

## Changes in the breeding biology of the Welcome Swallow (*Hirundo tahitica*) in New Zealand since colonisation

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**Abstract.** The Welcome Swallow was first recorded breeding in New Zealand in 1958, but is now common and widespread. Using nest record cards collected throughout New Zealand between 1962 and 1996 we investigated whether measures of breeding success showed temporal trends consistent with the effects of density dependence due to increased population densities. Controlling for potentially confounding factors, we found that: (i) breeding has occurred earlier in more recent years, (ii) nests in more recent years were more likely to produce fledglings, and (iii) there are no temporal trends in clutch size or the probability of at least one offspring failing to fledge. These results suggest that population densities have not yet reached the threshold at which density dependence limits breeding success. Earlier laying in more recent years is compatible with a response to global warming. As predicted for multiple-brooded species, clutch size exhibited a mid-season peak, the timing of which is consistent with the decline in the second half of the season being due to reduced foraging time. There was no evidence for a latitudinal gradient in clutch size within New Zealand.

### Introduction

Welcome Swallows (*Hirundo tahitica*) were first recorded in New Zealand in the 1920s and were first recorded breeding in 1958 (Michie 1959). Since then, the population has increased so that the species is now widespread and common in open, lowland areas, but is still expanding into areas at higher altitude (Heather and Robertson 1996).

Breeding success in birds can be reduced at high densities due to competition for resources (Newton 1992). Such density-dependent effects are frequently observed (Sinclair 1989) and have been demonstrated experimentally (e.g. Kempenaers and Dhondt 1992; Both 1998). In an invading species with a rapidly expanding population, such as the Welcome Swallow in New Zealand, we might expect breeding success to decline over time if population density increases past the point at which competition for resources begins to affect breeding success. Indeed, previous studies have observed that the clutch size of Welcome Swallows is higher in New Zealand than in Australia, and have suggested that this is a consequence of lower population densities in New Zealand due to recent colonisation (Edgar 1966; Tarburton 1993). However, these clutch size differences could be due to variation in factors other than population density: the same pattern is predicted from the general trend for clutch size to increase with increasing latitude (Lack 1947; Tarburton 1993). Other approaches are required to test the hypothesis that variation in population density is affect-

ing breeding success in New Zealand's Welcome Swallow population.

Our aim in this study was to test for temporal trends in the breeding success of Welcome Swallows, over the last four decades, using data from nest-record cards collected throughout New Zealand. We predicted that an increase in population density since colonisation would cause a decline in mean clutch size, a lower probability that nests would produce a fledgling, a higher probability that some offspring would fail to fledge, and a delay in first-egg date over time, if densities increase past the point where birds are competing for limited resources. A delayed first-egg date is predicted because reduced food availability, per individual, at higher densities would result in birds achieving breeding condition later in the year. In testing for density dependence we assume that local population densities are positively correlated with total population size. This assumption is justified as Welcome Swallows rarely form colonies and these are always very small (a few pairs only); therefore, as total population density increases so should local population density (Tarburton 1993; Heather and Robertson 1996).

In testing for these temporal trends, we control for other potentially confounding effects. Multi-brooded species, such as the Welcome Swallow, are expected to breed earlier than is optimum for rearing chicks in order to have sufficient time to produce subsequent broods (Crick *et al.* 1993). In these circumstances, we predicted that clutch size should peak at

intermediate laying dates, corresponding to the optimal period for chick rearing. Following Lack (1947), we also tested whether clutch size is positively related to latitude within New Zealand.

## Methods

Data were obtained from the Ornithological Society of New Zealand's nest-record card scheme, which is described by Robertson (1986). All cards that recorded nest contents on two or more visits were used in this study ( $n = 525$ ). These spanned the period 1962–96; 109 cards were available for 1962–70, 183 for 1971–80, 202 for 1981–90 and 30 for 1991–96. Response or explanatory variables could not be calculated from some of the cards, so sample sizes varied between analyses.

