Food-supplementing parents reduces their sons' song repertoire size

Liana Zanette[1],*, Michael Clinchy[2] and Ha-Cheol Sung[1]

[1]*Department of Biology, University of Western Ontario, London, Ontario N6A 5B7, Canada*
[2]*Department of Biology, University of Victoria, Victoria, British Columbia V8W 3N5, Canada*

Food-supplemented parents typically produce more offspring, as numerous experiments on vertebrate populations have shown. 'Propagule' (egg or neonate) size and parental care may also be affected, with implications concerning the adult quality of offspring, although few experiments have addressed whether food-supplementing one generation affects adult quality in the next. We conducted a food supplementation experiment on song sparrows (*Melospiza melodia*) and tested whether song repertoire size, a demonstrated indicator of male quality, differed between the adult sons of fed (food-supplemented) and unfed (non-food-supplemented) parents. Counterintuitively, fed parents produced sons with smaller adult song repertoires, who may thus be expected to contribute fewer offspring, and fewer grand-offspring, to the population. Fed and unfed parents invested equally in the total biomass of their clutches and broods, and average nestling condition was comparable, but because fed parents produced more offspring, average egg and nestling sizes were reduced. Fed and unfed parents apportioned care differently within their broods, and we suggest compensatory growth of offspring emerging from light eggs, or egg size itself, may have affected adult repertoire size. Conceivably, the conservation benefits of food-supplementing populations could attenuate over time if fed parents produce offspring of poorer quality than themselves.

Keywords: compensatory growth; egg size; intergenerational effects; maternal effects; offspring quality; propagule size

1. INTRODUCTION

Intergenerational effects arise when a parent's actions or circumstances affect the reproductive performance or adult survivorship of its offspring and possibly later descendants (Plaistow *et al.* 2006). When this is the case, the reproduction and survival of individuals reflect not only current environmental conditions, but also the environmental conditions experienced by their progenitors (reviews in Mousseau & Fox 1998; Lindström 1999; Metcalfe & Monaghan 2001), which can significantly affect population dynamics (Lindström 1999; Beckerman *et al.* 2002; Benton *et al.* 2005). Population models incorporating intergenerational effects typically assume there is a positive relationship between the parental environment and offspring quality (Ginsburg & Taneyhill 1994). However, several studies have shown that, in order to produce more offspring or lessen the burden on themselves, parents may produce poorer quality offspring when conditions are favourable because it is precisely when conditions are favourable that offspring quality is least likely to affect recruitment (Bernardo 1996; Sinervo *et al.* 2000; Plaistow *et al.* 2006; Russell *et al.* 2007).

Increased food availability clearly constitutes a favourable environmental circumstance. Numerous food supplementation experiments have shown that vertebrate populations normally increase in response to added food, in part because parents produce more offspring (reviews in Boutin 1990; Newton 1998; see also Zanette *et al.* 2006*a*,*b*; Schoech *et al.* 2008). Lindström (1999) argued

that over 100 years of laboratory work on vertebrate development unambiguously demonstrates that nutritional effects on 'propagule' (egg or neonate; Bernardo 1996) size and parental care can profoundly affect the morphology, immunocompetence and physiology of adult offspring. Consequently, it would be very surprising if food supplementation did not have intergenerational consequences. The intergenerational effects of such manipulations, however, have rarely been investigated (Lindström 1999), due in part to the fact that few such studies have examined effects over more than one year (Boutin 1990; Newton 1998).

Song complexity is a potential measure of intergenerational effects in songbirds. Song complexity is often positively correlated with survival and reproduction (e.g. Buchanan *et al.* 1999; Doutrelant *et al.* 2000), and thus generally reflects an adult male's quality. Being indelibly affected by early rearing conditions, song complexity ought to reflect intergenerational effects. During the early months of life, the brain nuclei associated with song learning grow rapidly and appear particularly sensitive to food intake rate (Nowicki *et al.* 1998, 2002). MacDonald *et al.* (2006), for example, showed that HVC (song control nuclei) volume was greater in song sparrow (*Melospiza melodia*) nestlings fed *ad libitum* compared with a food-restricted group (HVC volume being correlated with song repertoire size in the field; Pfaff *et al.* 2007). Female song sparrows prefer large song repertoires (Reid *et al.* 2004), and repertoire size is highly predictive of lifetime reproductive success (Reid *et al.* 2005). Thus, one might expect sons reared by food-supplemented parents to be better fed, leading to their

* Author for correspondence (lzanette@uwo.ca).

