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Survival of adult, territorial Longtailed Wagtails *Motacilla clara*: the effects of environmental factors and individual covariates

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ABSTRACT   *The Longtailed Wagtail is a non-migratory African passerine that is confined exclusively to small, fast-flowing rivers in a largely arboreal environment. The breeding adults hold permanent, life-long, linear territories in their riverine habitat and this makes it easy to locate colour-marked birds. They are confiding by nature and permit close approach, often to less than 10 m, and this allows their unique permutations of colour-rings to be read. Using data from the 21 year period, 1 August 1978 to 31 July 1999, of a dozen territories it has been shown that the breeding territories have not changed at all, even though there has been a continual, but slow turnover of territory holders. A total of 109 territorial adult birds were monitored for a total of 1121 bird-quarters and survival was estimated for each of four quarters in a year. The average survival rate is estimated at 68.8% yr^{-1} (95% confidence limits: 63.3% to 69.3%) and this is high for such a small bird (approximately 20 g) and there have been some remarkably long-lived individuals, e.g. 10 to 12 years. In this paper, a generalized linear model is built of the survival of territorial adults. It is shown that bigger birds have a higher survival rate and that there are seasonal differences in survival that are ascribable to the cost of breeding and possibly cost of moult. There is an underlying long-term quadratic trend in survival that is related to increasing environmental degradation and decreasing chemical pollution.*

1 Introduction

The Longtailed Wagtail *Motacilla clara* is the object of a long-term demographic study in southern Africa. The overall objective of the study is to develop an understanding of the lifetime reproductive success of individuals and how they

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contribute as individuals to the demography of the population as a whole. To date, descriptions have been provided of the type and dimensionality of the territories (Piper & Schultz, 1989), the timing of breeding and the fecundity of pairs (Piper, 1989) and the demographic structure of the population (Piper, 2001). The primary aim of this paper is to construct a set of biologically plausible and *a priori* models that lead to a deeper understanding of those factors that influence survival.

Longtailed Wagtails were caught opportunistically in the main study site and along other nearby rivers, once caught they were colour-ringed. The main study site was searched regularly and individuals were identified in the field using binoculars—each individual carried a unique permutation of colour-rings. Using these sightings' data from over 100 individuals that occupied a dozen territories for over two decades a database of many thousands of such sightings was assembled. This database was used to create a space-time diagram (Piper, 2001). In turn, this space-time diagram was used to monitor the survival of every individual territory-holder on a quarterly basis. Because almost every territory-holder was seen almost every quarter it was possible to estimate survival directly. This is equivalent to assuming that the sighting (= recapture) probability is unity. As a consequence it is not necessary to resort to the more complex Cormack-Jolly-Seber (CJS) methods (Burnham *et al.*, 1994). Territories for which this was not true were excluded from the analysis.

Many factors are thought to impact upon the survival of this little (approximately 20 g) African passerine that lives almost exclusively along small to medium streams, usually in a forested environment (Piper, 1997). To make sense of these factors they are grouped in two different ways: along a proximate to ultimate axis and along an individual to group axis (Fig. 1).

The concept of a proximate to ultimate axis is borrowed from evolutionary ecology (Endler, 1986, p. 43; Stearns, 1992, p. 153; Krebs & Davies, 1997, p. 4). A variable or factor is considered 'proximate' if it acts immediately on the survival of an individual, e.g. its size, or 'ultimate' if it acts at a distance, e.g. rainfall. In my opinion it is better to use a variable rated as 'ultimate' as an explanatory variable rather than one rated as 'proximate' because it is more likely to have greater biological significance. For instance, using a four-level factor for season is
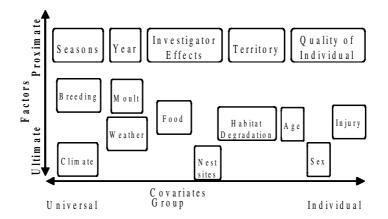

FIG. 1. Relationships among explanatory variables along the axes proximate to ultimate and universal, group and individual.

not as biologically useful as fitting factors that model the costs of breeding and moult, both of which vary seasonally.

The putative explanatory variables were classified as individual, group or universal, defined as follows. An 'individual' variable is one that may take on a different value for each individual in the population, e.g. wing length. A 'group' variable is one that may take on a different value for each group but has the same value for every member of a given group, e.g. territory takes on the value 2 for all those individuals who occupied the Palace Corner territory. In other words, the variable is homogeneous with respect to all members of the group. A 'universal' variable is one that takes on the same value for all members of the study population, e.g. rainfall.

The following putative explanatory variables were classified as 'proximate' and 'individual'—an individual's size and condition; as 'group'—territory; and as 'universal'—annual effects, seasonal effects and investigator effects. The following variables were classified as both 'ultimate' and 'universal'—cost of breeding, cost of moult, habitat degradation, rainfall and temperature. These variables are described below, as are their hypothesized effects on survival.

Size.   If the population is subject to stabilizing selection then it is to be expected that smaller and larger individuals will have lower lifetime reproductive success (LRS) and survival may be a component of this (Endler, 1986, pp. 4-5, 16 ff). Thus, middle-sized birds may survive better. However, if habitat degradation (see below) has an effect on survival then selection may be directional favouring either larger or smaller birds (e.g. Brown & Brown, 1998).

