



Ecological predictors of reduced avian reproductive investment in the southern hemisphere

Peter Samaš, Tomáš Grim, Mark E. Hauber, Phillip Cassey, Karel Weidinger and Karl L. Evans

P. Samaš (psamas@seznam.cz), T. Grim and K. Weidinger, Dept of Zoology and Laboratory of Ornithology, Palacky Univ., 17 listopadu 50, CZ-771 46 Olomouc, Czech Republic. – M. E. Hauber, Dept of Psychology, Hunter College and the Graduate Center of the City Univ. of New York, 695 Park Avenue, New York, NY 10065, USA. – P. Cassey, School of Earth and Environmental Sciences, Univ. of Adelaide, SA 5005, Australia. – K. L. Evans, Dept of Animal and Plant Sciences, Univ. of Sheffield, Sheffield, S10 2TN, UK.

Despite intensive research, the factors driving spatial patterns in life-history traits remain poorly understood. One of the most frequently documented, and paradoxically, least understood patterns, is the latitudinal gradient of increasing avian clutch size at higher latitudes. These gradients are less marked in the southern hemisphere, thus clutch sizes tend to be smaller at southern latitudes than at equivalent northern ones. We exploited a natural experiment provided by the introduction of European passerines to New Zealand (NZ) to test three widely proposed ecological drivers of this pattern, i.e. the nest predation, Ashmole's seasonality, and the breeding density hypotheses. We focus on the blackbird *Turdus merula* and the song thrush *T. philomelos* as founder effects do not have a major influence on the reproductive traits of their introduced populations. Both species laid smaller clutches in NZ than in Europe. These reductions had stabilised within one hundred years and were not associated with a compensatory increase in investment in individual offspring by laying larger eggs. In contrast to the nest predation hypothesis, daily nest predation rates were lower in NZ than in Europe. Smaller southern hemisphere clutches were associated with higher conspecific population densities and a relaxation of seasonal clutch size trends. These findings thus provide some support for both Ashmole's seasonality and the breeding density hypotheses. Analyses across 11 European passerines introduced to NZ suggest, however, that neither of these hypotheses provide general explanations of smaller clutches in the southern hemisphere. We suggest that reduced seasonality and lower nest predation promote increased breeding densities and adult survival in the southern hemisphere. The later may drive smaller southern clutch sizes by generating spatial variation in the outcome of the trade-off between reproductive investment and longevity.

Animal life-history traits exhibit strong geographic patterns (Gaston et al. 2008). Amongst the most consistent intra- and inter-specific patterns is the tendency for avian clutch size to covary positively with latitude, and to be smaller in the southern hemisphere than at equivalent northern latitudes. A diversity of mechanisms may drive these spatial patterns, and, despite decades of research, their relative contributions remain unclear (Lack 1947, Ashmole 1963, Evans et al. 2005, 2009a, Jetz et al. 2008).

One of the strongest candidates for a general driver of spatial variation in clutch size is Ashmole's seasonality hypothesis (Ashmole 1963). In seasonal environments, mortality during periods of low food supply, typically winter, reduces population size below that which the environment can support the following breeding season. Reduced intraspecific competition thus increases the per capita food supply during the breeding season enabling clutch size to be increased. The rapid increase in spring food availability may further promote larger clutches in seasonal environments (Stutchbury and Morton 2001). Therefore, individuals experiencing higher seasonality

should have larger clutch sizes than those in areas of lower seasonality. Whilst such patterns have been found in many studies, both intra- and inter-specifically, seasonality rarely provides a complete explanation of spatial variation in clutch size (Jetz et al. 2008), including smaller southern clutches (Evans et al. 2005). Temporal variation in resource availability during the breeding season can also contribute to intra-specific seasonal clutch size patterns. Single brooded species tend to exhibit a seasonal decline in clutch size, whilst multi-brooded species exhibit an initial increase in clutch size with a mid-season peak followed by a decline towards the end of the breeding season (Crick et al. 1993).

The nest predation hypothesis is also widely considered to be a strong driver of spatial patterns in clutch size (Skutch 1949, Martin et al. 2006, Cassey et al. 2009). It states that clutch size is typically reduced in regions with high predation rates, for example the tropics (Robinson et al. 2010, Remeš et al. 2012a). A number of mechanisms may contribute to this pattern (Roff 1992). Smaller clutches will be promoted in areas with high predation risk as the duration of the nesting period, and thus the cumulative

probability of predation, are reduced by decreasing the egg-laying period (because birds are physiologically constrained to lay no more than one egg per day; Hauber 2012). Smaller clutches also reduce the probability of nest predation at the chick stage because parents can reduce provisioning rates and, thus, the probability of visually and acoustically orientated predators detecting the nest (Skutch 1949, Haskell 1994, Martin et al. 2000). Alternatively, if provisioning rates are not reduced in small broods then chick development rates are increased, enabling chicks to fledge earlier, thus reducing the length of their exposure to nest predators (Martin and Briskie 2009). Finally, when predation risk is high, parents may lay smaller clutches to reduce investment in each nesting attempt because this increases the parental resources available for re-nesting within the same season, and increases the probability of adults surviving to another breeding season due to a trade-off between reproductive effort and survival (Martin 1995).

