Effect of population bottlenecks on the egg morphology of introduced birds in New Zealand

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Hatching failure is inversely correlated with population bottleneck size among exotic birds introduced to New Zealand, but the mechanism for this is unclear. We assess whether the bottlenecks these species experienced during their introduction have affected hatching failure through deleterious changes in egg morphology. We measured egg size and shape of 13 species that passed through bottlenecks of 11–800 individuals during their establishment in the 19th century. Eggs were also measured in the source populations ('pre-bottleneck') of each species to compare pre- and post-bottleneck egg morphology directly. Significant changes in egg volume were found in six of 13 species, with most laying smaller eggs in New Zealand. Egg shape changed in four of 13 species but there was no directional bias; two species developed more elongated eggs and two species broader eggs. There was no relationship between bottleneck size and change in egg volume, but species passing through severe bottlenecks had greater variability in egg volume and were more likely to have eggs that deviated in shape from their source populations. There was no relationship between changes in either egg volume or shape and rates of hatching failure. Further work is needed to assess whether changes in egg morphology have negative consequences on offspring fitness and whether the observed changes are the result of differing environmental conditions in the introduced range.

Keywords: egg shape, egg volume, hatching failure, introduced species, island birds.

Generally, around 10% of eggs that are not destroyed or predated during the incubation period fail to hatch (Koenig 1982). However, hatching failure in some endangered birds can exceed 50% and may limit population recovery (e.g. Jamieson & Ryan 2000, Briskie & Mackintosh 2004). The causes of hatching failure have only been studied in a few species, but can include environmental effects such as calcium deficiency (Patten 2007) or contamination by pollutants such as DDT, which may increase hatching failure through a reduction in shell thickness (Newton & Bogan 1974, Elliott *et al.* 1988). Increased hatching failure may also result from changes in the environment. Endangered species may be particularly at risk from this, as conservation strategies commonly involve translocations of a small number of individuals from one environment to another. For example, Jamieson and Ryan (2000) suggested that increased rates of hatching failure in the endangered Takahe *Porphyrio hochstetteri* were exacerbated by environmental differences between their native alpine range and the sea-level island habitats to which they were moved for conservation purposes.

As many endangered species have been reduced to small and fragmented populations, increased hatching failure could also result from genetic changes induced by population bottlenecks. Population bottlenecks are defined as abrupt and temporary reductions in population size. Depending on the size and duration of the bottleneck, populations may experience loss of genetic variation and increased inbreeding in the recovery stages, which decreases individual heterozygosity and can reduce fitness through increased expression of deleterious recessive alleles (Frankham *et al.* 2002, Keller & Waller 2002, Spielman *et al.* 2004). Known as

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inbreeding depression, this can take the form of increased hatching failure (Wildt *et al.* 1987, Kempenaers *et al.* 1996, Hale & Briskie 2007). Briskie and Mackintosh (2004) found increased hatching failure in both native and introduced species of birds in New Zealand that had experienced severe bottlenecks.

A population bottleneck that leads to genetic changes in the post-bottleneck population could increase hatching failure in a number of ways. First, population bottlenecks could increase infertility through the production of abnormal sperm or problems with fertilization (Roldan *et al.* 1998). Even when fertilized, an egg may still fail to hatch if genetic changes increase rates of embryo mortality through increased susceptibility to disease or increased expression of deleterious alleles during embryonic development (Sittmann *et al.* 1966). Secondly, genetic changes associated with severe bottlenecks might also increase hatching failure through problems with egg production that lead to abnormally sized and shaped eggs. For example, small eggs are less likely to hatch (Amundsen *et al.* 1996, Serrano *et al.* 2005) and changes in egg shape might reduce hatching success if this constrains embryonic development, alters the efficiency of gas exchange or heat transfer (Gosler *et al.* 2005), or affects the strength of the shell (Picman 1989, Smart 1991). Abnormally shaped eggs in domestic chickens show reduced hatchability (Narushin & Romanov 2002), suggesting that selection may favour not only an optimally sized egg but also an optimally shaped egg.