Condition.   It is known that nestlings and fledglings in better condition survive longer (e.g. O'Connor, 1979, for the Swift *Apus apus*). Among adults, those in better condition may hold better roosts (e.g. Summers *et al.*, 1987 for the Starling *Sturnus vulgaris*) and may be better able to survive starvation (e.g. Stokkan & Blix, 1986, for the Svalbard Rock Ptarmigan *Lagopus mutus*). This suggests that individuals in better condition could have higher survival rates.

Territory.   It has been shown that individuals on territories with lower survival rates are more likely to forsake them for other territories (Piper, 2001). In other words, it has already been shown that survival rates differ between territories.

Annual effects.   In some years, almost every pair produces at least one fledgling while in other years only a few pairs are productive. Thus, by analogy, it is to be expected that survival may also vary from year to year.

Seasonal effects.   In northern temperate climes birds have lower survival rates during the winter (e.g. O'Connor & Cawthorne, 1982) and so by analogy it is to be expected that the survival rates of Longtailed Wagtails could vary between quarters.

Investigator effects.   It is important to be mindful of the possible impact that trapping can have on survival (Houston, 1974). In a survey of 786 papers in which birds were marked and of 301 papers reporting the use of rings, only 1.6% commented on their use and only 0.3% reported or tested for harmful effects (Calvo & Furness, 1992). More recently (Smith & Inglis, 1999) reported an

increase in post-trapping mortality of the Woodpigeon *Columba palumbus*. Thus, it is necessary to model the possible deleterious effects of mist netting, handling, ringing and releasing an individual. This can be achieved by recording whether or not an individual was handled in a given quarter. However, prior to 1986, fewer searches were made on foot and so the space-time diagrams, and hence estimates of survival, are more heavily based on ringing data. After 1986, many more walks were conducted and survival was better estimated from sightings. Consequently, this investigator effect will have a different meaning before and after 1986.

Cost of breeding.   It has been shown that breeding is energetically expensive (e.g. Cichon *et al.*, 1998, for the Collared Flycatchers *Ficedula albicollis*) and so it is to be expected that this could translate into a lower survival rate (see Stearns, 1992, pp. 82-84, for a review of trade-offs between breeding and survival).

Cost of moult.   A complete annual moult in passerines is necessary but costly (Jenni & Winkler, 1994, pp. 4-5) and a reduction in survival during the period of moult is possible.

Habitat degradation.   Urban storm water runoff has increased throughout the study period as the surrounding plateau has become more densely settled and this has led to severe habitat degradation with most of the riparian vegetation having been washed away (personal observation). During the period 1976 to 1991 there was an increase in chemical pollution of the Palmiet River from textile factories in upper catchment but this declined in the 1990s as there was a relaxing of import restrictions in the post-Apartheid society with imported textiles depressing the local market (M. C. Cottrell, personal communication). From the early 1990s water quality increased.

Rainfall.   The primary productivity of the natural environment is driven by rainfall and temperature (Schulze, 1997). It is hypothesized that the higher the rainfall the higher the primary productivity and hence the greater the food base for Longtailed Wagtails. However, when it rains, even lightly, there is a rapid inflow of dirty and muddy water from the surrounding suburban storm water network (M. C. Cottrell, personal communication) and this inhibits foraging for some hours to days. This is because the birds seek the major portion of their food on, or just below the water's surface and do so by sight (personal observation). Also, when it is raining they cannot go about their usual foraging activities that normally take up most of the day (personal observation).

Temperature.   Invertebrates are more active on warmer days and less active on colder days and a day was defined as cold if it was below 20°C (it's Africa!) and warm if it was above 30°C (S. Pryke, personal communication).

  It is probable that survival could vary with food quality and quantity, an individual's sex and the presence of external abnormalities. However, no data were ever collected on food availability in the main study site. In the early years of the study no reliable method of sexing birds was available but this is now possible using a DNA-based technique; unfortunately, only a few individuals have been sexed in recent times. External physical abnormalities were noted on a number of

birds but these data were not collected consistently across the whole study population to be included in this analysis.

Because most birds were caught as free flying individuals of unknown age it was not possible to model senescence.

Only territorial birds in adult plumage were included in the study, thus avoiding the need to estimate the survival rate of immature individuals or non-territory holders.

The aim of this research is to elucidate those factors that influence the survival rate of territorial Longtailed Wagtails and to estimate the effect of each factor.

2 Methods

Study site.   The Longtailed Wagtail was studied in the deeply incised valley in which the Palmiet River (29°49′S; 30°55′E) flows through Westville, a suburb of the port city of Durban on the south-east coast of South Africa, in the Province of KwaZulu-Natal. The birds were trapped, ringed (= banded) and released along a 7 km stretch of the river. This constitutes the main study site; research was also carried out further upstream and on other rivers and streams in the vicinity and at other sites in South Africa. Details of the objectives of this study and the field methods used may be found elsewhere (Piper & Schultz, 1988).