It is routinely recognised that avian life history traits, including clutch size, typically respond to population size in a density-dependent manner (Perrins 1965, Ricklefs 1980). This density dependence partly arises through interactions with other mechanisms that influence clutch size, for example high population densities can increase the risk of nest predation (Schmidt and Whelan 1999). It is thus useful to take population density into account in analyses of spatial patterns in clutch size, but few studies do so. This is perhaps because such studies frequently rely upon the haphazard collection of data on nest contents by volunteers, often across multiple years, and thus associated data on population densities are rarely available.

Assessing causes and drivers of large scale patterns in life history traits is complicated because species occurring in different regions vary in numerous other traits that could confound geographic patterns in life history traits. Different regions will also differ markedly in habitat type, and will thus vary in a wide range of environmental factors making it difficult to distinguish these effects from those of primary interest, such as seasonality or predation risk. This limits the ability to assign underlying causality in comparative studies (Jetz et al. 2008). Such situations can be improved by exploiting natural experiments (*sensu* Diamond 1986) in which species are introduced to novel geographic locations where they occupy similar habitats to those in their ancestral range. As an example, many European bird species have been introduced from the United Kingdom (hereafter UK) to New Zealand (hereafter NZ) where they occur in urban and agricultural landscapes that are very similar to those in their native range, and experience a less seasonal environment in NZ (Evans et al. 2005; Table 1). The translocation history of these species is well documented (Thomson 1922, reviewed by Duncan et al. 2006), providing researchers with a rare opportunity to estimate the flexibility of avian breeding biology traits under a known historical ecological context (Briskie and Mackintosh 2004). Previous work exploited these natural experiments and documented smaller clutch sizes in the southern hemisphere, relative to ancestral populations at equivalent northern latitudes, but the mechanisms driving these patterns are still uncertain (Evans et al. 2005). Moreover, egg sizes are also reduced in NZ (Cassey et al. 2005, Congdon and Briskie 2010). This is

surprising as avian life history theory predicts that the smaller clutch sizes would be associated with larger eggs due to trade-offs between investment in offspring number (i.e. clutch size) and in individual offspring (i.e. egg size; reviewed by Roff 1992, Martin et al. 2006).

Here we advance previous analyses of clutch size variation between native European bird populations and conspecific introduced populations in NZ by simultaneously assessing both clutch size and egg size in the focal populations and taking nest predation rates and breeding population densities into account. Instead of relying upon nest record cards we use data from intensive fieldwork conducted by the same researchers in both regions. Whilst nest record cards are certainly valuable (Hušek et al. 2010), our approach of collecting original data on focal taxa increases methodological consistency, reducing the potential influence of confounding variables and enabling greater precision in estimating egg-laying dates (Weidinger 2001). We use the blackbird *Turdus merula* and song thrush *T. philomelos* as case studies because these species occupy similar habitats in the native and non-native ranges, and no major founder effects on their reproductive biology have been observed in the non-native range (Briskie and Mackintosh 2004, Congdon and Briskie 2010), presumably because relatively large numbers of individuals were introduced to NZ, i.e. ca 800 blackbirds and 400 song thrush between 1862 and 1879 (Thomson 1922).

Our primary objective is to utilize the natural experiment provided by human-mediated avian introductions from the northern to the southern hemisphere to assess whether spatial patterns in clutch size are driven by Ashmole's seasonality hypothesis, Skutch's nest predation hypothesis, or density dependence. We also test two additional hypotheses: a) reductions in clutch size are associated with increased egg size as predicted by avian life-history theory (Martin et al. 2006); and b) that changes in clutch size in response to novel southern hemisphere conditions are still in progress.

Material and methods

Study sites

European study populations were situated in the Czech Republic (hereafter CZ) at similar latitudes as the UK source populations (ca 50°N) from which *Turdus* thrushes were introduced to NZ. Although our northern hemisphere data were not collected in the general area of source populations (most likely rural southern England; Thomson 1922), this is not problematic because we are interested in between-hemisphere differences (i.e. differences independent of local variation within hemispheres). Moreover, the major aspect of climate that is most relevant for this study, seasonality, is more similar between the UK and CZ than between either of these locations and NZ (Table 1). Finally, there is negligible genetic divergence between blackbird populations in the UK and CZ (Evans et al. 2009b). We tested our hypotheses using novel data on nest predation, breeding densities and clutch characteristics that were collected from the same study populations,

Table 1. Climatic variables (1971–2000) across our study sites in Olomouc region in CZ (Tinklová 2007), Auckland region in NZ (NIWA 2012) and southern UK (UK Met Office 2012).

Climate variables	CZ	UK	NZ
Mean annual temperature (°C)	9.0	10.0	15.1
Annual range of mean monthly temperatures (°C)	22.3	13.5	9.0
Rainfall per year (mm)	529	767	1240
Range in monthly rainfall (mm)	92.1	119.4	71.0

temporal period and by the same workers using consistent methodology.

Data were collected in CZ at four sites, the cities of Brno and Olomouc and their respective adjacent areas of Bystřc and Chválkovice; in NZ data were collected from the cities of Auckland and Hamilton (Table 2). There is some evidence that clutch size can vary with the intensity of urban development, and we defined sites close to the geographic city centre and dominated by the built environment as urban, and defined sub-urban sites as those with less intensively developed areas that included non-built up areas, primarily semi-natural habitats (Chamberlain et al. 2009; Table 2).