We examined the effects of bottleneck size on egg morphology and hatching failure in introduced birds in New Zealand. Introduced species provide a good model for assessing the effects of bottlenecks on fitness traits such as egg morphology for several reasons. Acclimatization societies kept comprehensive records of the number of individuals released (Thomson 1922, Long 1981), thus providing an index of bottleneck size. Subsequent genetic analyses confirm that those species passing through the most severe bottlenecks have lost the most genetic variation (Merilä *et al.* 1996). Unlike endangered native birds, introduced bird species also provide the opportunity to compare traits before and after the bottleneck, as introduced species still have extant source populations that can act as pre-bottleneck 'controls'. In contrast, often the only populations available to study in endangered native birds have already experienced a bottleneck. By measuring the size and shape of eggs from both the source and naturalized populations of each species, we assessed whether changes in egg morphology correlated with either bottleneck size or hatching failure rates. Although it is likely that some changes in egg morphology may be due to environmental effects, such as differences in climate or food resources between the native and introduced ranges, differences in bottleneck size should also result in differences in egg morphology if passing through a severe bottleneck increases inbreeding and the frequency of abnormal eggs.

METHODS

Data on the egg morphology of 13 introduced passerine species were collected from both the source populations (primarily the UK) and the introduced range of New Zealand. We used only species for which numbers of birds released were known; thus bottleneck sizes ranged from 11 to 800 individuals (see Table 1). A combination of museum egg collections and field-observed clutches was used to gather data on the following species: Blackbird *Turdus merula*, Song Thrush *Turdus philomelos*, Dunnock *Prunella modularis*, Yellowhammer *Emberiza citrinella*, Cirl Bunting *Emberiza cirlus*, Goldfinch *Carduelis carduelis*, Redpoll *Carduelis flammea*, Greenfinch *Carduelis chloris*, Chaffinch *Fringilla coelebs*, Starling *Sturnus vulgaris*, Common Myna *Acridotheres tristis*, Skylark *Alauda arvensis* and House Sparrow *Passer domesticus*.

To estimate egg size and shape in the source population we measured 21–30 clutches per species (total 358 clutches) from egg collections housed in the British Museum, Tring. For 12 of the 13 species we examined, birds were introduced from England (Thomson 1922). The exception was the Common Myna, which was established in New Zealand from an introduced population in Australia, but that population was probably sourced originally from India. Only eggs clearly labelled as clutches from a single nest were used and we avoided measuring abnormally large 'clutches' that were likely to be the result of multiple nests. Where there was any doubt that a group of eggs did not represent a single clutch, only one egg was measured. For European species, we selected clutches collected from the southern half of England, the area from which most of the species in our sample were likely to have been 'sourced by the acclimatization societies for

introduction to New Zealand. The majority of eggs in this collection were obtained in the late 19th and early 20th centuries. Although population estimates of each species at this time are not available, only in the last few decades have widespread declines been reported (Hewson & Noble 2009) and we assumed they were relatively common at the time of collection. Even eggs of the Cirl Bunting, which is rare today in England, were available from an area that spanned southern England, suggesting they were still common at the time the eggs were collected. Clutches of the Common Myna were selected from across India, where the species is still common today. Thus, we assumed for our study that none of the source populations had experienced a severe population bottleneck, and by selecting clutches from across large geographical areas, we were able to capture the range of variation present in the source populations.

To measure egg morphology for the same species in the introduced range, we measured 260 clutches in the collections of the four main museums in New Zealand (Auckland Museum, National Museum Te Papa, Canterbury Museum and Otago Museum). The eggs in these collections date largely from the early to mid-20th century and were obtained from sites across the country. We also measured the eggs of a further 215 clutches at our field sites in Kaikoura (42°23′S, 173°37′E), Ward (41°48′S, 174°06′E) and Port Waikato (37°29′S, 174°46′E) during the breeding seasons of 2004–2006. Thus, data on egg morphology of introduced species in New Zealand were also collected over a wide geographical area, and differences are unlikely to be the result of local conditions. We used the same criteria for selecting and excluding clutches in the New Zealand museums as for those in the British Museum. For eggs measured in the field, we monitored nests to ensure that clutches were complete before egg measurements were collected.

All eggs were measured to the nearest 0.1 mm with callipers. The length and maximum width of each egg was measured and then an index of volume and shape was calculated using the following equations:

$$\text{Egg volume index} = \text{Length} \times \text{width}^2 \ (\text{in cm}^3)$$

$$\text{Egg shape index} = \text{Length/width}$$

The volume index provides a value approximately twice the actual volume (Hoyt 1979); we avoided using a constant to approximate 'true' volume for each species because the constant is related to the shape of the egg and we had no way of confirming its validity. The egg shape index is a measure of elongation; larger values indicate elongated eggs, while low values indicate shorter and broader egg shapes. As there was no relationship between change in egg shape and change in egg volume across species ($F_{1,11} = 0.67$, $P = 0.43$), we subsequently treated the two measures as independent traits relative to bottleneck size and rate of hatching failure.