Nests were coded as being successful if at least one chick fledged and as failing if at least one offspring, either an egg or chick, failed to produce a fledgling (we term such failure partial/total failure). Using these definitions, a single nesting attempt could experience both success and partial/total failure. It was sometimes possible to determine that a nest experienced partial/total failure, but not that it succeeded, i.e. any remaining offspring fledged. Therefore, to maximise our use of the data, success and partial/total failure were analysed using separate models. Consequently, although the variables explaining success and partial/total failure should be similar, they may not be identical.

Clutch size and first-egg dates were estimated using programs adapted from the British Trust for Ornithology's nest-record card scheme, which is described by Crick and Baillie (1996). Calculations assumed that nests were active on the date of each visit, unless evidence suggested otherwise, and that (i) eggs were laid daily, with a maximum delay of three days during laying, (ii) incubation lasted between 13 and 19 days, and (iii) the maximum hatching interval was three days. These parameter values were obtained from Disney (1988), Turner (1989), Tarburton (1993) and Heather and Robertson (1996). Laying date was calculated relative to the date of the winter solstice, which was set as Day 0, and controlled for the slight inter-annual variation in this date. First-egg dates were calculated as the mean of the minimum and maximum possible first-egg dates, but were used only if minimum and maximum dates differed by ten days or less. This ensured that first-egg dates were accurate to within five days.

### Statistical analyses

Data were analysed using multivariate regression modelling in SAS (Ver. 8). The 525 nests were not evenly spread across the country, but were clustered into 96 sites. Variables recorded from nests at the same site are likely to be correlated because these nests will share features in common, including similar habitat and climate. Clustering by site, leading to correlated responses in groups of nests, is likely to violate a core assumption of standard statistical models: that the error terms are independent. This will lead to standard error estimates that are smaller than the true values, resulting in overestimates of the significance of explanatory variables included in the model (i.e. a greater frequency of Type I errors).

We used two approaches to overcome the problem of non-independence due to the clustering of nests by site. First, when the response variable was normally distributed (as it was for clutch size and first-egg date) we fitted a linear mixed model, with site included as a random effect (Littell *et al.* 1996). This model assumed a common correlation between nests at the same site and zero correlation, or independence, between nests at different sites. Second, when the response variable was binary (as it was for nest success and partial/total failure) we fitted a Generalised Estimating Equations model (GEE), specifying a logit link function and binomial error distribution, with site included as a clustering variable. A GEE model is an extension of a Generalised Linear Model that allows for clustered observations

(Diggle *et al.* 1998), in this case by assuming a common correlation between nests in the same cluster and zero correlation between nests in different clusters (Alison 1999). Controlling for the clustering of data by site also controlled for any potential biases created by differences in observers' nest-recording behaviour (for example, the months in which data were collected), because only one observer contributed data for each site.

For clutch size, we included year, latitude, longitude, altitude, first-egg date and nest height as continuous explanatory variables, together with their squared terms so that simple non-linear relationships were modelled. We used the same variables to model first-egg date, except that clutch size replaced first-egg date as an explanatory variable. Full models, which contained all the explanatory variables, were constructed and the least significant variable was then deleted from the model. This process was repeated until a Minimum Adequate Model (MAM) was created in which all the explanatory variables retained in the model had a significant effect ( $P < 0.05$ ), as assessed by  $F$  ratios. In other words, model simplification was carried out using backward selection. The significance of site, as a clustering variable, was assessed by comparing the change in deviance of MAMs with and without site included as a random effect. This change in deviance was compared with the  $\chi^2$  distribution with one degree of freedom.

For nest success and partial/total failure, year, latitude, longitude, altitude, first-egg date, clutch size and nest height were included as continuous explanatory variables in GEE models, together with their squared terms. Model simplification was carried out using backward selection, with significance assessed using the Type III  $\chi^2$  values reported in the GEE output. All mean values are reported  $\pm$  one standard error.

## Results

Model results are presented in Table 1.

### Clutch size

Three nests had unusually large clutch sizes (one each of eight, nine and ten eggs). Following Heather and Robertson (1996), we assumed that these were laid by more than one female and these data were not used in subsequent analyses. The mean clutch size was  $4.04 \pm 0.05$  ( $n = 293$ ); both the median and modal clutch sizes were 4.