Data on clutch and egg sizes were collected in CZ during the northern springs and summers of 2004–2010 and in NZ during three consecutive austral breeding seasons 2007/2008, 2008/2009 and 2009/2010. Data on nest predation rates and breeding densities were collected in 2003–2006 in CZ and 2007–2010 in NZ. We did not collect additional data on predation rates or breeding densities in CZ during 2007–2010 because a) we reached sufficient sample sizes already in 2003–2006 (Results) and b) logistical trade-offs with other projects prevented us from collecting sufficient sample sizes in each field season during 2007–2010. Moreover, within each site there was limited annual variation in densities or predation risk (Results) suggesting that the minimal temporal mismatch in data collection would not bias our conclusions.

Table 2. Location and characteristics of study sites; urban sites are classified as those close to the geographic city centre and dominated by the built environment (e.g. urban parks and vegetation around housing estates), and sub-urban sites are those with less intensively developed areas that included non-built up areas, primarily semi-natural habitats (e.g. deciduous forest patches).

Locality	Region	Latitude	Longitude	Site
Chválkovice	CZ	49°35'N	17°17'E	sub-urban
Bystřc	CZ	49°14'N	16°30'E	sub-urban
Olomouc	CZ	49°35'N	17°15'E	urban
Brno	CZ	49°11'N	16°35'E	urban
Auckland	NZ	36°51'S	174°46'E	urban
Hamilton	NZ	37°46'S	175°16'E	urban

Data collection

Nest searching was conducted in both regions throughout the breeding season, i.e. from the last week of March to the end of July in CZ, and from the start of September to the end of January in NZ. It is likely, however, that a small number of particularly early and late broods were not detected, especially in NZ. We attempted to spread sampling effort uniformly across each site and across the duration of the fieldwork season and succeeded in the majority of sites (with the exception of CZ sub-urban sites, see below). Sampling effort was, however, particularly intensive during a two week period in the middle of the breeding season in order to obtain a precise estimate of the number of simultaneously active nests which was used as a proxy of breeding density. These intensive searches were conducted at sites with very similar habitat structure and comprised two sites in CZ (Olomouc, 33.7 ha; Chválkovice, 13.6 ha) in 2005 and 2006, and two urban NZ localities within Auckland (36.0 and 14.1 ha) in the 2008/2009 and 2009/2010 breeding seasons.

Nest contents were checked daily during laying, every one to three days during incubation and every one to four days during the nestling phase. Egg length and width were measured using digital callipers to the nearest 0.01 mm. Egg size was calculated using Hoyt's (1979) equation,

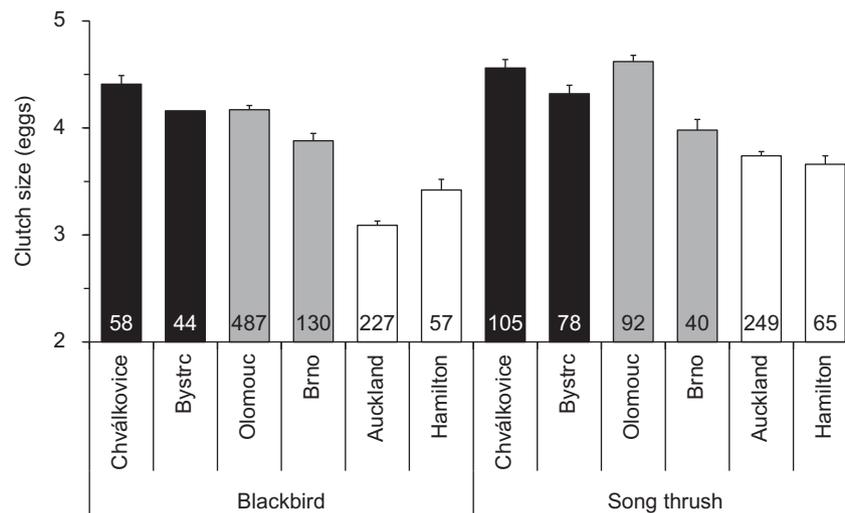


Figure 1. Variation in blackbird and song thrush clutch sizes (mean + SE) across study localities. Sample sizes (numbers of clutches) are given within bars. Data were collected in the Czech Republic in sub-urban (black bars) and urban sites (grey bars) and New Zealand urban sites (white bars).

i.e. egg volume (cm^3) = $0.51 \times \text{length (cm)} \times [\text{width (cm)}]^2$. We collected data on 1716 eggs and 1003 blackbird clutches, and 1040 eggs and 629 song thrush clutches. Sample sizes differ between egg size and clutch size analyses because for some nests we recorded final clutch size but were not able to measure the eggs due to early predation or limited accessibility.

To test whether reductions in the clutch size of NZ blackbird and song thrush populations have occurred during recent decades we used nest record card data collected by the Ornithological Society of New Zealand (OSNZ) during 1950–1998 (Robertson 1986).

To further test the predation, seasonality, and breeding density hypotheses, we obtained data on the proportional increase in breeding population densities, relative to those in the UK, of all 11 passerine species introduced from the UK to NZ from MacLeod et al. (2009). Data on the relative differences in NZ clutch size, relative to northern hemisphere populations, of these species were obtained from Evans et al. (2005).

Statistical analyses

All analyses were conducted using SAS 9.2 unless stated otherwise. Throughout this report, mean values of our results are provided \pm one standard error. First egg dates (FEG) were transformed prior to analysis so that they were directly comparable between regions and to take variation between years in the timing of breeding into account. This was achieved in two steps. First, FEG dates were centred around the mean so that for each species, region and year the mean FEG date equalled zero. Second, a constant was added so that the earliest FEG date then had a value of zero ensuring that all dates were positive before calculating square terms. We calculated egg size as the average egg volume of a complete clutch.