Marking.   Individual Longtailed Wagtails were caught opportunistically using mist-nets erected, before dawn, at right angles to the river. The birds were fitted with a metal ring issued by the South African ringing scheme (Safring) and a unique permutation of three or four colour-rings. Primary wing length was measured to the nearest 1 mm using a metal rule graduated in mm. The weight of each bird was estimated to 0.1 g by interpolating on a spring balance with 0.5 g graduations. The remiges and rectrices were inspected and checked for moult.

Monitoring.   The main study site was searched for marked birds by walking along the river, birds were visually identified using binoculars. The identity of each bird was established from its unique permutation of colour-rings. Each time a uniquely marked individual was sighted, the date, time and spatial location were recorded. From these data it was possible to draw a space-time diagram for each individual (Piper, 2001) and hence construct territory-occupation charts as well as infer which birds were mated pairs (Piper & Schultz, 1989).

Survival.   The year was divided up into four quarters: spring (August to October), summer (November to January), autumn (February to April) and winter (May to July). The wagtail year runs from 1 August in one calendar year until 31 July in the next year. Survival was monitored on a quarterly basis and an individual was reckoned to have survived a quarter if it was seen alive on or before the first day of the quarter and then seen alive on or after the last day of the same quarter. If a bird deserted its territory and moved to another territory before the end of the quarter and even if it was seen alive on the second territory then it was still recorded as a loss for that quarter, for the first territory.

Model formulation and fitting.   A generalized linear model (GLM) was constructed using the quarterly survival of each territorial individual as the binary response variable (0 = loss or death, 1 = survived). The logit was used as the link function

(McCullagh & Nelder, 1989). The various variables to be discussed below were entered into the model in linear combinations. The GLMs were fitted using Genstat (Anonymous, 1988). The goodness of fit of a model was assessed using the X^2 statistic in which the actual survival was compared with predicted survival; X^2 has the useful property that it is asymptotically distributed as χ^2 (Dobson, 1991).

Model selection and parameter estimation.   A small set of candidate models was formulated *a priori* and fitted. For each model the Akaike information criterion (AIC) was computed from the sum of the deviance and twice the number of model parameters (Burnham & Anderson, 1998). The difference in AIC between the ith model and the model with the lowest AIC was computed from $\Delta_i = \text{AIC}_i - \min_i(\text{AIC})$. The Akaike weights were computed from $w_i = \exp(-\frac{1}{2} \times \Delta_i)/\Sigma_i \text{Exp}(-\frac{1}{2} \times \Delta_i)$. The weighted estimate of a parameter, θ was computed from $\Sigma_i w_i \theta_i$, where θ_i was the estimate from the ith model.
   The explanatory variables, introduced above, are defined below.

Size.   The length of the primary portion of the wing was taken as a surrogate for the bird's overall size. Wing length was entered into the GLM as a linear variable, assuming directional selection or as a quadratic, assuming stabilizing selection.

Condition.   An index of condition was computed as the residual mass from a regression of mass against wing. Condition was entered into the GLM as a linear variable. Wing length and the condition index were averaged over all those occasions on which an individual was captured and measured and the averaged values were used in the GLMs.

Territory.   There were 11 territories in the main study site and so territory was entered into the GLM as an 11-level factor.

Annual effects.   The first study year was from 1 August 1976 to 31 July 1977 and all years were numbered sequentially thereafter; year 24 ended on 31 July 2000. Annual effects were entered into the GLM as a 21-level factor (21 years of data were used in the model—see below).

Seasonal effects.   The four quarters (i.e. spring, summer, autumn and winter) were entered into the GLM as a four-level factor.

Investigator effects.   If an individual was trapped in a given quarter then this was coded as 1, otherwise as zero. Two investigator effect variables were defined, one for the period prior to 1986 and the other for the period after, see above for the rationale.

Cost of breeding.   The onset of breeding is variable from year to year but is seldom before 15 August and never after the end of August and generally runs through to about 15 December (Piper, 1989). Hence breeding is assumed to run for 2.5 months in the spring quarter and 1.5 months in the summer quarter. Thus the cost of breeding is a variable that has the values (2.5/3, 1.5/3, 0, 0), i.e. (0.833, 0.5, 0, 0) for the four seasons spring, summer, autumn and winter, respectively. While individual variations in breeding performance were observed they have not been uniformly quantified.

Moult.   Nearly all individuals completed their post-nuptial primary feather moult between February and April, i.e. in the autumn quarter as defined in this study. A few birds initiated moult in January or completed their moult in May (personal observation). Thus, the cost of breeding is a variable that has the values (0, 0.5/3, 2.5/3, 0.5/3), i.e. (0, 0.167, 0.833, 0.167) for the four seasons spring, summer, autumn and winter, respectively. While many individuals were caught undergoing moult there is, as yet, insufficient data to quantify individual variations in the timing and duration of moult.

Habitat degradation.   The degradation of the physical environment due to urban water runoff is assumed to be a decreasing and linear function with time. The degradation of the water quality due to chemical pollution is assumed to be a concave quadratic function as water quality decreased during the 1970s and 1980s but has been improving since the early 1990s.

The extensive databank of the Computing Centre for Water Research (CCWR) at the University of Natal, Pietermaritzburg, South Africa, was searched for long-term weather stations near the main study site that had daily temperature and rainfall data for the entire study period. From these, a complete run of data was compiled for the study period.