2855

having larger song nuclei and a resulting larger song repertoire in adulthood, with positive effects on their reproductive performance.

An intergenerational effect of food supplementation on song complexity would be demonstrated as convincingly by a decrease as by an increase in the song repertoire size of sons. A growing number of studies suggest temporal variation in food intake may be as critical to development as the mean food intake rate. In the case of 'compensatory growth', whereby growth is accelerated following an earlier deficit, there may be lasting negative effects (Metcalfe & Monaghan 2001). Fisher *et al.* (2006), for example, showed that cognitive development was permanently impaired in zebra finches (*Taeniopygia guttata*) that experienced food restriction in the first 20 days post-hatch and were thereafter fed *ad libitum*. If food-supplemented mothers lay more, lighter eggs (Sinervo *et al.* 2000; Russell *et al.* 2007), this initial deficit could thus have negative consequences even if food-supplemented parents feed their young *ad libitum* (Wagner & Williams 2007). In this case, the sons of food-supplemented parents could, counterintuitively, end up having smaller song repertoires in adulthood. Laying more eggs could furthermore exaggerate the effects of compensatory growth, because laying a larger clutch may commonly create developmental asymmetries within the brood due to the increase in hatching asynchrony (Sockman *et al.* 2006). Recent work by Garamszegi *et al.* (2007) suggests egg composition or size could also have a dramatic effect on cognitive development affecting performance in adulthood, independent of the quality of parental care provided post-hatch.

We conducted a food supplementation experiment on song sparrows over three consecutive breeding seasons. Food-supplemented (fed) parents fledged more young over a season (Zanette *et al.* 2006a) partly because fed mothers laid more eggs (Zanette *et al.* 2006b), and partly because fed parents suffered both less nest predation and less partial brood loss (Zanette *et al.* 2006a). Fed parents were less physiologically stressed (Clinchy *et al.* 2004) and spent more time attending their nests, which reduced their vulnerability to nest predation (Duncan-Rastogi *et al.* 2006). Nest predation was nonetheless the principal determinant of annual reproductive success (Zanette *et al.* 2006a), and food supplementation and nest predation together had combined effects on egg production (Zanette *et al.* 2006b). In this paper, we test for potential intergenerational effects of our food supplementation experiment by looking at the adult song repertoire sizes of males reared by fed and unfed (non-food-supplemented) parents.

2. MATERIAL AND METHODS

(a) *Food supplementation*
Our study was conducted in the context of the same experiment described in Zanette *et al.* (2006a,b). We monitored song sparrows resident in Victoria, British Columbia, Canada, over three consecutive breeding seasons. On fed territories, supplementary feed consisting of equal proportions of millet and pellets high in fat and protein (45%) was provided *ad libitum* throughout the breeding season (for details see Zanette *et al.* 2006a,b).

(b) *Song repertoire size*
We recorded songs from male recruits the year following each year in which food was added. We did not survey for all male recruits but instead took advantage of instances when male territory owners were identified in the course of our work to establish the effects of food supplementation on female annual reproductive success (Zanette *et al.* 2006a,b). Recruits ringed as nestlings were identified by their colour combinations.

We located 444 nests containing 1510 eggs. By day 6 of brood rearing this number of potential young had been reduced to 500, of which only 377 fledged. By the year following fledging, 24 out of the likely 250 (500 divided by 2 sexes) males ringed as nestlings had become local territory owners whose repertoires we could record (9 from fed and 15 from unfed territories; all from different parents). This ratio of recruits (9 : 15) is not significantly different from the proportion of young fledged from each type of territory (158 : 214; Fisher's exact test $p = 0.676$), suggesting there was no treatment difference in local recruitment, although rigorously testing for an effect on survival from fledging to recruitment would require radio-tracking (Krebs 1999, p. 123), which was not done.

Song sparrow repertoires consist of several (6–14 in this study) highly stereotyped song types, each individual singing a fixed number (Cassidy 1993; Nordby *et al.* 2002). Songs were recorded using a Marantz PMD222 portable cassette recorder and Sennheiser ME66 microphone, and then digitized and classified into song types by visual inspection of their spectrograms using SYRINX (www.syrinxpc.com; following Cassidy 1993; Reid *et al.* 2005).

