledglings from different broods of paired birds 4A13185 and 4A13188 were guided to the same specific hedges and flowerbeds. These “nursery areas” provided cover and protection and the fledglings could be located here on most days. One of these nurseries was shared by two of the Olive Thrush broods with fledgling Cape Robins *Cossypha caffra*. During these times an alarm call of either species would invariably trigger an alarm call of the other. The fledglings of one brood of Olive Thrushes also shared the same tree with fledgling Cape White-eyes, fledgling Black-eyed Bulbuls *Pycnonotus tricolor* and fledgling Red-faced Mousebirds *Urocolius indicus* for most of one day.

One fledgling from brood RU03D (territory E), accompanied by a parent, was captured and ringed in a neighbouring territory B. While being handled the fledgling from territory E uttered alarm calls, which attracted the female from territory B, who chased the intruding parent back to territory E. The fledgling was released at the site of capture, but now did not respond to the calls of its own parents and remained in territory B. Although the female from territory B had nestlings (brood RU03A) of her own (Table 10.1), she remained with the fledgling

from territory E and started feeding it. Six hours later the fledgling was recaptured and relocated to its parents territory, where the adults soon started caring for it again. The female of brood RU03A then continued feeding her own nestlings.

One female built a new nest while caring for a dependent fledgling from the previous brood. Independent fledglings were seen in a territory occupied by an incubating female; the territory owners showed no aggression towards these fledglings, and although they were not colour-ringed they were possibly fledglings from the previous brood, reared in the same territory.

### **10.3 Discussion**

Reproductive rate is a function of clutch size and the number of broods per year, and clutch sizes are typically larger in similar species with the same number of broods per year in the northern hemisphere than in the southern hemisphere (Ghalambor and Martin 2001). The mean clutch size of the Olive Thrush in the Eastern Cape was 1.8 eggs, half that of suburban Blackbirds in England (Snow 1958). Post-fledgling parental care in passerine birds also tends to be longer in the southern hemisphere than in the northern hemisphere (Russell 2000).

The process of nest construction and nest materials used matches the description of Urban *et al.* (1997). Winterbottom (1966c) reported a case where a female had nearly finished building a nest, when she started building a new nest in the same tree; this is similar case to that where the nest kept on falling down and the female built a new nest in the same tree later.

Winterbottom (1966c) reported two nest that were re-used. Re-using a nest can be detrimental to the nestlings, because of an increasing population of ectoparasites in the nest (Earlé RA 1985). Leaving the nest dormant for long periods, perhaps together with the addition of fresh mud and leaves, could be effective control mechanisms against nest parasites (Bucher 1988).

Because the female starts incubating as soon as the first egg is laid (Urban *et al.* 1997), the laying date can be assumed to be the first date on which the female sits for most of the day. This was used to determine the incubation period from two nests, together with direct observations from a single nest, giving an incubation period of 14 days; this is in agreement with findings in other parts of the range of the Olive Thrush (Urban *et al.* 1997) and captive birds (Shore-Baily 1924).

Before flying to the nest with food for the nestlings, the male often perched nearby, sometimes in a tree adjacent to the nest tree. The male then regularly sang a few phrases softly. It is uncertain why the male does this; it may be that the male needs to inform the female of his identity and presence, before approaching the nest. The male also often sang near the nest when the female was away from the nest; this was possibly to inform the female that he was defending the nest in her absence.

Although no data on the causes of nest mortalities were collected, there was no evidence for partial nest losses. There were also no nests that were obviously lost as a result of bad weather, and failed nests were always empty, suggesting that predation was the cause.

In four of the broods studied, the fledglings were spatially separated, and observations suggested that the male cared for one fledgling, while the female cared for the other(s). One advantage of dividing the fledglings in this manner would be to protect them from predators. In one brood comprising a single fledgling, the female alone cared for the fledgling, while the male remained in the territory, feeding alone. During this time, wing, tail and body moult was visible in this male, suggesting the possibility that the onset of moult could have affected parental care in this individual. The female started moult about three weeks after the male. Timing of moult, relative clutch size and availability of food are some possible reasons for the different strategies adopted in the care for fledglings,

and hopefully further studies will shed some light on these aspects. It would be interesting to determine whether the sex of the fledglings relates to how they are “split” and which parent looks after which fledglings. Brood RU02B was split and the fledglings were last seen 23 days after fledging. The female laid eggs in the same nest (Brood RU02D) five days later; perhaps the fledglings of the first brood did not survive or reached independence at about 40 days old. Many birds begin a new brood before the fledglings from the previous brood are independent, requiring the parents to divide their duties (Tinbergen 1953). Therefore, when the Olive Thrush broods are split and the female is caring for one of the fledglings, she may not be able to start a new brood until the fledglings are independent.

The accidental experiment of releasing a fledgling in a neighbouring territory, suggests that Olive Thrushes may adopt fledglings in unusual circumstances, for example, when their own young have fledged, or are about to fledge.