Each clutch was assumed to have been laid by a different female and we treated each clutch as an independent data point, while the eggs within each clutch were considered dependent (we assumed they were laid by the same female). To avoid the pseudoreplication that would result if we treated each egg independently, we used a one-way nested analysis of variance (ANOVA) that partitioned variance between and within clutches to test for differences between the eggs of introduced and source populations for each species separately, with source as the categorical predictor. The null hypothesis was that there would be no differences in the volume or shape of eggs between these two populations. As clutch size differences may explain differences in egg size (Flux 2006), and as mean clutch size has decreased for several species in New Zealand (Evans *et al.* 2005), we also re-analysed our data by comparing egg morphology only between clutches of the same size. Due to sample sizes, this analysis was conducted only for the Song Thrush and Starling.

Bottleneck size estimates were taken from Thomson (1922) and Long (1981) and analysed following Briskie and Mackintosh (2004). This involved summing the number of birds released in each district to provide a total number of individuals released in New Zealand (Table 1). Where it was clear that a particular release was unsuccessful, these birds were not included in the estimate of bottleneck size. To test for an effect of bottleneck size or shape on egg size, we calculated mean percentage change using the formula:

$$\text{Mean \% change} = \frac{(\text{New Zealand mean} - \text{source mean}) \times 100}{\text{source mean}}$$

This allowed direct comparison among species despite variation in egg size and shape related to differences in body size. We then ran separate regressions to test for a relationship between bottleneck

size and percentage change in egg volume and differences in egg shape. Both egg volume and egg shape were arcsine square-root transformed to achieve normality. To avoid pseudoreplication, we took the average for all eggs within each clutch and then the means of each clutch to estimate a species-specific value for use in the regression analyses.

Severe bottlenecks may affect not only the average value of a trait but also its variance. This might occur if the deleterious effects of inbreeding result in large and non-directional deviations from the presumed optimal egg morphology present in the source population. We first calculated the coefficient of variation in both egg size and egg shape and then compared this with a regression analysis against population bottleneck size. Coefficients of variation were calculated using the means of each clutch, as the small number of eggs per clutch (two to four) makes it difficult to estimate within-female variation in egg morphology. Thus, this analysis compares between-clutch variation in egg volume and egg shape and we used it as a measure of whether severe bottlenecks increased variance in egg traits among females within a post-bottlenecked population.

To assess whether changes in egg morphology affected hatching failure rates, we then ran separate regressions with change in hatching failure rates (i.e. New Zealand hatching failure rate minus the hatching failure rate in the source population) against the percentage change in egg volume and difference in egg shape. Both variables were arcsine square-root transformed. Hatching failure rates for the New Zealand and source populations were taken from Briskie and Mackintosh (2004) and are based on the proportion of eggs that failed to hatch due to egg infertility or embryo mortality. Predation, desertion and the loss of eggs as a result of environmental factors (e.g. blown out of the nest) were not included. This information was collected from both New Zealand and the source countries for 12 of the 13 species. The Cirl Bunting was excluded from this part of the analysis as there is inadequate information on the rate of hatching failure in New Zealand for this species.

Our results are potentially confounded by phylogeny and differences in body size. To control for differences in adult body size across species (as egg size is typically larger in larger species), we used the percentage change in egg volume when testing for relationships with bottleneck size and hatching failure, instead of the actual difference between the New Zealand and source populations. As there is also some evidence to suggest that body size of adults has changed for some species since their introduction (C. Debruyne unpubl. data), we compared percentage change in body mass with percentage change in egg volume using body mass means from regional handbooks (Cramp 1977–1994, Higgins 1990–2006, Dunning 1993). If adult body size has decreased in New Zealand, this could have caused a decrease in egg size, independent of any effect of bottleneck size.