First-egg date had a significant effect on clutch size, which peaked at intermediate laying dates and varied by up to one egg during the season (Fig. 1). No other variables were retained in the MAM, which used data from 110 nesting attempts. In univariate models, there was a trend towards smaller clutch sizes in earlier years ( $P = 0.09$ ,  $n = 293$ ), with predicted clutch sizes falling by 0.4 of an egg between 1962 and 1996.

### First-egg date

The mean first-egg date was 123, which corresponds to 23 November when the winter solstice occurs on 22 June, as it does in most years. First-egg dates became significantly earlier with time, with predicted values advancing by 30 days between 1962 and 1995 (Fig. 2). Predicted first-egg dates were 52 days earlier in the easternmost localities ( $177.8^\circ\text{E}$ ) than in the westernmost localities ( $169.9^\circ\text{E}$ ). Although latitude and longitude covaried in our data set the significant

**Table 1. Minimum Adequate Models of breeding success of Welcome Swallows**

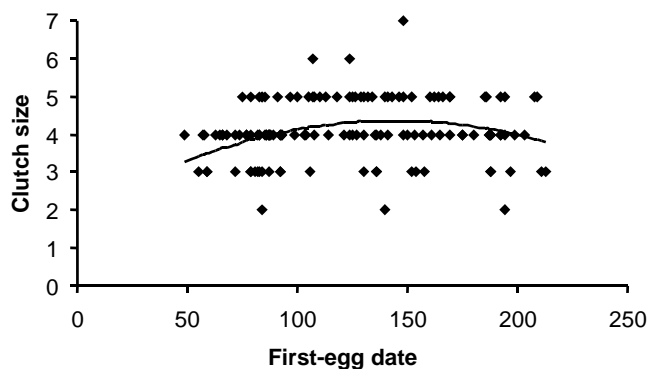
For details of the modelling process, see the Methods section.  $r^2$  values and the significance of random factors are not available for models fit using Generalised Estimating Equations. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; n.a., not applicable

Response variable	Fixed explanatory variables	Test statistics	Correlation coefficients	Model $r^2$	Random factors
Clutch size	First-egg date	$F_{1,46} = 10.08$ **	+0.035	0.58	Site $\chi^2 = 4.3$ *
	First-egg date <sup>2</sup>	$F_{1,46} = 8.64$ **	-0.00001		
First-egg date	Year	$F_{1,83} = 5.17$ *	Intercept = +1.866 -0.931	0.12	Site $\chi^2 = 3.8$ *
	Longitude	$F_{1,83} = 7.99$ **	-5.890		
	Altitude	$F_{1,83} = 7.71$ **	-0.389		
	Altitude <sup>2</sup>	$F_{1,83} = 6.28$ *	+0.001		
			Intercept = +2998.40		
Partial/total failure	Clutch size	$\chi^2 = 8.94$ **	-4.630	n.a.	n.a.
	Clutch size <sup>2</sup>	$\chi^2 = 8.55$ **	+0.562		
	Altitude	$\chi^2 = 4.10$ *	+0.010		
	Nest height	$\chi^2 = 4.95$ *	-0.579		
Nest success	Clutch size	$\chi^2 = 7.76$ **	Intercept = +10.389 +0.896	n.a.	n.a.
	Year	$\chi^2 = 5.48$ *	+0.077		
	Altitude	$\chi^2 = 4.29$ *	+0.067		
	Altitude <sup>2</sup>	$\chi^2 = 4.98$ *	-0.0006		
			Intercept = -155.694		

effect of longitude was not a consequence of its covariation with latitude, in these data, because latitude could not replace longitude from the model. First-egg dates were significantly influenced by altitude; they were predicted to decrease by 30 days between sea-level and intermediate altitudes (160 m), and then to increase by 70 days at the highest altitude (400 m). No other variables were retained in the MAM, which used data from 182 nesting attempts.