Following the recommendation of Grafen and Hails (2002), model selection was conducted using backward elimination of non-significant terms (from full models described below), whilst retaining the major variable of interest (i.e. region or FEG depending on the particular model) in the models regardless of its statistical significance (Grim et al. 2011). This enabled us to follow recommendations to report effect sizes for both significant and non-significant comparisons of our focal variables of interest (Nakagawa and Cuthill 2007). When the focal variables of interest were not significant their effect sizes and associated statistics are thus reported from models in which all non-significant non-focal variables have been removed. In order to take spatio-temporal variation into account year and site (both treated as categorical random effects) were included in all models (Grafen and Hails 2002).

We first assessed whether there was variation in clutch size or egg size between the urban and sub-urban CZ sites by constructing models of these response variables that included habitat type (a fixed factor), FEG and its squared term (FEG^2 ; to take non-linear seasonal trends into account), and the interactions between habitat type and FEG, and between habitat type and FEG^2 as additional predictors, together with year and site as random factors. The analyses of

egg size also included clutch size as an additional predictor. Habitat type had no statistical influence on clutch size or egg size in either focal species (Supplementary material Appendix 1, Table A1 and A2) so in all subsequent analyses we pooled data across habitat types.

To test the hypothesis that clutch sizes were smaller in NZ than in CZ, we modelled clutch size, using general linear mixed models with a normal error distribution, as a function of region, FEG, FEG^2 , the interactions between region and FEG, and between region and FEG^2 , together with year and site as random factors. We used the same approach and model structure to assess the effects of region on egg size, but included clutch size and its interaction with region as additional predictors.

The above analyses provide important information on how seasonal clutch size trends differ between regions, but because their primary focus was on assessing regional effects on clutch size they include data from the two CZ sub-urban localities (Chvátkovice, Bystrc) at which sampling effort was not fully standardised across the entire breeding season. We thus conducted additional analyses that excluded data from these sub-urban sites and modelled clutch size in CZ and NZ in separate models using FEG and FEG^2 as predictors together with year and site as random factors. We again followed the recommendations of Grafen and Hails (2002) and Nakagawa and Cuthill (2007), and used backward elimination of non-significant terms whilst retaining the major variables of interest (FEG and FEG^2) in the final models.

We tested the hypothesis that daily nest predation rates varied between regions using the logistic regression model developed by Aebischer (1999) which further develops Mayfield's method (Mayfield 1975). This model contained region (CZ vs NZ) and the spatio-temporal replicate (combination of breeding season and site) nested within region (four and three breeding seasons respectively for CZ and NZ) as predictors. We collected sufficient data for predation analyses from Auckland, Hamilton and Olomouc. The predation data for Olomouc have previously been reported by Strachoňová (2008) who helped us with field work in both CZ and NZ.

We tested the hypothesis that breeding densities differed between regions using the exact variant of the Mann–Whitney U-test, calculated in StatXact, as only four data points were available for each region. More generally, we tested the hypothesis that species with the largest increases in population density following their introduction to NZ exhibited the largest decreases in clutch size. We used data from all 11 European passerines introduced successfully to NZ; data on the magnitude of changes in clutch size were from Evans et al. (2005) and equivalent changes in population density were from MacLeod et al. (2009). These analyses were conducted taking species specific indices of reduced seasonality in NZ into account (from Evans et al. 2005). Phylogeny was accounted for using the PGLS methodology described in Evans et al. (2011), but this generated qualitatively identical results to those obtained without taking phylogeny into account and we only report the latter.

Finally, we tested the hypothesis that blackbirds and song thrush have continued to evolve smaller clutch sizes in NZ during recent decades by comparing the clutch sizes

we found in 2007–2009 with those reported from the same regions of NZ (Auckland and Hamilton) in the 1950s and 1960s using data from the OSNZ nest record scheme. We did so using Welsch's t-test for unequal variances (Ruxton 2006). In addition, we constructed multiple regression models of the clutch size recorded in the OSNZ scheme for our study area between 1950 and 1998 (blackbird) and 1956 and 1986 (song thrush); the time periods differed between species due to the variation in the availability of nest record cards. These models included year and its square term, FEG and FEG² as continuous predictors together with NZ locality (Hamilton or Auckland) as a fixed two level factor.

Results

Effects of region on clutch size, egg size and seasonal clutch size patterns

Mean blackbird clutch size was larger in CZ, by approximately one egg than in NZ (CZ: 4.13 ± 0.03 , $n = 735$; NZ: 3.15 ± 0.04 , $n = 284$; Fig. 1). The final multiple regression model of blackbird clutch size retained, in addition to region, seasonal effects (FEG and FEG²) and their interaction with region (Table 3). Song thrush clutch size was larger by 0.7 of an egg in CZ (4.44 ± 0.04 , $n = 315$) than NZ (3.73 ± 0.03 , $n = 314$; Fig. 1). The final model for song thrush clutch size again retained, in addition to region, seasonal effects (FEG and FEG²) and their interaction with region (Table 3).

Mean blackbird egg sizes were similar in CZ (6.77 ± 0.03 cm³, $n = 325$ clutches) and NZ (6.94 ± 0.05 cm³, $n = 209$), and neither region ($F_{1,519} = 0.62$, $p = 0.43$), nor any other predictors were retained in the final model. Song thrush egg size was bigger in CZ (5.96 ± 0.07 cm³, $n = 54$) than in NZ populations (5.67 ± 0.04 cm³, $n = 218$), and this significant effect of region ($F_{1,271} = 13.63$, $p = 0.0003$) was the only predictor retained in the final model of song thrush egg size.

