MONITORING TERRITORY, SURVIVAL AND BREEDING IN THE LONGTAILED WAGTAIL

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INTRODUCTION

The Longtailed Wagtail Motacilla clara has been studied in the Palmiet Nature Reserve, Westville, Natal $(29^\circ49\mathrm{S},\ 30^\circ55\mathrm{E},\ \mathrm{Figure}$ 1 overleaf) since October 1976. The study site is a 7,08 km stretch of the Palmiet River. This long-term, life-history study has three components: territory, breeding and survival, and our aim in this note is to describe, in some detail, the ringing techniques and observational methods we have used.

While the procedures described here apply to our data collection programme over a number of years we have used a data set collected between 1 August 1986 and 3 July 1987 to illustrate the results; this period is referred to as the 'study period'. The results of the study of territory have been presented elsewhere (Piper and Schultz in prep.) as have the breeding data (Piper in prep.) and these results are summarised below. New data on survival are presented here, as is a preliminary conjecture on population dynamics.

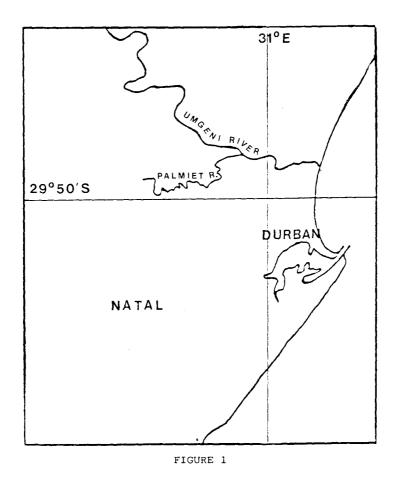
We use this note to illustrate the importance of acquiring a theoretical background against which to conduct an intensive colour ringing study.

METHODS

When we began ringing wagtails, it was a case of "let's colour ring the 'Waggies' and see where they go and what they do" (Piper 1980, 1982). However, we realised that in order to understand what was happening in the population we needed to have a deeper theoretical understanding of territoriality and population biology. We present a precis of the relevant literature for $\varepsilon_{\hat{\epsilon}}$ ch component of our study.

TERRITORY

A definition is provided for the term 'territory', a classification of territory 'types' is presented, as is a method for determining which birds constitute a pair. A working definition of territory, after Davies and Houston (1984: 148) is: "a more or less exclusive area defended by an individual or group". Thus territory is composed of three elements: - 'who' is 'where' and 'when' are they there.



LOCATION OF STUDY SITE NEAR DURBAN

From observations of other songbirds (Davies 1985) a three-tier system of territory defence is to be expected: "Song ... a long-range signal that deters potential trespassers, visual displays ... repel actual trespassers and then, if an intruder persists, it is chased and attacked.".

A functional classification of avian territories, based upon Hinde (1956), is presented in Perrins and Birkhead (1983: 10ff). Of the six categories, type A is the all-purpose territory described as: "a large defended area within which all activities, such as roosting, courtship, mating, nesting and feeding occur.".

Of the many spatio-temporal associations that occur between adult birds, it is said of breeding pairs (Hinde 1985) that "When paired, the mates often tend to keep together for much of the time, and may show a special type of searching behaviour if they lose contact.".

Based on the above definitions and concepts, the following colour-ringing scheme and observational procedures were devised.

Colour ringing

In order to establish the 'who' it was necessary to provide each bird with a unique (to the human observer) identity. To this end birds were caught and fitted with a set of coloured plastic rings. Capture was effected using a 6 m (sometimes 9 m or 12 m), 35mm, four-shelf mistnet strung at right angles across the river. Each bird was ringed with a 3 mm stainless steel, numbered ring supplied by the South African Bird Ringing Unit (SAFRING) on its right leg. In addition, another three coloured plastic rings were attached, one to the right leg above the metal ring and two to the left leg. The six colours used were white (coded as 'W', on the computer coding forms), blue ('B'), red ('R'), yellow ('Y'), green ('G') and swart ('S'; the Afrikaans word 'swart' rather than the English 'black' was used so as to avoid the black/blue confusion when coding the data using a single letter).

It was foreseen that the supply of colour rings would be a problem so no distinction was made between light and dark greens and light and dark blues. Colours which could have been misidentified were avoided. Confusion could have arisen because of colour rings fading or because observations were made in a poorly-lit forest environment, thus colours such as purple, pink and orange were not used. Nevertheless, some yellow rings faded to white and this complicated unambiguous identification; these yellow rings were replaced.