Rainfall.   From the records of daily rainfall two summary statistics were computed for each quarter: total rainfall and number of days of rain.

Temperature.   The mean daily minimum and mean daily maximum temperatures were computed for each quarter as were the number of 'hot' days and 'cold' days per quarter. A day was defined as cold if $T < 20°C$ and hot if $T > 30°C$.

This long-term study of survival in the Longtailed Wagtail began on 5 October 1976 and the last census was conducted on 10 June 2001, a total of 24 years and 8 months. The study is ongoing. A total of 539 Longtailed Wagtails have been ringed at all study sites, 411 of them were caught at least once in the main study site, the total number of times individuals have been caught and processed is 1122 with 877 of those being in the main study site. Thus, each bird has been processed 2.13 times in the main study site and 2.08 times overall. A total of 353 ringing excursions were made, 269 of these in the Palmiet River valley, i.e. 1.19 per month overall and 0.91 per month in the main study site. An average of 3.18 individuals were caught per excursion overall and 3.26 in the main study site.

Although the first Longtailed Wagtail was caught and ringed on 5 October 1976 the first territory-holder was only recognized at the start of November 1977. It was only by the end of the 1977/1978-year that all the territories had been located and mapped and most of the territory holders marked. Thus, this analysis begins on 1 August 1978. The last territory-holder was located in June 2001. Because of limitations in collecting, collating and correcting the weather data used in these analyses, the last year for which the data are available is 1998/1999. Thus, the analyses end on 31 July 1999, i.e. a total of 21 years. Of the 13 permanent and four temporary territories located and monitored in the main study site there is only enough consistent data to model survival in 11 of the permanent territories and one temporary territory, i.e. a total of 12.

Of the 411 individuals caught and processed in the main study site only 139 of them settled long enough in a territory to be recognized and monitored as a territory holder; these birds form the basis of this analysis. The time they spent on a territory varied from a single quarter up to 45 quarters (i.e. a decade) for the two longest surviving individuals. The oldest bird was last seen just over 12 years from when it was first ringed. These 139 individuals were noted alive as territory holders at the start of 1252 bird-quarters.

A total of 324 adults were weighed and measured 695 times. Of the 150 individuals weighted and measured at least twice, only four had a standard deviation (sd) of primary wing length greater than 2 mm and only two had a sd(mass) > 2 g, thus these measurements may be considered repeatable. From a regression of weight on wing length the condition index was equated to the residual = observed mass − predicted mass = Observed mass − $(3.783 + 0.20456 \times \text{wing})$.

Not all the territorial birds were weighed and measured and so data from only 109 individuals spread over 1121 bird-quarters could be used in this analysis.

In this study, the survival of a pair of territory holders on 12 territories over 21 years was monitored on a quarterly basis. Of the potential $21 \times 12 \times 4 \times 2 = 2016$ bird-quarters a total of 1121 bird-quarters were actually recorded, i.e. 55.6%. The difference is attributed to territory-holders that were not adequately weighed or measured, territories that were not filled for sometime after the previous occupier had died and new territory holders who acquired a vacant territory but were left unringed by me for some time.

Three groups of models are proposed *a priori* and these are based on current insights into survival process of passerines in general and this study species in particular (see introduction for references). The three groups are a constant, models based on proximate variables and models based on all variables. In these models, care has been exercised in choosing variables so that the potential for confounding and redundancy is minimized.

The first model (model A, Table 1) is a constant only.

There are six models that are based on proximate variables only (models B-G, Table 1). In all of these the investigator effects (i.e. caught pre- and post-1986) are included because they are thought to play a large part. Three of the models then include one of the main effects, i.e. season, year and territory (models B, C and D, respectively, Table 1). The remaining three models (E-G, Table 1) all include season, year and territory as well as size and condition. Size is included as a linear variable, i.e. assuming directional selection or as a quadratic variable, i.e. assuming stabilizing selection (models E and G respectively, Table 1). The last model in this group also includes condition (model F, Table 1).

There are seven models based on all variables (models H-N, Table 1). All these models include the pre-1986 investigator effect, size and habitat degradation. The first three models (H-J, Table 1) include either the cost of breeding or the cost of moult or both; these models have the minimum number of explanatory variables. The remaining models all include cost of breeding and cost of moult. In these models, cost of breeding and cost of moult replace season while habitat degradation, as a quadratic function, replaces year but territory is excluded altogether. The next three models (K-M, Table 1) include the two mean temperature variables, numbers of cold and hot days and the rainfall variables (models J, K and L respectively, Table 1). The last model includes all the weather variables (model M, Table 1).

No models were formulated with interaction effects.