(c) *Eggs and nestlings*
Eggs were weighed to 0.05 g. On day 6 post-hatch, nestlings were ringed, weighed to 0.1 g and had their tarsi measured to 0.1 mm. Blood was collected to assess physiological condition in the final year of food supplementation. Nutritional stress has been shown to have significant impacts on corticosterone, plasma glucose and haematocrit levels (e.g. Clinchy *et al.* 2004; Pravosudov & Kitaysky 2006), and Kempster *et al.* (2007) showed that differences in food-provisioning rate significantly affected each of these in a hand-rearing experiment on song sparrow nestlings in the laboratory. Plasma glucose was measured immediately after blood extraction (AccuSoft Advantage blood glucose monitor). The remaining blood was centrifuged, measured for haematocrit, and plasma was drawn off and frozen at $-20°C$ until processing. Corticosterone was measured in samples of 5–21 µl of plasma via radioimmunoassay (Wingfield *et al.* 1992).

(d) *Statistical analyses*
We compared the sizes of the song repertoires sung by the adult sons of fed and unfed parents using a one-way ANOVA.

To test the effects of food supplementation on propagule size, we began by addressing whether fed and unfed mothers differed in their total investment in egg biomass and then tested for differences in mean egg mass per clutch using one-way ANOVAs. To address whether fed and unfed parents differed in their total investment in nestling biomass, we first examined the cumulative mass of nestlings per brood and then tested for differences in mean nestling mass per brood, again using one-way ANOVAs. Finally, we tested for treatment effects on nestling structural size by conducting a one-way ANOVA on mean nestling tarsus length per brood.

To test the effects of food supplementation on the condition of free-living song sparrow nestlings, we evaluated the same four indices that Kempster *et al.* (2007) showed were sensitive to food-provisioning rate in the laboratory, namely (i) corticosterone, (ii) plasma glucose and (iii) haematocrit levels and (iv) mass corrected for body size (i.e. mass/tarsus^3); all of these were compared between our two treatments using one-way ANOVAs.

To assess whether laying more eggs (as fed mothers did; Zanette *et al.* 2006*b*) increased asymmetries within the clutch or brood (Sockman *et al.* 2006), we used one-way ANOVAs to compare the within-nest variance in egg mass, and in nestling mass, between our two treatments.

Next, we looked specifically at the 24 recruits whose songs we recorded. We could never identify which egg any given nestling hatched from but do know the mass of our recruits as day 6 nestlings, the mass of their nest-mates and the mean egg mass of the 24 clutches from which they hatched. To assess the relative development of recruits, we conducted two one-way repeated-measures ANOVAs testing for between-treatment differences in (i) the recruit's day 6 nestling mass versus the mean mass of its nest-mates, and (ii) the recruit's growth to day 6 versus the mean growth of its nest-mates. We estimated growth to day 6 by assuming the mass of the egg the recruit hatched from was comparable with that of all others in the clutch from which it hatched (which is not unreasonable, given the results of our analysis of the within-nest variance in egg mass; see below). Finally, we used Spearman rank correlations to evaluate the relationships between a recruit's repertoire size and its day 6 nestling size, as well as the mean egg mass of the clutch from which it hatched. Because roughly one-third of all nests were found after hatch (Zanette *et al.* 2006*b*), the sample sizes in both analyses regarding our recruits and egg mass are smaller than those involving only nestling size. Similarly, because corticosterone, plasma glucose and haematocrit were not assayed in all nestlings, it eventuated that too few recruits had been assayed to permit meaningful analyses of these measures of nestling condition.

All data were tested for normality and homogeneity of error variances prior to conducting parametric tests. In the Results, we report only values for statistical terms that were significant or where non-significant terms are relevant to the Discussion. The descriptive statistics reported are means ±s.e.

3. RESULTS

Food supplementation evidently had an intergenerational effect since the adult sons of fed parents had significantly different song repertoire sizes than the adult sons of unfed parents. Counterintuitively, we found that the sons of fed parents had smaller repertoires (figure 1*a*; $F_{1,22}=5.4$, $p=0.030$).