To test for the effects of phylogeny, we used the programme CAIC (Comparative Analysis by Independent Contrasts, Purvis & Rambaut 1994). Egg morphology is likely to be similar in closely related species and the phylogenetic analysis was run to control for variation due to common ancestry. We used a phylogeny based on the DNA classification of passerine birds by Johansson *et al.* (2008). The CAIC method calculates 'contrasts' between species (i.e. differences that have arisen since they shared a common ancestor), and then compares these contrasts with that of the other variable of interest (e.g. bottleneck size). Regressions were forced through the origin (Harvey & Pagel 1991). We present regression analyses using both the raw data and the raw data when controlled for possible phylogenetic effects.

RESULTS

Changes in egg morphology

Significant differences in egg morphology were found between the New Zealand and source populations for nine of 13 species (Table 1). Six species showed changes in egg volume between the New Zealand populations and their source populations, ranging from a decrease of 3.3% in the Dunnock to a decrease of 8.6% in the Yellowhammer. No species experienced a significant increase in egg volume between their source and New Zealand populations. Significant changes in egg shape were found for four species (Table 1). Song Thrush and Chaffinch eggs were, on average, narrower and more elongated in New Zealand compared with their source populations, whereas Common Myna and Goldfinch eggs were shorter and broader in their introduced populations (Table 1).

For Song Thrush and Starling, egg volume was still significantly smaller in New Zealand when

Table 1. Comparison of egg volume and egg shape between source and introduced (New Zealand, NZ) populations and the number of birds released (bottleneck size), including the number of clutches measured (n), mean egg volume, and mean egg shape indices and their significance levels as tested using nested general linear models (*denotes significant at $P < 0.05$). Volume and shape were transformed (arcsine square-root) to meet the assumptions of these tests.

	n			Mean volume (LW^2)				Mean shape (L/W)			
Species	Source	NZ	Bottleneck size	Source	NZ	Direction of change	P	Source	NZ	Direction of change	P
1. Cirl Bunting	21	7	11	5.34	5.20	0	0.21	1.307	1.324	0	0.53
2. Common Myna	30	16	70	13.37	13.62	0	0.52	1.380	1.334	−	0.019*
3. Greenfinch	28	31	100	4.52	4.27	−	0.041*	1.378	1.409	0	0.18
4. Dunnock	29	41	250	4.28	4.14	−	0.044*	1.356	1.346	0	0.63
5. Skylark	25	26	399	6.79	6.72	0	0.75	1.411	1.394	0	0.050
6. Song Thrush	30	88	400	12.08	11.42	−	0.0019*	1.297	1.321	+	0.0097*
7. Yellowhammer	25	33	401	5.79	5.29	−	< 0.001*	1.325	1.335	0	0.42
8. House Sparrow	30	23	419	5.37	5.19	−	0.40	1.402	1.408	0	0.56
9. Redpoll	25	18	450	2.43	2.45	0	0.74	1.305	1.315	0	0.15
10. Goldfinch	25	23	500	2.84	2.78	0	0.55	1.347	1.313	−	0.0099*
11. Chaffinch	30	42	501	3.98	4.12	0	0.17	1.305	1.346	+	0.0040*
12. Starling	30	56	653	13.80	13.03	−	< 0.001*	1.400	1.400	0	0.82
13. Blackbird	30	71	800	13.70	13.14	−	0.021*	1.379	1.379	0	0.90

only same-sized clutches were used (Song Thrush clutches of four eggs: $F_{1,56} = 11.4$, $P = 0.0014$; Starling clutches of five eggs: $F_{1,24} = 12.1$, $P = 0.0019$). Song Thrush eggs were 7.8% smaller and Starling eggs 11.6% smaller in New Zealand than in their native range. However, the significant difference in shape for Song Thrush eggs was no longer significant ($F_{1,56} = 1.68$, $P = 0.20$).

There was no significant relationship between changes in egg volume and changes in body size between New Zealand and the source populations ($F_{1,11} = 0.62$, $P = 0.45$). This result did not change when controlled for phylogeny ($F_{1,11} = 0.92$, $P = 0.36$). Thus, the decline in egg size in some introduced species was not the result of a concomitant decrease in adult body size.