TABLE 1. Summary of GLMs fitted

	Model													
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Constant	+					+	+	+	+	+	+	+	+	+
Factors: Seasons		+			+	+	+							
Years			+		+	+	+							
Caught, pre '86		+	+	+	+	+	+	+	+	+	+	+	+	+
Caught, post '86		+	+	+	+	+	+	+	+	+	+	+	+	+
Territories				+										
Wing					+	+	+	+	+	+	+	+	+	+
Wing-squared						+								
Condition							+							
Habitat degradation								+	+	+	+	+	+	+
Cost of breeding								+	+	+	+	+	+	+
Cost of moult										+	+	+	+	+
Mean max. temp. °C									+		+	+		+
Mean min. temp. °C										+		+		+
Days below 20°C												+		+
Days above 30°C												+		+
Quarterly rainfall													+	+
Days of rain													+	+
Deviance: Resid	674.2	636.9	580.1	643.2	562.4	562.3	561.2	600.9	608.4	600.3	600.2	599.0	598.2	597.3
Deg of Freedom	1120	1115	1096	1107	1092	1091	1090	1115	1115	1113	1111	1109	1111	1107
X²	100.0	99.9	99.5	99.9	98.9	98.9	99.1	101.8	101.9	101.9	101.8	101.5	101.1	100.8
P	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
R²	—	4.3%	8.9%	3.8%	12.1%	12.1%	12.2%	7.5%	6.6%	7.5%	7.6%	7.9%	8.0%	8.3%
Residuals	0	0	0	0	1	1	1	1	0	1	1	1	1	1
Leverage	0	75	40	20	31	26	27	45	42	25	12	22	21	17
Warnings	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Parameters	1	6	25	14	29	30	30	6	6	8	10	12	10	14
AIC	676.2	648.9	630.1	671.2	620.4	622.3	621.2	612.9	620.4	616.3	620.2	623.0	618.2	625.3
Delta(AIC)	63.3	36.0	17.2	58.3	7.5	9.4	8.3	0.0	7.5	3.4	7.3	10.1	5.3	12.4
Exp(−0.5*Delta(AIC))	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.2	0.0	0.0	0.1	0.0
Akaike weights	0.0%	0.0%	0.0%	0.0%	1.7%	0.7%	1.2%	73.5%	1.7%	13.4%	1.9%	0.5%	5.2%	0.1%

Notes: AIC Minimum (Model H). Sum of Exp(−0.5*Delta(AIC)) = 1.4.

3 Results

A total of 14 GLMs were fitted but four of these had Akaike weights of less than 0.1% and so were ignored in this analysis (Table 1). Model H had the lowest AIC differing by 3.4 units from the next best model (Table 1). While model H was the best model, its Akaike weight of 73.5% was not so high that the other models could be ignored; it has been recommended that a 'best' model should not be used alone if its Akaike weight is less than 90% (Burnham & Anderson, 1998, p. 157). Because of this, the ten best models with Akaike weights greater than 0.1% were used to provide weighted estimates of the variable coefficients as well as weighted unconditional estimates of the standard errors (Table 2).

The survival rate, averaged over all bird-quarters was 68.8% yr^{-1} (95% limits 63.4-73.7%), similar to an earlier estimate of 65.5% (± 2.5%) (Piper, 2001), which was based on a slightly smaller data set. However, both these estimates are much lower than the first estimate of 85.1% yr^{-1} for this species (Piper, 1994), which was based on a much smaller data set that included some years with high survival rates. By way of example, the survival rate during 1986/87 was high with 75 bird-quarters of whom 73 survived, i.e. a rate of 90% yr^{-1}. These estimates for *M. clara* are about 12-19% higher than the estimates of annual survival for three congeneric species in Britain: *M. alba* 49.7% (se 6.9%) yr^{-1} (Baillie & McCulloch, 1993), *M. flava* 53.3% yr^{-1} (Siriwardena *et al.*, 1998) and *M. cinerea* 46.3% (se 7.9%) yr^{-1} (S. Freeman in Piper, 2001).

The differences in survival are largest between spring and summer and decrease monotonically between quarters thereafter with spring having the lowest and winter the highest survival rates (models E-G, Table 1; Fig. 2, Table 2).

When modelling temporal variation using study year it was found that all the pre-1985/1986 survival rates were high (models E-G, Table 1; Fig. 3; Table 2) and this was due to the pre-1986 investigator effect, see below. The high survival rate during the 1986/87 study year was not a result of investigator effect, it was real, see comments above.

Of the two investigator effects, the pre-1986 effect had a large and significant coefficient (Table 2). In an average quarter the survival rate was 68.8% p.a. but if the bird was caught and processed during that quarter, prior to 1986, then the survival rate was estimated to decease to 0.3% p.a. (0.01-5.37%)! This is due to the way survival was monitored prior to 1986. From the 1986/1987-study year the post-1986 investigator effect increased the average survival rate from 68.8% p.a. to 74.1% (56-86), a small but statistically non-significant change. Why this effect should be positive is not known.

The variations in survival between territories were small and of no significance (model D, Table 1) and were not included in the analysis. This conclusion is in contrast to that of Piper (2001) where it was found that there were significant variations in survival between territories but no cognisance was taken in that analysis of investigator effects.

Wing length as a surrogate for size was included in the models as a linear variable with a highly significant coefficient (Table 2). However, the quadratic term was not significant (model F, Tables 1 and 2). The implication of this is that there is directional selection with larger birds having the advantage. All else being equal, a small bird with a wing of 74 mm will have an annual survival rate of 47% (43-52%). A large bird with a wing of 84 mm will have an annual survival rate of 83% (81-85%).