Considering food effects on propagule size, total clutch mass did not differ between fed and unfed mothers (fed, 10.1 ± 0.23 g; unfed, 10.1 ± 0.22; $F_{1,189}=0.4$, $p=0.84$), indicating that each invested equally in total egg biomass per nest. Where fed and unfed mothers did differ was in how this biomass was distributed, since fed mothers distributed it among more eggs (Zanette *et al.* 2006*b*), with the result that the mean mass of each egg laid by fed mothers was significantly lighter than that of eggs laid by unfed mothers (figure 1*b*; $F_{1,190}=5.8$, $p=0.017$). Similarly, total day 6 brood mass did not differ between fed and unfed parents (fed, 41.8 ± 2.15 g; unfed, 41.5 ± 2.16;
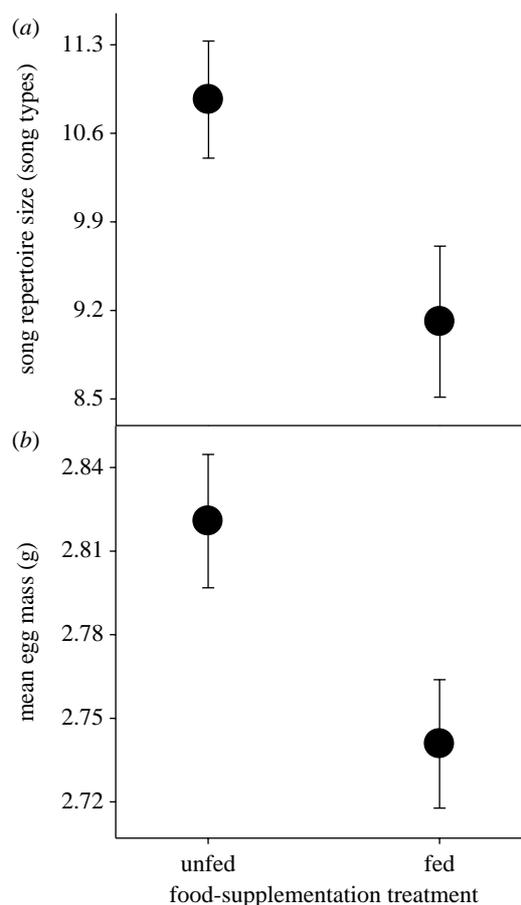

Figure 1. Effects of food-supplementing parents on (*a*) the adult song repertoire size of their sons and (*b*) mean egg mass. 'Fed' identifies food-supplemented parents, whereas 'unfed' refers to non-food-supplemented parents. Values are means ±s.e.

$F_{1,184}=0.0$, $p=0.88$), indicating that fed and unfed parents each invested equally in the total nestling biomass produced per nest. Again, where they did differ was in the number of nestlings (Zanette *et al.* 2006*a*), with the result that the mean mass of each day 6 nestling in nests of fed parents was significantly lighter than that of nestlings in nests of unfed parents (fed, 15.5 g ± 0.30 g; unfed, 16.4 ± 0.30; $F_{1,183}=7.8$, $p=0.006$). Fed nestlings were on average also structurally smaller, the mean tarsus length of fed nestlings (18.04 ± 0.14 mm) being shorter than that of unfed nestlings (18.49 ± 0.16; $F_{1,183}=4.4$, $p=0.038$).

Fed and unfed parents appeared to have provided comparable care to their broods, on average, since none of the four indices of condition we evaluated differed significantly between fed and unfed nestlings (corticosterone: fed, 12.6 ± 1.42 ng ml^{-1}; unfed, 13.7 ± 1.39; $F_{1,25}=0.3$, $p=0.57$; plasma glucose: fed, 21.2 ± 0.35 mg dl^{-1}; unfed, 22.0 ± 0.29; $F_{1,17}=3.4$, $p=0.08$; haematocrit: fed, 47.9 ± 0.58; unfed, 47.8 ± 0.58; $F_{1,25}=0.0$, $p=0.93$; mass/tarsus^3: fed, 2.6 ± 0.06 × 10^{-3}; unfed, 2.5 ± 0.07; $F_{1,185}=0.8$, $p=0.36$).

Although evidently providing comparable care to the brood as a whole, fed parents appeared to apportion their care within the brood differently than unfed parents since we found evidence of greater developmental asymmetry within fed broods. Whereas the eggs of fed and unfed mothers were equally variable (fed, 0.015 ± 0.002 g; unfed, 0.018 ± 0.002; $F_{1,190}=0.7$, $p=0.41$), by day 6 of
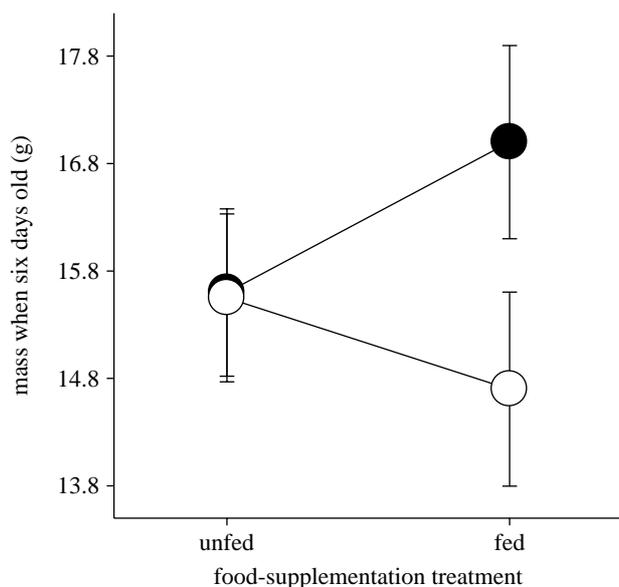
Figure 2. Mass as day 6 nestlings of sons whose songs we later recorded (recruits, filled circles) when compared with their nest-mates (open circles) in the broods of fed (food-supplemented) and unfed (non-food-supplemented) parents. Values are means ±s.e.