Effect of bottleneck size on egg morphology

There was no relationship between bottleneck size and the percentage change in egg volume across all species ($F_{1,11} = 0.043$, $P = 0.84$) and this was not significant when controlled for phylogeny ($F_{1,11} = 0.64$, $P = 0.44$). The relationship remained non-significant if absolute change in egg volume (i.e. the magnitude of difference between populations regardless of direction) was compared with bottleneck size ($F_{1,11} = 0.21$, $P = 0.66$). Again, this result was not significant when controlled for phylogeny ($F_{1,11} = 1.20$, $P = 0.30$). However, there

was a significant inverse relationship between bottleneck size and the coefficient of variation in egg volume (Fig. 1a; $F_{1,11} = 4.82$, $P = 0.050$). In other words, the eggs of those species passing through the most severe bottlenecks were more variable in size in New Zealand populations compared with species passing through larger bottlenecks. This relationship held once potential phylogenetic effects were controlled for (Fig. 1b; $F_{1,11} = 11.9$, $P = 0.0054$).

There was a significant inverse relationship between bottleneck size and absolute change in egg shape (i.e. the magnitude of change in egg shape regardless of its direction; Fig. 2a; $F_{1,11} = 6.63$, $P = 0.026$), and this relationship remained significant when phylogeny was controlled for (Fig. 2b; $F_{1,11} = 6.29$, $P = 0.029$). However, there was no significant relationship between bottleneck size and change in egg shape across species ($F_{1,11} = 0.02$, $P = 0.89$), or when controlling for phylogeny ($F_{1,11} = 0.23$, $P = 0.64$). In other words, those species that passed through the most severe bottlenecks showed the largest deviations in egg shape from their source populations, although the direction of the deviations (more elongated vs. broader eggs) was not related to bottleneck size. Unlike egg volume, there was no relationship between the coefficient of variation in egg shape and bottleneck size ($F_{1,10} = 0.83$, $P = 0.38$) and this relationship did not change when phylogeny was controlled for ($F_{1,11} = 0.13$, $P = 0.72$).
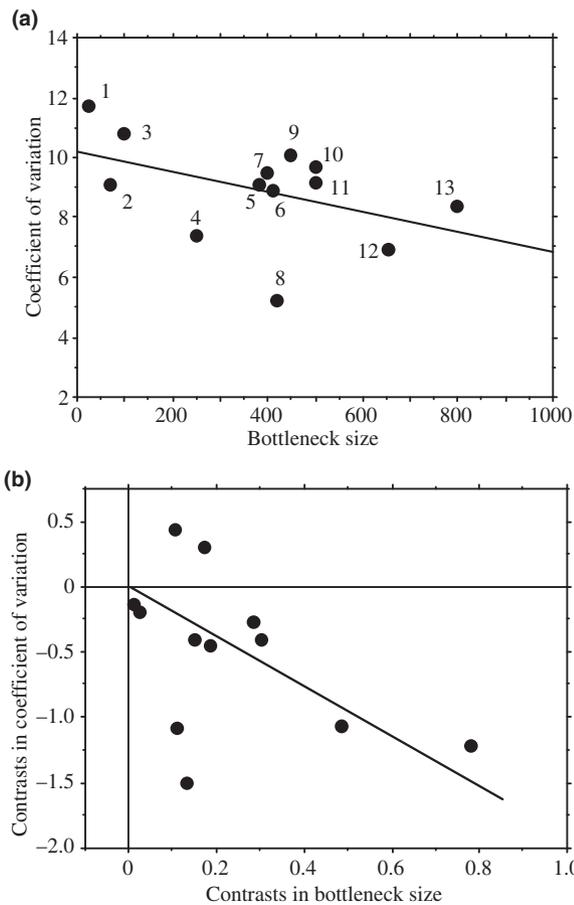
Figure 1. Bottleneck size vs. variation in egg volume. (a) Coefficient of variation (CV) of egg volume in relation to bottleneck size among 13 species of birds introduced to New Zealand. (b) Relationship between contrasts in the CV of egg volume and contrasts in bottleneck size. Species codes as in Table 1.

Figure 2. Bottleneck size vs. change in egg shape. (a) Mean change in egg shape in relation to bottleneck size among 13 species of birds introduced to New Zealand. (b) Relationship between contrasts in the change of egg shape and contrasts in bottleneck size. Species codes as in Table 1.