With the metal ring on the lower right there are 180 distinct (i.e. unique) colour combinations, with no colour repeated twice on the left leg. These were all utilized in the period 1976 to 1986 and in 1987 a new series was started in which the metal ring was put atop the colour ring on the right leg. This has made another 180 combinations available. On seeing a bird its combination was recorded in the field notebook as it appeared on the bird, i.e.: -

	Left	Right	
Top	G	R	
Bottom	R	М	

This represents the bird with the colour combination: - green over red on the left leg and red over metal on the right leg. No linear conventions (e.g. GR/RM or RG/MR for the above colour combination) were used when writing the data in the field notebook because of possible errors in recording and subsequent transcription. All partial and doubtful identifications were rejected.

Spatial location

The river was divided into 16 successive sections and each was given a letter to denote that section, e.g. from the bottom of Palmiet Drive to the bottom of old New Germany Road is section 'G' (Figure 2). Within each section along the river physical features were identified, named and given a numerical code, e.g. a felled tree across a small cascade became 'Log-rapids' denoted 'G72'. Place codes were allocated to 138 features along 7,08 km of river, i.e. an average of one code for each 51 m. Each bird observed was recorded as being at the nearest upstream place code, e.g. 'G7200' if it was at, or below 'G72' and in the If it was more than 10 m from the edge of the river then river. For example: the bird was coded as this fact was recorded. 'G72L3' if it was 20 m to 30 m to the left (facing downstream), or as 'G72R5' if it was 40 m to 50 m to the right of the river. In order that planimetric distances be computed for each interdistance between each feature was place-code interval, the distance between each feature was measured along the bed of the river (without correction for slope) using a 100 m metal tape graduated in units of 0,01 m. A number of features were identified on a 1/10 000 orthophoto and these, together with the trace of the river, were digitally captured using a digitizer, the data being stored on computer. A bird's recorded position will be within plus or minus 51 m of its true position.

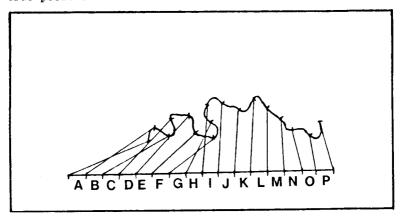


FIGURE 2

DEMARCATION OF SECTIONS ALONG PALMIET RIVER

Time

All observations were recorded by date (as day, month and year) and time, to the nearest minute, local time which is two hours ahead of Greenwich Mean Time. While the measurement of time is internally consistent within any one day to the nearest minute, time may have varied absolutely between days by up to 5 minutes.

Territory monitoring

During the breeding season the following method for monitoring the territorial adults was adopted: - the river was searched, top to bottom, two afternoons a week, covering the top seven territories in one afternoon and the bottom seven on the other, with the central territory being covered twice. In the non-breeding season the river was walked once per week, thus monitoring the territories every second week. On Saturdays an attempt was made to catch and colour ring unringed individuals, or birds which had lost colour rings.

Social behaviour

Special attention was paid to behaviour patterns which could yield clues to territory boundaries and their defence. Notes were kept of all calls and displays, the identity of the birds performing them and all other birds seen in the vicinity.

POPULATION BIOLOGY

The important population parameters are fecundity (or natality), survival (or mortality) and dispersal (i.e. emigration and immigration), see Perrins and Birkhead (1983: 105ff). So far we have not had the resources to set up satisfactory programmes to track emigration and immigration; hence we will only describe our breeding and survival monitoring schemes.

Nest sites

All potential nest sites (being cliffs, bridges and sometimes trees) were photographed and the nest sites used were marked on the photographs. Active nest sites were located by inspecting all previously used nest sites, by searching likely looking areas, by watching for signs of nest building (and refurbishment) as well as by watching birds carrying nesting materials. Some nests were only found after completion when an adult was flushed off the nest as the observer walked by. For each site the following observations were made: -

A. Location. The position of the nest site on its substrate, e.g. tree, bridge (in a hole or on a protrusion), cliff face (on a slope or ledge, vegetated or bare); the height of the nest above the river and the horizontal distance from the "low water's edge".

- B. Nest dimensions. Cup diameter and depth were measured just after completion (or refurbishment), maximum nest height and maximum base diameter; trailing vegetation, if present, was not included in the outer dimensions of the nest.
- C. Materials, mode of construction, the nature of the nest lining and the addition of trailing vegetation.
- D. Timing. The onset of nest building, its duration, its relationship to nuptial behaviour and breeding in the case of a subsequent nest; a distinction was made between the time taken to build a new nest and that required to refurbish an existing nest.

Eggs

All completed nests were checked and their contents noted. Observations were made on the number of eggs, their shape and colouring using a mirror-stick (attached to an extension, if necessary) and illuminating the nest contents with a dry-cell-battery torch. If it was possible to reach into a nest then the contents were extracted. When first handled, eggs were marked with a Roman numeral using a felt-tipped marker pen. The eggs were marked in strict laying sequence, if known. Weights of eggs were interpolated to 0,05 g using a 0,4 g sachet and a 10 g spring balance graduated in 0,2 g. The egg temperature was rated as 'stone cold', 'cool, but not cold' and 'warm' by gently placing each egg on the observers' moistened lips.