*Partial/total failure*

Clutch size had a significant and quadratic effect on the probability of partial/total failure. The lowest partial/total failure probabilities occurred at intermediate clutch sizes of 4.1 (Fig. 3). Altitude had a significant and positive effect on the

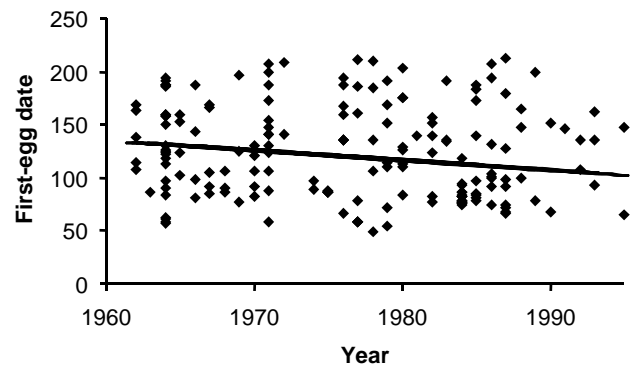


**Fig. 1.** Relationship between clutch size and laying date, i.e. first-egg date. Diamonds represent the original data; the black line represents predicted values from the Minimum Adequate Model. First-egg date equals zero on the date of the winter solstice.

probability of partial/total failure: predicted probability of partial/total failure increased from 0.5 at 2 m to 0.9 at the highest altitude for which data were available (150 m). The predicted probability of partial/total failure declined with increasing nest height, and decreased from 0.8, for nests at almost ground level, to nearly zero for nests at 13.5 m, the highest observed height. No other variables were retained in the MAM, which used data from 142 nesting attempts.

*Nest success*

The probability of nest success increased significantly over time; predicted probabilities changed from 0.6 for nests in 1962 to 0.95 for nests in 1995. Clutch size also had a positive



**Fig. 2.** Relationship between year and laying date, i.e. first-egg date. Diamonds represent the original data. The black line represents the values predicted from the Minimum Adequate Model, over the observed range of years, while holding other continuous variables at their mean value. First-egg date equals zero on the date of the winter solstice.

effect on success probability, with predicted probabilities increasing from 0.22, for single-egg clutches, to 0.98 for clutches of seven. Altitude had a significant and quadratic effect on the probability of success: predicted probabilities increased from 0.5 at sea level to 0.8 at intermediate altitude (75 m) and then declined to 0.02 at the highest altitudes for which data were available (150 m). No other variables were retained in the MAM, which used data from 136 nesting attempts.

## Discussion

### *Temporal changes in breeding success*

Our results do not show a temporal decline in breeding success of Welcome Swallows over the four decades since they colonised New Zealand. Such a decline would be predicted in an invading population if its density had increased past the point at which individuals were competing for limited resources. Instead, we found no significant temporal trend in clutch size or the probability of at least one offspring failing to fledge, although if density dependence occurred in only the most recent years of our data set we may not be able to detect its effects. In more recent years Welcome Swallows have bred earlier in New Zealand and have a higher probability of nest success (producing at least one fledgling). These temporal trends are opposite to those predicted for an invading population subject to density-dependent competition as density increases with time. The simplest explanation for these results is that population densities for Welcome Swallows in New Zealand are still below the threshold at which density dependence in breeding success is exhibited.

Our finding that Welcome Swallows are breeding earlier in New Zealand in recent years is intriguing. Similar trends toward earlier laying in bird populations in the United Kingdom and North America have been attributed to global warming (Crick *et al.* 1997; Crick and Sparks 1999; Dunn and Winkler 1999). In New Zealand, the most rapid warming

over the last 150 years has occurred since ~1950 (Salinger *et al.* 1993), coinciding with the period of colonisation by the Welcome Swallow. While the amount of variation explained by the model is fairly small, the possibility that global warming has affected the breeding biology of birds in Australasia warrants further research.

### *Optimum clutch size*

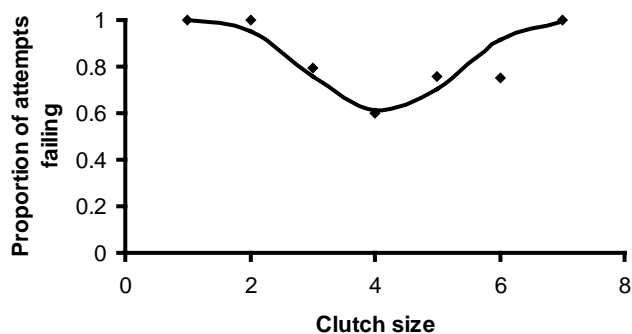
Partial/total failure rates were predicted to be lowest in clutches of 4.12 eggs. The close similarity between this value and the mean clutch size (4.04) suggests that Welcome Swallows may optimise their clutch size to maximise the probability of all their eggs producing fledglings.