Effect of changes in egg morphology on hatching failure

Across all species, there was no relationship between the difference in hatching failure between New Zealand and the source population and either change in egg volume ($F_{1,10} = 0.19$, $P = 0.68$) or absolute change in egg volume ($F_{1,10} = 0.11$, $P = 0.75$). Hatching failure was also not significantly related to the coefficient of variation in egg volume ($F_{1,10} = 0.77$, $P = 0.40$). None of these relationships was significant when controlled for phylogeny (change in egg volume: $F_{1,10} = 1.85$, $P = 0.20$; absolute change in egg volume: $F_{1,10} = 0.91$, $P = 0.36$; coefficient of variation in egg volume: $F_{1,10} = 0.19$, $P = 0.21$). Thus, the
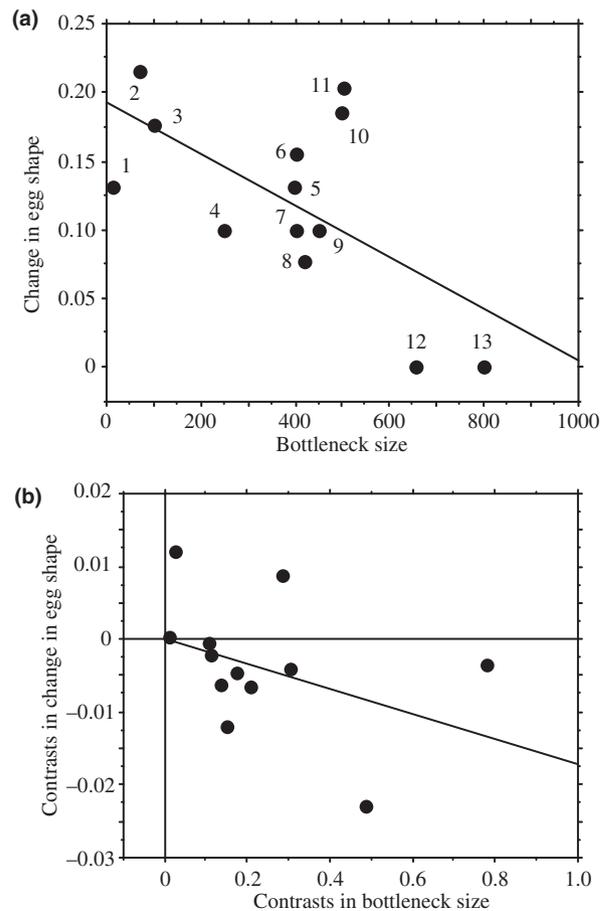
changes in egg volume between New Zealand and the source populations do not appear to be related to higher levels of hatching failure.

Increased hatching failure among introduced species in New Zealand was not related either to change in egg shape ($F_{1,10} = 3.16$, $P = 0.11$) or to absolute change in egg shape ($F_{1,10} = 3.09$, $P = 0.11$). The coefficient of variation in egg shape among the New Zealand populations was also not significantly correlated with rates of hatching failure ($F_{1,10} = 0.83$, $P = 0.38$). None of these relationships was significant when controlled for phylogeny (change in egg shape: $F_{1,10} = 2.99$, $P = 0.12$; absolute change in egg shape: $F_{1,10} = 3.17$, $P = 0.10$; coefficient of variation in egg shape: $F_{1,11} = 2.95$, $P = 0.12$). Thus, changes in egg shape did not appear to explain higher levels

DISCUSSION

Some of the birds introduced to New Zealand in the 19th century now lay eggs that are smaller than and different in shape from those of their source populations. At least some of these changes in egg morphology can be attributed to the effects of passing through a severe population bottleneck during their establishment, although contrary to our expectation, they do not appear to explain the increased levels of hatching failure that have previously been found in some introduced species (Briskie & Mackintosh 2004).

It might be expected that the increased variance in egg volume and greater deviation in egg shape of species passing through the most severe bottlenecks would have led to lower hatching success. Lower hatching success has been reported in nests of other species, with eggs that are smaller or larger than average (e.g. Nordskog & Hassan 1971, Simmons 1997, Williams 2001), and it is likely that large deviations in egg shape may also reduce hatching success (Narushin & Romanov 2002), although Encabo et al. (2001) did not find any such effect in Great Tits Parus major or Blackbirds. The magnitude of changes in egg volume found here (~3–9%) may not be sufficient to affect hatching success, but exactly how much an egg must decrease in size before it has a quantifiable fitness effect is unknown. Williams (2001) chemically induced captive Zebra Finches Taeniopygia guttata to lay eggs 8% smaller than average, which resulted in increased hatching failure, but had no effect on offspring condition. An 18% decrease in egg size in a later study was sufficient to reduce significantly both hatching success and offspring condition (Wagner & Williams 2007). Hence, the average changes in egg volume we observed in New Zealand birds were close to the range expected to affect hatching success, but less than half the decrease that resulted in decreased nestling condition in captive Zebra Finches.