Blackbird clutch size in CZ peaked in the middle of the breeding season, when clutches contained an extra egg compared to clutch sizes at the start and the end of the breeding season (Table 4; Fig. 2a). There was no evidence for seasonal trends in blackbird clutch sizes in NZ with only 0.1 egg difference between maximum and minimum clutch size (Table 4; Fig. 2b); this contrast in regional clutch size trends is also indicated by the significant interaction between region and first egg date in models that combine data from both regions (Table 3). Whilst the egg laying period appears to be shorter in NZ blackbirds than that in CZ, we consider it likely that we missed some early and late broods in NZ so do not further analyse or discuss such patterns. In CZ song thrush clutch size exhibited a mid-seasonal peak (Table 4; Fig. 2c) with maximum and minimum clutch sizes differing by 0.8, whilst in NZ there was a linear decline in clutch size with maximum and minimum clutch sizes differing by 0.8 (Table 4; Fig. 2d). These data thus indicate that song thrush clutch size exhibits divergent seasonal trends in CZ and NZ, confirming the significant interaction between region and first egg date in models that combined data from both regions (Table 3).

Regional effects on daily nest predation rates and breeding densities

Daily blackbird nest predation rates were consistently spatio-temporally higher in CZ than in NZ (CZ: mean = 0.0525, 95% confidence intervals (CIs) 0.0461–0.0598, $n = 585$ nests/6160 exposure nest-days; NZ: mean = 0.0277, 95% CIs 0.0207–0.0369, $n = 316/2444$; $\chi^2_1 = 18.64$, $DF = 1$, $p < 0.0001$, Fig. 3). Song thrush populations also had higher daily nest predation rates in CZ than NZ (CZ: mean = 0.0515, 95% CIs 0.0423–0.0626, $n = 220/2204$; NZ: mean = 0.0248, 95% CIs 0.0174–0.0352, $n = 324/2436$; $\chi^2_1 = 15.37$, $DF = 1$, $p < 0.001$).

Breeding densities were analysed as samples defined by a particular year and study site combination giving four samples for each species from each region (Fig. 4). Breeding

Table 3. Clutch size variation between regions, Czech Republic (CZ) and New Zealand (NZ). FEG is first egg laying date and FEG² is its quadratic term. Year and site are modelled as random variables and are forced into all models. These models include data from sub-urban sites at which sampling effort was not standardised across the breeding season, thus sample sizes are larger than those in Table 4 in which data from such sites are excluded. Parameter estimates for region are given for NZ relative to a reference level of zero for CZ.

Species	Predictor	z	F	DDF	p	Estimate ± SE
Blackbird	Year	1.06			0.14	0.01 ± 0.01
	Site	1.39			0.08	0.04 ± 0.03
	Intercept					3.20 ± 0.16
	Region		25.59	997	<0.0001	−0.89 ± 0.18
	FEG		6.84	997	0.009	0.002 ± 0.01
	FEG ²		6.53	997	0.01	−0.000006 ± 0.0007
	Region × FEG		5.65	997	0.02	−0.03 ± 0.01
	Region × FEG ²		6.08	997	0.01	0.0003 ± 0.00008
Song thrush	Year	0.08			0.47	0.0002 ± 0.003
	Site	1.26			0.10	0.06 ± 0.05
	Intercept					3.74 ± 0.19
	Region		6.49	612	0.01	−0.58 ± 0.23
	FEG		8.98	612	0.003	0.005 ± 0.006
	FEG ²		14.79	612	0.0001	−0.0009 ± 0.00005
	Region × FEG		5.21	612	0.02	−0.03 ± 0.01
	Region × FEG ²		5.21	612	0.02	0.0003 ± 0.0001

Table 4. The relationship between clutch size and first egg date (FEG) in the Czech Republic (CZ) and New Zealand (NZ) in multiple regression analyses conducted separately for each region. Year and site were modelled as random variables and were forced into all models. We report statistics and effect sizes also for non-significant focal variables, i.e. FEG and FEG^2 , which is a recommended practice (Nakagawa and Cuthill 2007). In the NZ song thrush model the random effects were non-estimable; however, conclusions remained identical when the random effects were removed or when the year and site were included as fixed (instead of random) effects (results not shown).

Species	Region	Predictor	z	F	DDF	p	Estimate \pm SE
Blackbird	CZ	Year	1.09			0.14	
		Site	0.66			0.25	
		Intercept					3.99 \pm 0.19
	NZ	FEG		18.10	605	<0.0001	0.03 \pm 0.07
		FEG ²		18.79	605	<0.0001	-0.0002 \pm 0.00005
		Year	0.28			0.39	
Song thrush	CZ	Site	0.65			0.26	
		Intercept					3.25 \pm 0.17
		FEG		0.14	278	0.71	0.0006 \pm 0.002
	NZ	FEG ²		0.52	277	0.47	-0.00004 \pm 0.00006
		Year	0.99			0.16	
		Site	0.65			0.26	
Song thrush	CZ	Intercept					4.31 \pm 0.30
		FEG		6.99	122	0.01	0.03 \pm 0.01
		FEG ²		9.52	122	0.003	-0.0004 \pm 0.0001
	NZ	Year	-			-	
		Site	-			-	
		Intercept					3.98 \pm 0.08
NZ	FEG		13.36	308	0.0003	-0.005 \pm 0.001	
	FEG ²		3.75	307	0.054	-0.00009 \pm 0.00005	