### *Seasonal trend in clutch size*

Seasonal changes in clutch size follow the pattern predicted for multi-brooded species: an initial increase followed by a decline (Klomp 1970; Crick *et al.* 1993). Such a pattern is expected to arise as seasonal reproductive success is determined by the number of broods that parents can raise during the breeding season, not simply by the success of a single brood. Therefore, individuals in multi-brooded species should be selected to start breeding before the date when their optimal clutch size is greatest, while single-brooded species should await this date before laying. Other multi-brooded hirundines, such as the Barn Swallow (*Hirundo rustica*), exhibit a linear seasonal decline in clutch size. This pattern may arise because the constraint of long-distance migration prevents these species from initiating breeding at the optimum date for rearing more than one brood (Crick *et al.* 1993; Banbura and Zielinski 1998). The presence of a unimodal relationship between clutch size and laying date in a non-migratory hirundine is compatible with the theory that migratory status influences the laying date–clutch size relationship in multi-brooded species.

Late seasonal declines in clutch size may occur for two non-mutually exclusive reasons. The timing hypothesis argues that environmental conditions deteriorate during the season, resulting in a causal link between the timing of breeding and reproductive success (e.g. Verhulst *et al.* 1995; Nilsson 2000). The quality hypothesis proposes that the correlation between the timing of reproduction and breeding success occurs due to variation in individual quality, as lower-quality birds breed later and produce fewer eggs (e.g. Hansson *et al.* 2000; Christians *et al.* 2001).

The parameter estimates obtained from our model predict that clutch sizes would peak in nests initiated on 11 November. Chicks will fledge from these nests during the summer solstice, when the time available for foraging is at a maximum. Clutch size thus peaks at the point in the season when subsequent conditions for rearing chicks may be particularly favourable. From this perspective our data are consistent with the timing hypothesis for seasonal declines in clutch size, concurring with other studies of seasonal declines in



**Fig. 3.** Relationship between clutch size and the probability of partial/total failure, i.e. at least one offspring not fledging. Diamonds represent probabilities calculated from the original data. The black line represents the values predicted by the Minimum Adequate Model, over the observed range of clutch sizes, while holding other continuous variables at their mean value.

clutch size in hirundines (e.g. Winkler and Allen 1996). Variation in individual quality may, however, also influence the relationship.

#### *Latitudinal trend in clutch size*

There was no evidence that clutch size was related to latitude within New Zealand. An evolutionary time-lag, due to insufficient time since colonisation for clutch size to have adjusted to local environmental conditions, could explain the lack of an effect. This is unlikely, however, as the heritability of clutch size is generally low in birds, including other hirundines (Banbura and Zielinski 2000; Christians 2002). Although an Australian study also failed to find an effect of latitude on clutch size in Welcome Swallows (Marchant and Fullagar 1983), the larger clutch sizes in New Zealand than in Australia (Tarburton 1993) are consistent with the predicted latitudinal trend. Much stronger effects of latitude on hirundine clutch sizes have been found in the Northern Hemisphere, although these studies cover a wider latitudinal range (e.g. Møller 1984; Dunn *et al.* 2000). One possibility is that latitudinal trends in clutch size are weaker in the Southern than in the Northern Hemisphere (Moreau 1944; Yom-Tov 1987, 1994; but see Cardillo 2002).

#### *Nest height*

The probability of partial/total failure decreased with increasing nest height. This may be a consequence of higher nests being more inaccessible to the mammalian nest predators, such as the Brown Rat (*Rattus norvegicus*), Black Rat (*R. rattus*), Domestic Cat (*Felis catus*) and the mustelids *Mustela erminea*, *M. furo*, and *M. nivalis*, that have been introduced to the islands since human colonisation (Holdaway 1999).

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