The changes in egg shape we observed included both greater elongation (long, tapered egg shapes) and greater width (short, broad egg shapes). The direction of change varied between species but was inversely related to bottleneck size. Large deviations in egg shape could imply that these changes were the result of genetic problems associated with inbreeding. Our results suggest the negative effects of severe population bottlenecks may lead to increased deviation in egg shape away from that found in the source population, but whether the magnitude of the changes we observed is sufficient to affect the fitness of post-bottlenecked populations is not clear from our study.

As with changes in egg shape, increased variability in egg volume as bottleneck severity increases suggests a link with the inability of individuals in the post-bottleneck population to produce eggs of a presumed optimal size. Understanding changes in egg size in any species is confounded by variability due to clutch size, female condition and age, environmental conditions, and differences between years (Christians 2002). As our data are based on egg collections that cover a variety of geographical locations, years, clutch sizes and females, we have assumed the noise introduced by these factors is random with respect to bottleneck size. Without further data on egg size variation in the New Zealand populations of each species, we cannot rule out other potential explanations for increased variability in egg size, although the differences in egg volume remained in Song Thrushes and Starlings once we controlled for clutch size. However, it seems unlikely that the relationship between increased variation in egg volume and bottleneck size arises solely from confounding variables unless there is a direct link between bottleneck size and, for example, age structure of the population or environmental factors. Instead, our data are consistent with a reduced ability of birds in post-bottleneck populations to produce eggs near a presumed optimum size, and could be interpreted as an outcome of increased inbreeding depression in those species that passed through the most severe population bottlenecks.

Despite evidence of changes in both egg size and egg shape, we did not find any correlations between these changes and levels of hatching failure. An obvious criticism is that our measures of both hatching failure and changes in egg morphology are too crude to detect anything but the strongest pattern. For example, combining all nests to calculate a 'species-specific' rate of hatching failure and comparing it with similarly calculated values for egg volume and shape might mask intraspecific effects in species in which the number of individuals affected is relatively small (as might be expected in species passing through moderate bottlenecks). It is possible that individuals that deviate most in

egg size and shape experience higher hatching failure, but any such effect would have been offset by combining the data with individuals showing little deviation. As our data were based primarily on museum specimens, it was not possible to correlate features of egg morphology with hatching success within each species, and such studies now need to be undertaken to determine whether the changes in egg morphology we observed affect hatching success at an individual level.

It has been suggested that morphological traits such as body size and egg size are less affected by inbreeding than other life-history traits, such as offspring survival (de Rose & Roff 1999). It is possible therefore that the changes in egg volume we observed may not be due to bottlenecks but rather that smaller eggs may be adaptive in New Zealand. Adaptive changes in egg morphology could be a result of novel selection pressures due to different predation regimes or patterns of adult mortality, but studies of such changes have been made in only a few introduced New Zealand birds (e.g. MacLeod *et al.* 2005). Alternatively, changes in egg morphology could be a non-adaptive outcome of environmental conditions in the introduced range, such as lower availability of essential nutrients and minerals (e.g. calcium), which could constrain egg production (Patten 2007).

Previous workers have also looked for changes in egg size among some of the species introduced to New Zealand (Cassey *et al.* 2005, Flux 2006). In both studies, data were taken from published records and may have included some data from populations other than the known source, whereas we directly measured eggs from collections in both the UK and New Zealand. Although the use of museum collections can introduce other problems (e.g. potential bias in collection, potential for mismatched clutches; Lack 1947), it did allow us to collect information directly from the same geographical source of the founding populations and with the same methods and instruments as we used in the New Zealand samples. As a number of introduced species also lay smaller clutches in New Zealand than in their source populations (Evans *et al.* 2005), and egg size can vary with clutch size, Flux (2006) suggested that changes in egg size among introduced species may simply be an artefact of clutch size differences between source and introduced ranges. Although we cannot rule out this possibility entirely, Song Thrushes and Starlings in our analysis had smaller eggs in New Zealand

even when comparing the equivalent clutch size. Thus, it seems that introduced birds in New Zealand have experienced changes in both clutch size and egg morphology, and that at least some of these changes may be due to the effects of population bottlenecks.

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