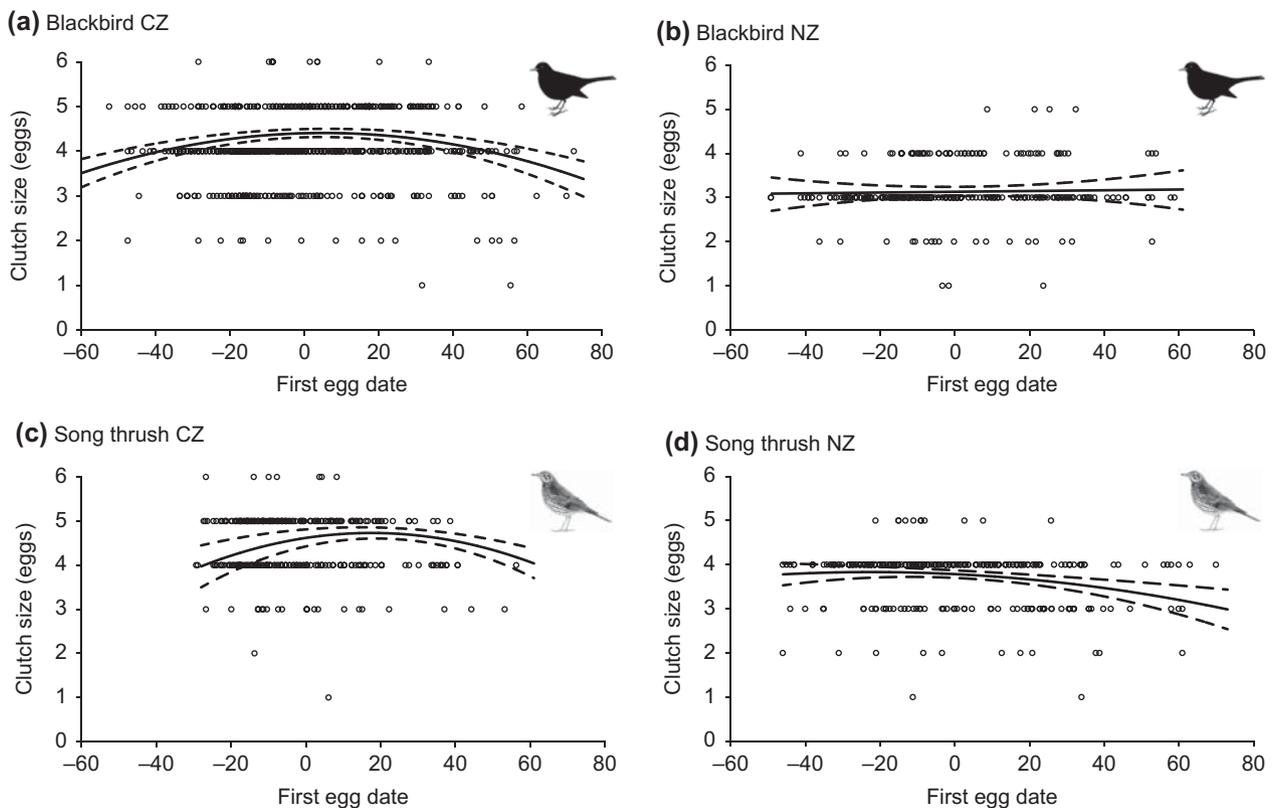


Figure 2. Seasonal variation in clutch size (number of eggs) of the blackbird in the Czech Republic (CZ) (a) and New Zealand (NZ) (b) and the song thrush in Czech Republic (c) and New Zealand (d). Fitted solid lines are from models presented in Table 3 (dashed lines represent 95% confidence intervals). Outlying data-points representing two clutches (most likely parasitized by conspecifics) with 8 eggs and one with 7 eggs are not displayed in (a) and (c), although these data were included in statistical analyses. We centred 'first egg date' values by mean for each species/year/region combination separately, so that day zero corresponded to the average date of laying across species, years and regions. This ensured that seasonal patterns in clutch size were directly comparable between species, years and regions.

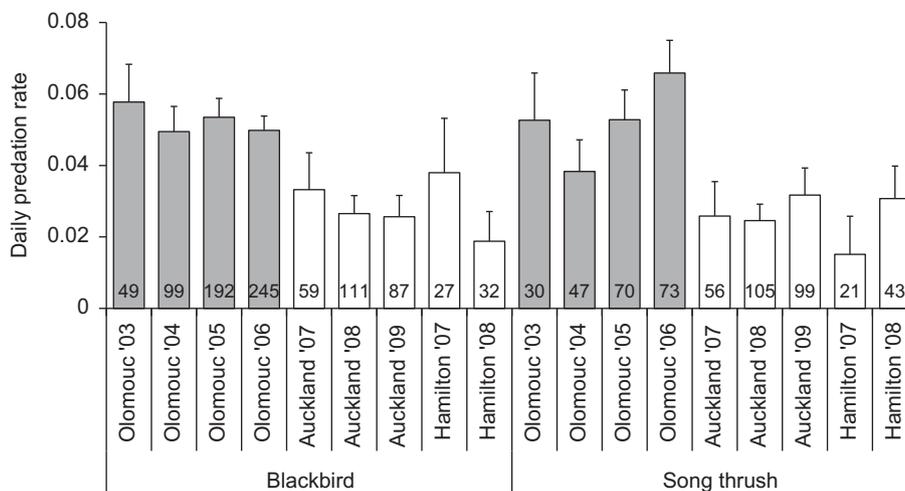


Figure 3. Daily predation rates (estimate + SE) of blackbird and song thrush nests across different urban localities and years in the Czech Republic (grey bars; data from Strachoňová 2008) and in New Zealand (white bars). Sample sizes (number of nests) are given within bars. SE were calculated following Johnson (1979).