Incubation and brooding

Each known nest was approached stealthily in an attempt to determine whether the nestlings were being brooded. If an adult flew off the nest its colour combination (i.e. identity) was noted.

Feeding

The identity of adults carrying food items to the nest was recorded as was the nature of the food item, if identifiable.

Growth

On each nest visit the number of nestlings, alive or dead, was recorded. If the nest was accessible, the nestlings were removed and weighed. A 50 g balance graduated in 0,5 g intervals was used and weights were interpolated to 0,1 g. The development of feathers and other external anatomical features was recorded, as well as the presence (or absence) of egg tooth and yolk sac.

Ontogeny

Observations were made on learning and behaviour of both the nestlings and the fledglings. Reactions of nestlings to the edge of the nest being tapped and to 'pisshing' were recorded. Fledglings were watched and records kept of their ability to fly, beg, follow their parents, attend to the 'End-of-Territory' calls (see Piper and Schultz in prep.) and forage on their own.

Post-fledging dependence period

The fledglings and their parents were followed and observed. Records were kept of when the adults were sufficiently free to commence the next breeding attempt and when the fledglings were able, or were forced, to disperse.

Survival

The spatio-temporal occurrence of each colour-ringed bird was recorded and used to monitor dispersal, territory occupancy and survival. A wall-chart was prepared for each 'wagtail year' (i.e. spring to winter = August to July) and used to monitor, graphically, the survival of each of the territory holders.

DATA CAPTURE

On encountering one or more birds during the census walks, the following data were collected: time, and time accuracy; place code, and spatial accuracy; colour combination; type of observation, e.g. sighting; activity, e.g. foraging; nest associated activity, e.g. feeding young; social behaviour, e.g. interactions between two or more birds; calls, e.g. contact; substrate, e.g. small rocks in river; abnormality, e.g. bird limping; and age, e.g. juvenile.

All observations were recorded in a field notebook. These were then transcribed to computer coding forms using one- to five-character codes for each of the items described above. In addition, a free-format field was used for entering non-coded information, queries and speculations. The data forms were then submitted for key punching and validation. The data were subjected to range checks and a detailed manual examination to eliminate errors. Since mid-1987 a data capture routine written by one of us (D.M.S.) has been used for direct capture and validation on a home micro-computer; this has eliminated having to pay for key punching while also reducing data capture errors.

Other species

Records, in the same format as that above, were kept of all observations of the following species also encountered in the study site: - Hamerkop Scopus umbretta, African Black Duck Anas sparsa, Spotted Eagle Owl Bubo africanus, African Pied Wagtail M. aguimp and Cape Wagtail M. capensis.

RESULTS

During the 12-month study period a total of 2 102 observations were made and entered on the computer. Of these, 194 records were excluded as they related to other species; also excluded were 142 records concerned with environmental observations (e.g. weather), thus leaving 1 766 sight records of Longtailed Wagtails spread across 52 different days (excluding visits for the purposes of recording nest contents), with about 34 records per day. The search rate was just over four times per month or once a week. There were 1 295 observations of 30 individually recognisable (i.e. colour-ringed) birds, 399 observations of unringed birds and 72 observations of birds where only part of the colour combination was seen or where, in retrospect, the identification was thought to be in error. The total of 1 694 usable records was further reduced to 1 654 by eliminating 40 records of birds seen on rivers other than the Palmiet. were observed at 135 of the 138 marked places. Coalescing all those records for the same bird at a place-day yields a birdplace-day, of which there are 947, i.e. there was an average of 1,75 observations per bird-place-day. The data may be further agglomerated by pooling all the observations, over time, for a given bird at a given place to yield a bird-place; there were 427 bird-places. The territory summaries presented below are drawn from Piper and Schultz (in prep.) and the breeding biology results from Piper (in prep.).

Territory dimensionality

It was found that birds held strictly linear territories, i.e. they confined all their activities (e.g. foraging, courtship, nest building, and raising of young) to the river and a narrow zone on either side of it. The territory is linear, i.e. unidimensional, so far as a bird's position in the territory can be uniquely determined in terms of a single measurement: the distance downstream from the top of the territory.

Territory type

Longtailed Wagtails hold a type A, i.e. a general purpose, territory. Within this territory all activities (e.g. foraging, roosting, courtship, mating and nesting) occur and territory holders seldom leave their territory.

Territory size

The sizes of the territories varied, in length, from 400 to 900 m with a mean of 590 m, which yields equivalent densities of 11,1 to 25,0 pairs/10 km with a mean of 16,9 pairs/10 km.

