

## Changes in egg size of exotic passerines introduced to New Zealand

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**Abstract** Bird species introduced to New Zealand from high northern latitudes are expected to change their breeding behaviour to conform to well-known geographic gradients in avian reproductive parameters. Here, we demonstrate reductions in average egg size and clutch volume for eight species of exotic passerine originating in the UK, and show that the magnitudes of these reductions appear to trade-off against reductions in annual variation in clutch size. Possible reasons for the trade-off are discussed.

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### INTRODUCTION

The global distributions of 13 European passerine species have been extended through their successful introduction into New Zealand (Duncan *et al.* 2005). In a number of cases these birds have been so successful that they have spread to become more widely distributed than native New Zealand species (Cassey 2001). New Zealand potentially represents a different selective environment for these species. In particular, it is well-known that the clutch sizes tend to be smaller in the southern hemisphere and fledging periods longer than at equivalent northern latitudes (Lack 1948), implying that species are responding to different selection pressures (qualitative or quantitative) on breeding in the different hemispheres (e.g. Chown *et al.* 2004). Thus, as exotic species have colonised New Zealand from Europe we might expect their breeding biology to have diverged from that of their native ancestors.

Recently, Evans *et al.* (2005) used data from the Ornithological Society of New Zealand (OSNZ) and British Trust for Ornithology (BTO) nest record schemes to test for such changes in 11 species of

passerine introduced to New Zealand (NZ) from the United Kingdom (UK). They showed that nine of these species had significantly smaller clutches in NZ than in UK, as expected from differences between hemispheres in clutch size (see also Niethammer 1970). Further, these species showed less seasonal variation in clutch size in NZ relative to UK. Both of these changes concur with predictions of Ashmole's hypothesis (Ashmole 1963) viz. that increased seasonality at high northern latitudes produces greater resource abundance per adult bird in the breeding season, resulting in larger clutch sizes but also more seasonal variation in clutch size. If Ashmole's hypothesis was the only explanation, however, clutch size change should also have been correlated with the change in seasonal clutch size variation, but these variables were uncorrelated (Evans *et al.* 2005).

The number of eggs laid is only one way by which birds can modify their investment in a clutch. They can also change egg size. Egg size data for exotic passerines in New Zealand were not available to Evans *et al.* (2005), but have subsequently become so for eight species through extensive fieldwork on the North Island (Cassey *et al.* 2005). Here, we combine these data with measures of egg size from UK, and with the data from Evans *et al.* (2005), to substantially extend their results by considering

**Table 1** Average fresh egg size measurements for eight exotic passerine species introduced to New Zealand and their proportional change in average egg volume (Volume) measured as  $(\text{Volume}_{\text{NZ}} - \text{Volume}_{\text{UK}}) / \text{Volume}_{\text{NZ}}$ .

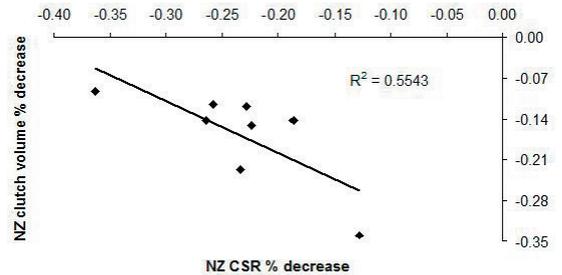
Common name	Species name	New Zealand length x breadth (mm)	Cramp <i>et al.</i> (1977-1994) length x breadth (mm)	$\Delta\text{Volume}$
song thrush	<i>Turdus philomelos</i>	27.6 x 20.5	27.5 x 20.8	-0.03
blackbird	<i>Turdus merula</i>	29.0 x 21.2	29.3 x 21.4	-0.03
starling	<i>Sturnus vulgaris</i>	29.1 x 20.9	29.7 x 21.2	-0.05
sparrow	<i>Passer domesticus</i>	22.0 x 15.8	22.2 x 15.7	-0.01
chaffinch	<i>Fringilla coelebs</i>	18.6 x 14.1	19.9 x 14.7	-0.16
goldfinch	<i>Carduelis carduelis</i>	16.6 x 12.5	17.0 x 12.8	-0.08
greenfinch	<i>Carduelis chloris</i>	19.8 x 14.1	20.6 x 14.8	-0.14
yellowhammer	<i>Emberiza citrinella</i>	21.3 x 15.7	21.7 x 16.4	-0.11

changes in clutch volume. We explicitly test the relationship between seasonal variation in clutch size and clutch volume. If Ashmole's hypothesis is correct then we expect reduced seasonality in clutch size in NZ to correlate with decreasing clutch volume.