TABLE 2. Computation of model parameters (part 1)

| | Model | | | | | | | | | | Weighted |
	E	F	G	H	I	J	K	L	M	N	value
Constant	−9.570	−9.360	−8.940	−9.000	−9.780	−8.880	−8.100	−5.610	−9.400	−6.090	−8.992
se	5.600	5.590	5.600	5.300	5.270	5.310	6.380	8.800	5.310	8.890	5.362
Summer	0.358	0.357	0.361								0.359
se	0.278	0.278	0.278								0.278
Autumn	0.799	0.797	0.800								0.799
se	0.317	0.317	0.317								0.317
Winter	0.984	0.983	0.998								0.988
se	0.344	0.344	0.345								0.344
Years—2	5.100	5.100	5.000								5.067
se	24.800	24.800	24.800								24.800
3	7.200	7.200	7.200								7.200
se	13.300	13.300	13.200								13.267
4	1.290	1.300	1.180								1.256
se	1.420	1.420	1.420								1.421
5	0.540	0.540	0.500								0.527
se	1.280	1.280	1.280								1.280
6	−0.350	−0.350	−0.400								−0.366
se	1.280	1.280	1.280								1.280
7	−0.200	−0.210	−0.300								−0.234
se	1.290	1.290	1.290								1.291
8	0.680	0.670	0.560								0.639
se	1.540	1.540	1.540								1.541
9	0.750	0.750	0.680								0.727
se	1.350	1.350	1.350								1.350
10	5.440	5.440	5.380								5.420
se	7.850	7.850	7.830								7.844
11	5.370	5.380	5.310								5.352
se	7.600	7.600	7.590								7.597
12	−1.790	−1.780	−1.850								−1.808
se	1.090	1.090	1.090								1.090
13	−1.880	−1.880	−1.950								−1.903
se	1.100	1.100	1.100								1.100
14	−1.500	−1.500	−1.580								−1.526
se	1.120	1.120	1.130								1.124
15	−1.140	−1.140	−1.210								−1.163
se	1.180	1.180	1.190								1.184
16	−2.570	−2.570	−2.590								−2.577
se	1.090	1.090	1.090								1.090
17	−2.240	−2.230	−2.250								−2.241
se	1.100	1.100	1.100								1.100
18	−2.100	−2.100	−2.100								−2.100
se	1.100	1.100	1.100								1.100
19	−0.990	−0.990	−0.980								−0.987
se	1.180	1.180	1.180								1.180
20	−1.550	−1.550	−1.510								−1.537
se	1.130	1.130	1.130								1.130
21	−2.040	−2.030	−2.000								−2.025
se	1.090	1.090	1.090								1.090
22	−1.940	−1.940	−1.920								−1.933
se	1.090	1.090	1.090								1.090
23	−1.530	−1.540	−1.520								−1.529
se	1.110	1.110	1.110								1.110

TABLE 2. Computation of model parameters (part 2)

	Model										Weighted value
	E	F	G	H	I	J	K	L	M	N	
Caught, pre'86	−3.349	−3.347	−3.353	−3.518	−3.612	−3.504	−3.499	−3.487	−3.425	−3.418	−3.506
se	0.693	0.693	0.694	0.547	0.547	0.548	0.549	0.548	0.548	0.549	0.554
Caught, post'86	0.201	0.197	0.207			0.221	0.221	0.252	0.275	0.295	0.231
se	0.355	0.355	0.355			0.338	0.399	0.340	0.341	0.342	0.347
Wing	0.164	0.161	0.156	0.148	0.149	0.148	0.148	0.149	0.155	0.155	0.149
se	0.070	0.070	0.070	0.067	0.067	0.067	0.067	0.067	0.067	0.068	0.067
Wing-squared		−0.009									−0.009
se		0.034									0.034
Condition			0.163								0.163
			0.148								0.148
Habitat deg. Linear				−0.804	−0.812	−0.826	−0.822	−0.831	−0.819	−0.822	−0.809
se				0.187	0.187	0.190	0.195	0.195	0.190	0.194	0.188
quadratic				0.652	0.661	0.647	0.650	0.659	0.629	0.641	0.650
se				0.175	0.175	0.174	0.174	0.175	0.174	0.175	0.175
Cost of breeding				−1.122		−1.274	−1.310	−0.658	−1.106	−0.639	−1.143
se				0.312		0.486	0.705	0.957	0.558	0.977	0.367
Cost of moult				0.898	−0.237	−0.162	0.257	−0.205	0.082	−0.125	
se					0.393	0.578	0.770	0.903	0.635	0.953	0.664
Mean max. temp.°C							−0.041	0.007		−0.018	−0.031
se							0.205	0.250		0.269	0.218
Mean min. temp.°C							0.012	−0.148		−0.106	−0.025
se							0.118	0.211		0.242	0.154
Days below 20°C								−0.020		−0.018	−0.019
se								0.025		0.025	0.025
Days above 30°C								−0.040		−0.029	−0.037
se								0.056		0.057	0.056
Quarterly rainfall									0.001	0.001	0.001
se									0.001	0.001	0.001
Days of rain									−0.017	−0.019	−0.017
se									0.014	0.020	0.014
Akaike weights	1.7%	0.7%	1.2%	73.5%	1.7%	13.4%	1.9%	0.5%	5.2%	0.1%	

The use of the mass residual as a condition index was included in one model (G, Table 1) but its coefficient was not statistically significant (Table 2) and the Akaike weight for the model was only 1.2% and it is concluded that the condition index has a low explanatory power.