Breeding and fecundity

Only territorial birds breed and they tend to use the same nest sites year after year and will even use an extant nest if it can be refurbished easily. They may lay one to four eggs, but usually lay two or three. They average 2,55 breeding attempts

per pair per season with 2,14 eggs per clutch and 0,65 fledglings per attempt. This means that there are an average of 1,55 fledglings produced per pair per annum.

Survival

Of the 19 marked, territory-holding birds alive at the beginning of the study period there were 18 still alive at the year's end (Table 1 overleaf). This yields an estimate of survival rate of 18/19 = 94,74 % per annum (95 % confidence limits of 73,97 % to 99,87 %; Diem and Lentner 1970:85).

DISCUSSION

Much of science consists of putting numbers to ideas that have been expressed earlier in qualitative terms. The Reverend Robert Godfrey, who lived much of his adult life in the Transkei, clearly understood much about the type and dimensionality of Longtailed Wagtail territories when he wrote: -

"For delicacy of colouring, grace of movement and fearlessness of mankind, few of the smaller forest-birds can compare with the Grey-backed Wagtail ... [which] ... occurs in isolated, resident pairs, each haunting a strip of river." (Godfrey 1927: 9)

What we have done is to quantify his observations and hypothesis.

The population data shown above lead to an interesting conclusion: assuming that adult male and female mortality is equal and that the male to female sex ratio is 1:1, then the adult survival rate of 73,97 % to 99,87 % p.a. implies that the annual recruitment of territorial adults must be 2*(100-99,87)/100 = 0,0026 to 2*(100-73,97)/100 = 0,5206 individuals per pair. The annual productivity of 1,55 fleglings is 2,97 times greater than recruitment and this implies a loss of about 70,5 % of the fledglings produced; i.e. many more fledglings disperse earn year than are needed to fill the vacancies in the population of territorial adults. However, two caveats must be made. Firstly there are considerable year-to-year variations survival and productivity, thus these may not be typical figures. Secondly the Palmiet is probably a prime area and may serve to populate other poorer areas; there is a danger in regarding a small system, such as the Palmiet, as 'closed'. preliminary estimates show that survival is an important parameter in the population dynamics of these tropical passerines and we should avoid the Euro-centric view that most research effort should go into monitoring breeding (to repeat a previously stated view: Piper 1987).

TABLE 1
SUMMARY OF TERRITORY OCCUPANTS AND SURVIVAL

	TERRITORY HOLDER AT 01.08.86			TERRITORY HOLDER AT 31.07.87		
TERRITORY NAME	BIRD	RING NO.	RINGED	BIRD	RING NO.	RINGED
Blair Athol Blair Athol	UUUUUU AUUUUU	BB28057	Ca.11/85	บบบบบบ		>
Palace Corner Palace	USBUYA	BB28084	09/03/85			-
Corner	UWSUGA	BB28063	28/09/84			>
May's pair May's pair	UWBUYA UUUUUU	BB28066	01/10/84	UGWUAW UUUUUU	BB28100	21/02/87
Fairy cliff Fairy cliff		BB20610 BB28002	03/09/77 14/11/81			
Caefron Avenue Caefron Avenue	UBWUWA	BB29288	15/03/81	UWGUWA	BB28083	24/11/84
Sportsfield Sportsfield	UYWUYA	BB28086 BB28052	05/04/85 03/09/83		BB20003	24/11/84
Entrance Entrance	URWURA URGUGA	BB28018 BB40109	30/10/82 01/02/79			
Dusky pool Dusky pool	UWSURA UWGUBA	BB28081 251561	24/11/84 22/09/84			
Minicascade Minicascade		BB29957 BB28079	01/06/80 24/11/84			\Rightarrow
Debris cliff Debris	USWUBA	BB28050	29/01/83			
cliff	UWBUGA	BB40293	27/12/80	ļ 		├
Longtill Longtill	UYRURA UUUUUU	BB28074	03/11/84	UGRUSA	BB28090	13/09/86
University University	UGSUAG UUUUUU	BB28076	03/11/84	טטטטטט		

The bird which did not survive was UWBUYA, a bird in May's pair territory.

Looking back on our initial proposal to undertake a colourringing study we see that very little ringing activity was required. The ratio of field work dedicated to seaching for and observing colour-ringed birds exceeded the time devoted to ringing by somewhere between 3:1 and 5:1. However, the rewards in raw-data and knowledge are probably in excess of 100:1, this bears out the maxim that 'ringing is a tool, not an end in itself'.

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Most of the ringers who attended the meeting in Johannesburg are featured in this group picture. The author of the report opposite is wearing dark glasses and failing to obscure the only standing figure, who is recognisable even at this scale. Get out your magnifying glass and see how many others you can recognise. James Harrison, SABAP Co-ordinator, took the photograph.