## METHODS

Cassey *et al.* (2005) measured 350 eggs from 148 naturally occurring clutches during the breeding season of 2003-2004 for eight exotic passerine species: song thrush (*Turdus philomelos*;  $n$  [number of clutches] = 38), blackbird (*T. merula*;  $n = 32$ ), starling (*Sturnus vulgaris*;  $n = 29$ ), greenfinch (*Carduelis chloris*;  $n = 9$ ), goldfinch (*C. carduelis*;  $n = 11$ ), chaffinch (*Fringilla coelebs*;  $n = 11$ ), yellowhammer (*Emberiza citrinella*;  $n = 3$ ), and house sparrow (*Passer domesticus*;  $n = 15$ ). Eggs were measured using Vernier callipers and precision electronic scales, and their breadth, length, and mass recorded. Average egg sizes (breadth and length) for these same species in their UK ranges were estimated from references in *Handbook of the birds of Europe, the Middle East and North Africa Vols 1-9* (Cramp *et al.* 1977-1994). We first compared egg sizes to test for differences between NZ and UK. Clearly, if egg sizes have not changed, patterns for changes in clutch volume will not differ from those in clutch size shown by Evans *et al.* (2005).

Evans *et al.* (2005) obtained clutch size data for each of the eight species from national nest record card schemes organised by the BTO (Crick *et al.* 2003), and OSNZ (Robertson 1986). The UK data spanned the years 1923-2000 and comprised 39,595 nest records, and the NZ data covered the period 1925-2002 and comprised 3,350 nest records. In both data sets the vast majority of data were from the most recent decades. Founder populations of the eight species were mainly introduced from UK between 1862 and 1885 (Thomson 1922), and so the



**Figure 1** The significant negative relationship between proportional change in clutch size ratio (CSR) in New Zealand and proportional change in clutch volume (CV); slope =  $-0.89 \pm 0.32$ ,  $R^2 = 0.55$  ( $\alpha = 0.05$ ).

New Zealand nest record data mainly related to breeding attempts after the species had had several dozens of generations to respond to selection pressures in their new environment.

Following Hoyt (1979), egg volume ( $\text{cm}^3$ ) was calculated as  $0.00051 \times \text{length} \times \text{breadth}^2$  and clutch volume (CV) was the product of average egg volume and average clutch size.

Evans *et al.* (2005) predicted that, if Ashmole's hypothesis is correct, smaller average clutch sizes in the southern hemisphere will be associated with less seasonal conditions, reflected in longer breeding seasons and less relative variation in clutch size throughout that season. Within-season variation in clutch size is assumed to reflect variation in resources available to the birds. We quantified temporal variation in clutch size as the ratio of the maximum and minimum clutch sizes observed during the season (CSR). The proportional changes in CV and CSR between UK and NZ were then expressed as  $(\text{CV}_{\text{NZ}} - \text{CV}_{\text{UK}}) / \text{CV}_{\text{NZ}}$  and  $(\text{CSR}_{\text{NZ}} - \text{CSR}_{\text{UK}}) / \text{CSR}_{\text{NZ}}$ . Proportional changes were arcsine transformed for subsequent analysis. Linear regressions across species were conducted using the program R (Ihaka

& Gentleman 1996). We also performed the analysis controlling for phylogenetic non-independence using the method of phylogenetic generalised least squares (PGLS) (Grafen 1989; Martins & Hansen 1997; Garland & Ives 2000; Freckleton *et al.* 2002) and the phylogenetic hypothesis for the relatedness among these species as specified in Cassey *et al.* (2005). However, this method revealed no phylogenetic correlation in these data, and hence we report only the analyses across species.