The behaviour of the sexes during the breeding cycle differs, and the following characteristics can be used to assist in distinguishing the sexes:

- Only the female builds the nest.
- Only the female incubates.
- Only the female brooded the nestlings in this study.
- Only the male sings.
- When feeding nestlings, the female typically flies directly to the nest, whereas the male perches nearby first, often singing softly.
- The female stays at the nest for longer after feeding the nestlings, often a couple of minutes, whereas the male typically leaves the nest within a minute.

## 11 Diet and feeding

### 11.1 Introduction

Thrushes are particularly cosmopolitan in their diets, and although some *Monticola* species are more restricted to animal foods (Clement and Hathway 2000) most *Turdus* species feed predominantly on a mixture of invertebrates and fruit. They can hear the underground movements of invertebrates and retrieve these with amazing accuracy (Clement and Hathway 2000). The diet of the Olive Thrush is well known (Koen 1992, Kopij 2000, Maclean 1993, McLachlan and Liversidge 1978, Urban *et al.* 1997, Winterbottom 1966c), but some of these data are from studies of the Karoo Thrush (Table 11.1).

**Table 11.1:** Food items: those listed by Winterbottom (1966c) refer to *T. o. olivaceus*, but the other items may refer to *T. smithi* or any of the races of *T. olivaceus*

Winterbottom (1966c)	McLachlan and Liversidge (1978)	Maclean (1993)
Dates		Insects
Cotoneaster		Spiders
Berries		Lizards
Cheese		Chameleons
Apple-cores		Nestlings
Bread	Seed	Seed
Guavas	Fruit	Fruit
Pears		
Grapes		
Apples		
Snails	Snails	Molluscs
Worms	Worms	
Boiled fish	Grasshoppers	Fish
	Caterpillars	

Sanders *et al.* (1997) experimentally demonstrated that Olive Thrushes<sup>4</sup> can select ripe fruit based on colour. Absence of beak marks on unripe fruit additionally suggested that free-living thrushes did not sample by taste.

Olive Thrushes may cause damage to grapes, strawberries and other commercial fruit, but only 3% of reports from a survey of 41 households included the Olive Thrush, which was lower than for all other frugivorous birds considered (Siegfried 1967). In gardens in Bloemfontein during winter, Karoo Thrushes fed mainly on *Celtis Africana*, *Ligustrum vulgare*, *Bequaertiodendron magalis-montana*, *Crataegus* spp. and *Olea europaea* (Kopij 2000).

## 11.2 Results

Food brought to nestlings included termite alates, earthworms, cut worm Noctuidae, Scarab beetle Scarabaeidae and other larvae, apple, berries of stinkwood *Celtis* sp., *Carissa* sp. and *Cotoneaster* sp., and flesh from the seeds of the cycad *Encephalartos altensteinii*. Small earthworms seem to be particularly important in the diet of young nestlings.

On one occasion a female appeared to be teaching a 24-day old fledgling to feed: The female first dropped food on the ground near where the fledgling was perched, after which she flew up to the fledgling, which started begging. The female then returned to the ground. After the third repetition of this behaviour the fledgling followed the female to the ground, where she picked up the food and offered it to the fledgling. When the fledgling gaped and begged, the female dropped the food instead of feeding it to the fledgling. The female then pecked at the food. The fledgling continued begging, so the female offered the food to the fledgling again and repeated the process after dropping the food closer to the fledgling. When the fledgling continued to beg, the female eventually fed it. Fledglings often drop fruit that the parents try to feed them; the parents will then

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<sup>4</sup> Based on distribution this study investigated food selection of the Karoo Thrush

retrieve the fruit and repeat the process until the fledgling swallows the food. This does not seem to happen with invertebrate food.

The young were also led to drinking water by their parents and sources included birdbaths, puddles at sprinkler systems and drips from air-conditioners.

### **11.3 Discussion**

The foraging techniques and varied diet of many *Turdus* thrushes are similar to those of the Blackbird (Clement and Hathway 2000). The wide range of feeding styles of the Olive Thrush, combined with its varied diet, and the availability of water may be important factors in its ability to remain resident in part of its range throughout the year. Water is likely a limiting factor resulting in the possible lack of a minor breeding period of the Karoo Thrush in the drier inland habitat, and may also provide an explanation for the seasonal winter migration of Olive Thrushes in mountainous regions. Water and food availability is also likely to affect the size of territories (Newton 1998). Birds in suburbia benefit from watered gardens, birdbaths and a variety of exotic fruiting plants.

## 12 Interactions with other animals

### 12.1 Introduction

Territorial Olive Thrushes are aggressive towards conspecifics, which may be the reason for attacking their reflections in mirrors and windows (A. Craig, personal communication); “The habit of fighting its own reflection is widespread in passerine birds, especially, perhaps, in the Olive Thrush” (Winterbottom 1964). They are aggressive towards other members of the Turdidae, and in three encounters with Orange Thrushes, the larger Olive Thrushes chased the smaller Orange Thrushes (Earlé and Oatley 1983).