Habitat degradation was fitted as a quadratic function to model both the changes in the physical environment and water quality and both the coefficients of the linear and quadratic terms were statistically significant (Table 2). The models in which they were included (H-N, Table 1) accounted for 96.3% of the Akaike
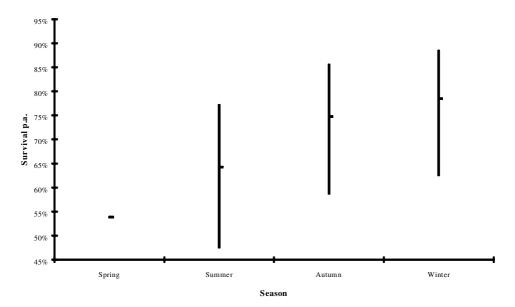
FIG. 2. Variation in survival (95% confidence limits) by season (i.e. quarter) after correcting for investigator effects (Model B, Table 1).

weights (Table 1). As hypothesized, the habitat degraded strongly through the 1970s and 1980s and then increased through the 1990s (Fig. 3).

The cost of breeding was statistically significant in the best model, i.e. H and overall (Tables 1 and 2) but showed considerable variation from model to model. The coefficient was considerably lower and not statistically significant in two models (L and N, Table 1), which were the only two models that included temperature data relating to the number of hot and cold days, thus indicating an interaction. The coefficient for cost of breeding was -1.143 (Table 2) and the weight vector for breeding across the four quarters was (0.833, 0.5, 0, 0), see methods. Thus, the decrease in the logit of survival will be the product of -1.143 and this vector, i.e. $(-0.9525, -0.5715, 0, 0)$ and this may be compared with the change in the logit for the four seasons of (0, 0.358, 0.799, 0.984) (Table 2). The 'shape' of these two vectors is fairly close, suggesting that cost of breeding is a plausible explanatory variable.

The coefficient for the cost of moult showed considerable variation, even changing sign! Only when cost of moult was entered on its own (model I, Table 1) was it statistically significant (Table 2). It is concluded that this is not a useful explanatory variable.

None of the weather variables was statistically significant (Table 2) and the models in which they were included only contributed 7.7% to the total Akaike weight (Table 1).

Lastly, all the models fitted the data well as adjudged by the X^2 statistic (Table 1) and it would seem as if the models are under-dispersed.

4 Discussion

The estimate of survival of 68.8% yr^{-1} for this African wagtail is much higher, by about 15%, than that for any other European wagtail species studied to date

(Baillie & McCulloch, 1993; Siriwardena *et al.*, 1998; S. Freeman in Piper, 2001). It has been known for some time that Longtailed Wagtails have the potential to live much longer (Piper, 1987) than either of the congeneric *M. cinerea* or *M. alba*, which have been ringed in much greater numbers, but have never had individuals that survived as long (Mead, 1985). Two territory holders in this study held their territories for 45 consecutive quarters (i.e. $11\frac{1}{4}$ years) and one survived for 12 years from the time first caught when it was in adult plumage. Longevities of 10 + years, as recorded in this study, are not exceptional for African passerines, longevities of 6 to 25.3 years have been recorded for nine species of robin (Oatley, 1998).

This species inhabits the sub-tropics of southern Africa where it has been shown that there is a broad trend for insectivorous passerines to be much longer-lived than species of the same genus in northern temperate climes (Peach *et al.*, 2001). A sample of African insectivores was shown to have a median survival rate of about 72% yr^{-1} compared with an average survival rate of 49.4% yr^{-1} for European species of similar phylogeny. It was shown that this difference was not due to differences in body mass or migratory tendencies (Peach *et al.*, 2001). Thus, this result conforms to the pattern currently being established in which it is hypothesized that insectivorous passerines in sub-tropical Africa have evolved different life history trade-offs with small clutch sizes and high survival rates. Providing estimates of high survival rates in sub-tropical and tropical passerines, especially in the southern hemisphere, is important for the ongoing debate on the evolution of life-history strategies, especially in unpredictable habitats (Johnson *et al.*, 1997).

The estimate of survival produced by this set of models is an underestimate for three reasons. First, some birds transferred to another territory before the end of a quarter—there is a tendency for them to do this if they are in a territory with a lower than average survival rate (Piper, 2001). An estimated 13 of the 100 losses recorded in this study were of birds that transferred to another territory but were actually recorded as losses. This increases the average annual survival rate from 68.8% to 72.4%. Second, some birds may have survived part-way into the next quarter but died before their territory was searched and so they would have been recorded as having been lost during the previous quarter. The effects of this bias have not been quantified. Third, birds were noted as being territory holders the first time they were seen on a territory but were only included in the survival analysis at the start of next full quarter—on average this under-enumerated an individual's life-span by half a quarter. Similarly, if an individual was last recorded at the end of the last full quarter in which it was alive, again this loses half a quarter on average. Given that birds hold territories for a mean of 10.3 quarters, this extra quarter represents a bias of about 2.4%, i.e. the annual survival rate could be as high as 71.2%. These three biases are all in the same direction and so the actual estimate of survival is conservative. Furthermore, there is no reason to suspect that these biases are heterogeneous with respect to time and space.