## RESULTS

Average egg volume was lower in NZ than in UK for all eight passerines (Table 1), and the decrease was significant across the sample (Paired 2-sample  $t = -3.82$ ,  $n = 8$ ,  $P < 0.01$ ). Across species, the decrease in average egg volume was not associated with the previously observed change in average clutch size between regions (slope =  $-0.06$ ,  $se = 0.51$ ,  $n = 8$ ,  $R^2 < 0.01$ ,  $P = 0.91$ ), and neither was it associated with the change in CSR between regions (slope =  $-0.54$ ,  $se = 0.27$ ,  $n = 8$ ,  $R^2 = 0.40$ ,  $P = 0.09$ ). However, there was a significant negative relationship between proportional change in CV and CSR following introduction to New Zealand (Figure 1).

## DISCUSSION

The processes by which populations diverge constitute important and dynamic parts of the ecological past of all species, yet, they can be extremely difficult to study based solely on observations from extant distributions. A wide range of biotic and/or abiotic factors may drive differences between populations, but inferences about the causes of such differences can also be confounded if, as is usually the case, the precise historical relationships between populations are unclear. Exotic species thus represent a useful natural experiment in that the history of the exotic population is often well-known, allowing comparisons between populations that are unambiguously related. Differences between the taxa can thus be assigned to the period following translocation, even if the causes of those differences may still be difficult to pin down.

Niethammer (1970) was the first to show differences in breeding parameters for passerine bird species translocated from UK to NZ, finding reduced clutch sizes in six species (blackbird, song thrush, starling, chaffinch, goldfinch, house sparrow). MacMillan (1985) showed that the same was true for greenfinch. Evans *et al.* (2005) were able to confirm these differences and show additional reductions in clutch size for skylark (*Alauda arvensis*) and dunnoek (*Prunella modularis*). As far as we are aware, this is the first study to demonstrate declines in egg volume in NZ for the seven species for which Niethammer (1970) and MacMillan

(1985) demonstrated clutch size reductions, plus the yellowhammer. The changes in both clutch size and egg volume imply reduced investment in average clutches in NZ relative to UK. Whether this also translates into an overall decline in reproductive effort over the course of a year, or over the lifetime of an individual bird, awaits better data on changes in both number of broods per year and longevity.

The changes in clutch size, combined with changes in the annual variation in clutch size, are consistent with Ashmole's hypothesis: declines in clutch size are correlated with an overall shift from more to less seasonal conditions (Evans *et al.* 2005). However, a substantial shortcoming with Ashmole's hypothesis as an explanation for these changes is that it predicts that species showing the greatest declines in clutch size should also be those experiencing the greatest shift in seasonality, and hence those species with the largest changes in CSR. Yet, Evans *et al.* (2005) were unable to demonstrate a positive correlation between clutch size decrease and change in CSR for these passerines. When egg size is added to the equation, and change in clutch size is replaced by change in CV, a significant *negative* correlation with CSR results. Rather than the largest changes in clutch size variation leading to the largest changes in CV, these changes trade off. This suggests that selection for reduction in the investment a bird places in each clutch in NZ may be achieved in one of two ways: a species either reduces the annual variation in clutch size in NZ, or it reduces its CV, but not both together.

There are two possible reasons for this trade-off. First, species are limited by the magnitude of either of these traits in their UK habitats. For example, species with relatively low CSR in UK may not be able to lower CSR much further in NZ. Similar arguments may also apply to CV. If either was the case, however, we would expect a correlation between CSR (or CV) in UK and the proportional change in that trait following introduction to NZ. In fact, the proportional change in CSR following introduction to NZ was unrelated to CSR in UK ( $r = -0.04$ ,  $n = 8$ ,  $P = 0.91$ ), and similarly there was no relationship between proportional change in CV following introduction to NZ and CV in the UK ( $r = 0.43$ ,  $n = 8$ ,  $P = 0.29$ ).