There have been no reports of associations with mammals, but the Orange Thrush has been observed attending a foraging mole-rat *Cryptomys* sp. (Dean and Macdonald 1981). This behaviour has also been recorded for several species of robins (Oatley and Arnott 1998: 204).

Tree (1967) reported on a pair of Cape Thrushes feeding a fledgling Red-chested Cuckoo *Cuculus solitarius* at the Grahamstown sewage works; this is the only record of *T. olivaceus* as a brood parasite host. Cape Sparrows *Passer melanurus* used an Olive Thrush nest after the thrushes had left (Winterbottom 1966c).

Olive Thrushes have been taken as prey by Hobby Falcons *Falco subbuteo* (Pepler 1991) and Booted Eagle *Hieraaetus pennatus* (Steyn and Grobler 1981). Cats, traffic and other human influences are one of the main causes of deaths of robins in urban environments (Oatley and Arnott 1998: 250) and this is likely to be the same for suburban Olive Thrushes.

Mention has already been made of interactions with other bird species during territorial defence, alarm calls used to warn against cats and raptors, and the sharing of nurseries with Cape Robins.

## **12.2 Other observations**

A male Olive Thrush caught invertebrates from the leading edge of a Golden Mole *Amblysomus* sp. (most likely *A. hottentotus*) surface tunnel. As the mole moved forward, insects were disturbed and the thrush fed on these. It is likely that annelids could be found this way too.

Laughing Doves *Streptopelia senegalensis* used old Olive Thrush nests, one of them twice and another once. The two nests were in the same area and it is not certain if it was the same dove on all three occasions. One of the Laughing Dove broods failed (the nearly fledged young was found dead below the nest), but the fates of the other two are uncertain.

These suburban Olive Thrushes can become very accustomed to humans and often seem tamer than their true forest counterparts. In forests, the presence of Olive Thrushes was typically first revealed by the “tsik” call, and it was generally necessary to remain quiet for a while before the thrushes would continue with their normal behaviour. In suburbia they often ignored people if a reasonable distance was kept, sometimes as little as two metres.

### **13 General conclusion**

When I first started colour-ringing Olive Thrushes in my garden to study their behaviour, I had no intension of submitting the results for a degree in Zoology. There were therefore no clearly defined questions for which answers were sought from the beginning. As the work progressed and some of the results were published, it seemed sensible to rewrite these in the form of a thesis for degree purposes. This work, therefore, is a general investigation into the life of suburban Olive Thrushes, dealing with aspects such as basic biology, morphology and distribution.

The study demonstrates the importance of colour-ringing as a technique to investigate the biology of bird species, especially where the sexes are alike, such as the Olive Thrush. It also highlights the usefulness of colour-ringing fledglings for species where post-fledgling parental care is high. Generally such studies are rarely done, supposedly because of the impression that pre-reproductive mortality rates are high, resulting in small returns for a high investment of effort. Such efforts are however very important if we are to improve our understanding of the life-histories of species and inter-specific trends.

Geographical variation is common in most measurable attributes of birds from the timing of moult and biometrics to life-history parameters such as clutch size and survival rates of different age classes. More work is needed on African species with large geographical distributions, such as the Olive Thrush, to understand how such parameters vary with latitude and climate within a species, and how they scale in relation to one another. One advantage of intra-specific comparisons is that there are no phylogenetic effects of inheritance to be taken into consideration (Bennett and Owens 2002), i.e. any differences would be expected to result from adaptation to local conditions. Such trends within species could then be compared to trends between closely related species to test the

generalisations of latitudinal variation in mass, size of protruding body parts, clutch size and adult survival rate.

One aspect that has made this study easy and inexpensive is that it has mostly happened on my front doorstep. I have been able to search for, and study, colour-ringed birds on my way to and from work, during lunch breaks and weekends, without needing to travel. Differences in life-history traits between suburban and rural Blackbirds have been found and such differences would also be predicted for Olive Thrushes. Studying Olive Thrushes in their wild habitats, such as indigenous forests, would require considerably more effort and finance, however, than studying their tamer suburban counterparts.

This study also provides a platform for asking new questions about the Olive Thrush and its relationship to the Karoo Thrush. Differences in the biology of the Olive Thrush and the Karoo Thrush and possible interactions where they are sympatric require further investigation. Future research could ask questions such as: What factors influence the survival rates of dependent and independent fledglings? How much variation is there in clutch size, reproductive rate and nesting success between different pairs? How does song vary between males and are the songs between males in neighbouring territories more similar to each other than those of distant males? How different are the song and calls of the Karoo Thrush to those of the Olive Thrush?

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