The best GLM (model H, Table 1) had an Akaike weight of 73.5% and included four explanatory variables: pre-1986 investigator effect, wing length, habitat degradation and cost of breeding. These variables are included in those models that make up nearly 95% of the Akaike weights and so they are discussed first.

The pre-1986 investigator effect measured the loss of information when assuming that mist netting was an adequate tool for monitoring survival—it clearly was not. After 1986, an intensive resighting programme was instituted with the result that almost every bird was resighted during every quarter, provided it was still alive and had not deserted its territory. The post-1986 investigator effect was positive,

although not statistically significant, suggesting that catching and handling birds had no impact on their survival. Notwithstanding, it is important nevertheless, to be mindful of the possible impact that trapping can have on survival (Houston, 1974; Calvo & Furness, 1992; Smith & Inglis, 1999).

Wing length was used as a surrogate for size and was included in the model as a linear, but definitely not as a quadratic, variable. The implication of this is that there was directional selection (Endler, 1986; Stearns, 1992) favouring the largest individuals that had a predicted survival rate almost twice as large as that of the smallest individuals, i.e. 87% versus 47%. Directional selection has been noted in the Barn Swallows *Hirundo rustica* in the northern USA (Brown & Brown, 1998). However, there is an alternative explanation. If there is sexual dimorphism, as yet undetected, and if the larger sex had higher survival, then this would also accord with these results without having to invoke directional selection.

The obvious degradation of the physical habitat (as measured by loss of riparian vegetation) and equally obvious improvement of water quality (as evidenced by increasing numbers of piscivores) is reflected in the long-term changes in survival as modelled by the quadratic habitat degradation variable. The shape of the fitted quadratic is correct, i.e. concave upwards and the minimum is at the appropriate time, i.e. early 1990s (Fig. 3).

There is a *prima facie* case for breeding having a real cost, in other words a trade-off between breeding and survival. In the two quarters in which breeding was concentrated, spring and summer, survival was lowest. In a meta-analysis of European populations of Blue Tit *Parus caeruleus* and Great Tit *P. major* there exists a significant inverse relationship between productivity (measured as fledglings
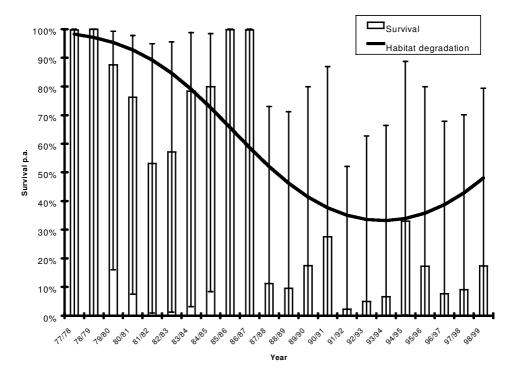

FIG. 3. Variation in survival (95% confidence limits) by study-year (i.e. quarter) after correcting for investigator effects (Model C, Table 1), bars and quadratic trend ascribable to habitat degradation curve.

per female per season) and adult annual survival (Dhondt, 2001). It is recom-
mended that this hypothesized trade-off be tested in this species by quantifying the
breeding activity of each individual in the spring and summer quarters of each year
and then correlating this with subsequent survival.

The proximate variables that play little or no part in the ten best models were
season, study year, territory and condition.

Season, or quarter, is a proximate variable that contains little biological informa-
tion. Its place was taken by two ultimate variables: cost of breeding and, to a lesser
extent, cost of moult. This was welcomed because these latter two variables are
biologically more meaningful.

The proximate variable study year was only included in models that contributed
less than 2.6% to the total Akaike weights (Table 1). Because it is a factor with 20
levels it is heavily penalized by the AIC even though it is more flexible in modelling
year-to-year variations than the quadratic function, i.e. habitat degradation, that
replaces it.

The variation in survival between territories was evident, but small (Model D,
Table 1), the coefficients are not shown.

On the one hand it is surprising that the condition was not an important
explanatory variable. It is intuitive that birds in better condition should have better
survival prospects. However, condition may only be important at some times of
the year, presumably when food is in short supply, but the condition index as used
here was averaged over all those occasions that a bird was captured.

The weather variables were included in models that together had Akaike weights
of less than 7.7% and thus were of little explanatory value.

There were no statistically significant differences in survival that could be
attributed to territory.

Not enough birds were trapped while moulting to estimate date of onset and
duration of moult. Many birds used in this analysis were never caught during the
autumn quarter when they moult. It is thus impossible to estimate directly the cost
of moult in this study. Furthermore, if an attempt is made to catch them too often
they become net-shy.

In this study, it would not have been possible to rely solely on capture-recapture
to amass enough observations with which to estimate survival because of the time
and effort needed to continually recapture so many birds. It takes the best part of
a morning to catch a territorial pair while a census walk of all the territories can
be undertaken in the same period of time. Thus, for this species, resightings yield
10-times as much data per unit effort.

The primary aim of this paper was to elucidate biologically important sources of
variation in survival in order to quantify them in the Longtailed Wagtail and this
has been achieved.

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