Second, phenotypic plasticity may influence the ability of species to change their breeding parameters. It has been shown that egg size is probably a less plastic trait than clutch size (Arroyo *et al.* 1998). However, the fact that species have changed their egg size following introduction to NZ suggests some advantage to the change if it is indeed possible. Perhaps, only the most phenotypically plastic species can respond to different reproductive selection pressures in NZ by decreasing their CVs rather than their annual variation in clutch size. We

tested this idea by comparing change in CV with the geographical range size of the species across Europe, on the assumption that species with the widest distributions have the greatest potential for phenotypic plasticity (West-Eberhard 2003). Those species that had reduced their CVs the most were indeed those with the largest European ranges ( $\log_{10}$  geographical ranges:  $r = -0.72$ ,  $n = 8$ ,  $P < 0.05$ ; range data kindly supplied by R.D. Gregory). This last result is based on the unsupported assumption that the ability to vary CV has greater reproductive benefits than other changes to breeding behaviour.

Although other hypotheses for the trade-off between reductions in CV and CSR may be suggested, the existence of this trade-off clearly has important implications for understanding specific changes in breeding biology in different environments. Further study is now required to test whether the ability to vary CV has the greatest reproductive benefits, whether these traits do indeed vary in their plasticity, and the generality of the observed trade-off across other populations and species.

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#### LITERATURE CITED

- Arroyo, B.; Leroux, A.; Bretagnolle, V. 1998. Patterns of egg and clutch variation in the Montagu's Harrier. *Journal of Raptor Research* 32: 136-142.
- Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b: 458-473.
- Cassey, P. 2001. Determining variation in the success of New Zealand land birds. *Global Ecology & Biogeography* 10: 161-172.
- Cassey, P.; Ewen, J.G.; Boulton, R.L.; Blackburn, T.M.; Möller, A.P.; Biard, C.; Olson, V.; Karadas, F. 2005. Egg carotenoids in passerine birds introduced to New Zealand: relations to ecological factors, integument coloration and phylogeny. *Functional Ecology* in press.
- Chown, S.L.; Sinclair, B.J.; Leinas, H.P.; Gaston, K.J. 2004. Hemispheric asymmetries in biodiversity – A serious matter for ecology. *PLoS Biology* 2: 1701-1707.
- Cramp, S.; Simmons, K.E.L.; Perrins, C.M. 1977-1994. *Handbook of the birds of Europe, the Middle East and North Africa Vols 1-9*. Oxford University Press, Oxford.
- Crick, H.Q.P.; Baillie, S.R.; Leech, D.I. 2003. The UK nest record scheme: its value for science and conservation. *Bird Study* 50: 254-270.
- Duncan, R.P.; Blackburn, T.M.; Cassey, P. 2005. Factors affecting the release, establishment and spread of introduced birds in New Zealand. In Allen, R.B.; Lee, W.G. (eds.). *Biological invasions in New Zealand*. Springer-Verlag, Berlin.
- Evans, K.L.; Duncan, R.P.; Blackburn, T.M.; Crick, H.Q.P. 2005. Investigating geographic variation in clutch size using a natural experiment. *Functional Ecology* 19: 616-624.
- Freckleton, R.P.; Harvey, P.H.; Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of the evidence. *American Naturalist* 160: 712-726.
- Garland, T.; Ives, A.R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist* 155: 346-364.
- Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society, London, B* 326: 119-157.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96: 73-77.
- Ihaka, R.; Gentleman, R. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5: 299-314.
- Lack, D. 1948. The significance of clutch-size. Part III.—Some interspecific comparisons. *Ibis* 90: 25-45.
- Martins, E. P.; T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* 149: 646-667.
- MacMillan, B.W.H. 1985. Breeding of greenfinches in Hawke's Bay, New Zealand. *Notornis* 32: 85-93.
- Niethammer, G. 1970. Clutch sizes of introduced European passeriformes in New Zealand. *Notornis* 17: 214-222.
- Robertson, H.A. 1986. OSNZ nest record scheme instructions. *Notornis* 33: 53-57.
- Thomson, G.M. 1922. *The naturalisation of plants and animals in New Zealand*. Cambridge University Press, Cambridge.
- West-Eberhard, M.J. 2003. *Developmental plasticity and evolution*. Oxford University Press, Oxford.