densities were consistently spatio-temporally lower in CZ than NZ in both blackbird and song thrush (statistical results were identical for both species: $U = 2.3$, $n_1 = 4$, $n_2 = 4$, exact $p = 0.029$; Fig. 4).

Across the 11 passerine species introduced from the UK to NZ, those with the largest increase in population density in NZ have the smallest decrease in clutch size ($r^2 = 0.54$, $p = 0.02$), and this effect remains (partial $r^2 = 0.50$, $p = 0.02$) when taking the non-significant species specific indices of seasonality (partial $r^2 = 0.01$, $p = 0.72$) into account (Fig. 5).

Temporal changes in clutch size within NZ populations

Mean blackbird clutch size in the Auckland and Hamilton areas during the 1950s and 1960s recorded in OSNZ nest record cards was 3.29 ± 0.09 ($n = 70$) compared with a current mean in this area of 3.15 ± 0.04 ($n = 284$;

Welsch's t -test, $t_{98} = 1.42$, $p = 0.16$). Mean song thrush clutch size in the Auckland and Hamilton areas during the 1950s and 1960s recorded in OSNZ nest record cards was 3.69 ± 0.09 ($n = 54$) compared with a current mean in this area of 3.73 ± 0.04 ($n = 314$; Welsch's t -test, $t_{75} = 0.41$, $p = 0.69$). Multiple regression analyses that took FEG, FEG² and area into account confirmed that there was no significant change in either blackbird or song thrush clutch size within the Auckland and Hamilton areas since the 1950s (blackbird: year $F_{1,80} = 1.99$, $p = 0.16$; year² $F_{1,79} = 0.37$, $p = 0.55$; song thrush: year $F_{1,67} = 0.23$, $p = 0.63$; year² $F_{1,66} = 0.49$, $p = 0.49$).

Discussion

Blackbirds and song thrush laid smaller clutches in New Zealand than at equivalent latitudes in the northern hemisphere. These reductions in clutch size appear to have

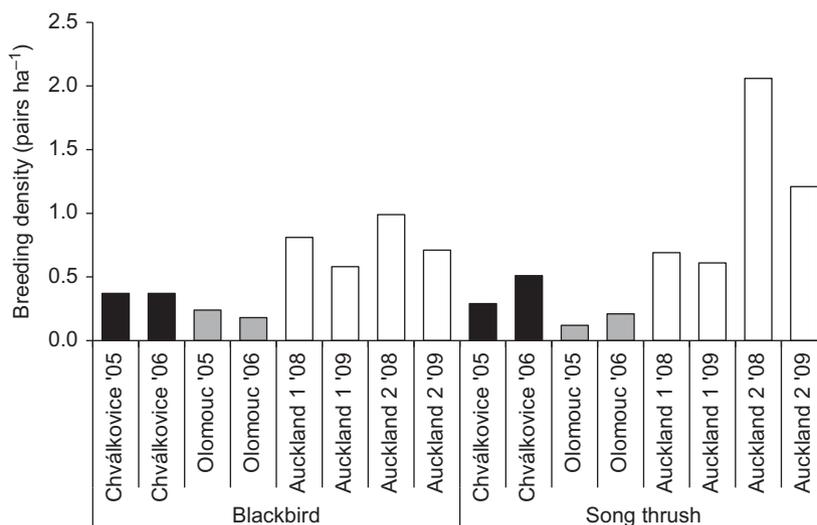


Figure 4. Breeding density estimates (pairs ha⁻¹) for blackbirds and song thrush across years and spatial replicates in the Czech Republic in sub-urban (black bars) and urban sites (grey bars) and New Zealand (white bars). Auckland 1 = Botanic Gardens, Auckland 2 = Western Springs. See Methods for details.

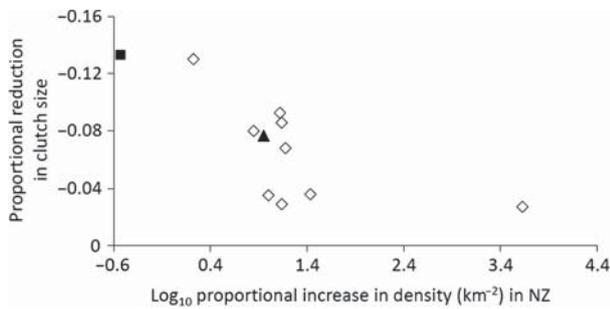


Figure 5. The proportional reduction in clutch size of 11 passerines introduced from the United Kingdom (UK) to New Zealand (NZ) is smallest in species with the greatest increase in population density in NZ relative to the UK. The blackbird and song thrush are indicated respectively by the solid square and triangle. Density data are from MacLeod et al. (2009), clutch size data and seasonality indices are from Evans et al. (2005).

occurred within one hundred years of the introductions of these species from the UK to NZ and, given the typical lifespan of 2–3 yr in both species (Robinson 2005), must have occurred within considerably less than one hundred generations. This suggests a rapid response to novel environmental conditions, although it remains unclear what the relative contributions of genetic traits and phenotypic plasticity may have been. Total reproductive investment per clutch is now lower in the southern hemisphere as we found no evidence for a compensatory increase in egg size in NZ blackbirds, and NZ song thrush in fact laid significantly smaller eggs than those in CZ. This pattern contrasts with the widely documented trade-off between investment in offspring number and investment in individual offspring (Hauber 2003), which predicts that reduced clutches in the southern hemisphere will be associated with larger egg sizes (Roff 1992). Egg size is ultimately constrained by female body size and geographic gradients in body size, such as Bergman's rule, can influence the direction of the association between clutch size and egg size at different spatial scales (Horak et al. 1995, Encabo et al. 2002). Whilst the mechanisms that break-down the trade-off between the predicted clutch size and egg size trade-offs in our focal populations remain unknown, it is notable that NZ adult blackbirds and song thrush are smaller than their ancestral source populations in a number of biometrics, including measures of skeletal size (Debruyne 2008). It is thus possible that reduced female body size contributes to the smaller egg size in the southern hemisphere. Mechanisms that reduce reproductive investment with regard to clutch size, such as reduced per capita resource availability due to reduced seasonality (Ashmole 1963), could also limit investment in individual offspring and further promote smaller eggs in NZ.

Blackbirds and song thrush exhibited relaxation of seasonal clutch size trends in the southern hemisphere, and this relaxation was more marked in blackbirds which is the species that exhibited the larger reduction in clutch size in the southern hemisphere (reduced by one egg compared to 0.7 of an egg in the song thrush). This association between the magnitude of reduced seasonality and reduced clutch size is compatible with Ashmole's hypothesis in that

reduced seasonality would promote smaller clutches in the southern hemisphere. However, a previous analysis of 11 passerines introduced from the UK to NZ found that the magnitude of divergence in seasonal clutch size patterns was not associated with the magnitude to which clutch size decreased in NZ, suggesting that Ashmole's hypothesis was not a general driver of smaller clutches in NZ (Evans et al. 2005). The novel interspecific analysis that we report here confirms that this is also the case when taking into account the changes in species' breeding population densities between the two regions.

One of the most prominent alternative hypotheses for spatial variation in clutch size is the nest predation hypothesis, which predicts greater nest predation rates in regions with smaller clutches (Skutch 1949). In contrast to its predictions we found that nest predation rates were consistently lower in NZ across years, localities and study species. It thus seems highly unlikely that higher nest predation rates are driving the reduced clutch sizes in NZ, especially as nest predation rates in New Zealand were lower in previous decades than is currently the case (Remeš et al. 2012b).

Both blackbird and song thrush population densities in our NZ study localities were more than twice those at sites at equivalent northern latitudes. These higher southern hemisphere densities could contribute to reduced southern hemisphere clutch sizes through density dependence effects. These patterns confirm previous work reporting higher song thrush and blackbird population densities in NZ than Europe, together with higher densities in most of the passerine species that have been introduced from Europe to NZ (MacLeod et al. 2009). However, we find that the species with the largest increase in population density in NZ have the smallest decrease in clutch size, and so the breeding density hypothesis also cannot provide a general explanation for smaller clutch sizes in NZ.

Spatial patterns in clutch size variation are one of the most frequently documented trends in avian life history traits. We find that clutch sizes are reduced in the southern hemisphere, compared to those at equivalent northern latitudes, even when focusing on avian populations in sites containing substantial proportions of urban development. Urbanisation is widely considered to homogenise species assemblages and their life history traits (Crocì et al. 2008, Evans et al. 2011), and can alter ecological variables at other, large scale spatial patterns, such as latitudinal gradients in species richness and species–energy relationships (Evans et al. 2009c, Pautasso et al. 2011). It is perhaps therefore surprising that urban development did not alter the nature of large scale intraspecific spatial patterns in avian clutch size in our dataset, since we found no evidence that urban and sub-urban populations in the CZ differed in their clutch size.

We provide evidence that, within our focal avian study system, smaller southern clutches are not associated with one of the frequently proposed drivers of such patterns, i.e. increased nest predation rates. Southern blackbird and song thrush populations did occur at higher population densities and experienced reduced seasonality compared to equivalent northern populations, patterns that are compatible with Ashmole's seasonality and the breeding density hypotheses for smaller clutch sizes in the southern hemisphere. Despite

this, there is no evidence that these hypotheses generally drive the reductions in clutch size observed across a larger suite of bird species introduced to New Zealand. Reduced seasonality is, however, associated with milder winters that could promote relatively higher population densities and greater longevity in southern populations. In addition, the lower nest predation rates that we document could also promote greater longevity (in particular, for incubating females) and, thus, higher population densities. Other factors, such as reduced abundance and diversity of aerial predators in NZ (Marchant and Higgins 1993, Bell and Lawrence 2009), could also contribute to higher adult survival rates. Reduced clutch sizes in the southern hemisphere might result from the trade-off between reproductive investment and longevity (Roff 1992), but further tests are required to distinguish and test the predictions of this adult-survival hypothesis from its alternatives.

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Supplementary material (Appendix E7927 at < www.oikosoffice.lu.se/appendix >). Appendix 1.