brood rearing the nestlings of fed parents were more than twice as variable in mass as those of unfed parents (fed, 5.0 ± 0.52 g; unfed, 2.2 ± 0.60; $F_{1,147} = 12.3$, $p < 0.001$).

That there was greater variation in nestling mass in fed broods was clearly evident when we looked specifically at the nests from which our recruits fledged (figure 2). Recruits that fledged from fed nests were much heavier than their nest-mates, whereas there was virtually no difference in mass between recruits and their nest-mates in unfed nests, leading to a significant food treatment by nestling identity interaction (figure 2; $F_{1,12} = 5.8$, $p = 0.033$). Consistent with the greater mass of fed recruits being a function of compensatory growth following hatching from a lighter egg, recruits from fed nests evidently gained mass faster than their nest-mates (recruit, 2.4 ± 0.14 g day^{-1}; nest-mates, 2.0 ± 0.15), whereas recruits and their nest-mates in unfed nests gained mass at roughly the same rate (recruit, 2.2 ± 0.13; nest-mates, 2.3 ± 0.14), again leading to a significant food treatment by nestling identity interaction ($F_{1,9} = 6.0$, $p = 0.037$). Also consistent with compensatory growth entailing achieving the same eventual size, there was no significant difference in mass between fed and unfed recruits (figure 2; $F_{1,18} = 3.0$, $p = 0.10$). Not surprisingly, since fed and unfed recruits did not differ in mass by day 6 of brood rearing, song repertoire size was not significantly correlated with day 6 nestling size; neither was it significantly correlated with the mean egg mass of the clutch from which the recruit hatched.

4. DISCUSSION

Food-supplementing parents had an intergenerational effect since it significantly affected the size of the song repertoires sung by their adult sons (figure 1a). Counter-intuitively, the sons of fed parents had smaller repertoires. Fed and unfed parents invested equally in the total biomass of eggs and nestlings produced per nest.

Fed parents divided this biomass among more eggs and nestlings, with the result that mean egg mass (figure 1b), mean nestling mass and mean nestling tarsus length were all significantly smaller than for unfed parents. Fed and unfed parents provided comparable care to their broods as a whole, since there were no significant treatment effects on the four indices of nestling condition we evaluated, which earlier laboratory work showed were sensitive to differences in food-provisioning rate. Fed and unfed parents apparently apportioned care differently within their broods, since nestling mass was significantly more variable in fed broods, whereas there was no treatment effect on variation in egg mass. Treatment effects on nestling variability were evident in the broods of the recruits whose songs we later recorded (figure 2), since recruits from fed nests were heavier and grew faster than their nest-mates, whereas this was not so in unfed nests. Fed recruits evidently experienced compensatory growth after hatching from a lighter egg (figure 1b), since by day 6 of brood-rearing they were not significantly different in size from unfed recruits (figure 2) and this compensatory growth may explain their smaller song repertoire sizes (figure 1a).

Reid *et al.* (2005) recently analysed a 20-year dataset and reported that song sparrow males with larger song repertoires recruited both more independent offspring and more grand-offspring. Consequently, the reproductive performance of sons can be inferred to have been affected by the effect of parental food supplementation on their song repertoire sizes, reported here. Taken together, our results and Reid *et al.*'s (2005) point to food supplementation potentially having effects on vertebrate populations that extend not only one but two generations into the future.

Parents would presumably do best by increasing both offspring quantity *and* quality. The fact that fed parents increased the former but not the latter suggests they were constrained from doing so. Egg production and brood rearing are both costly activities (Monaghan & Nager 1997; Monaghan *et al.* 1998). In our system, the fate of most nests (58%; Zanette *et al.* 2006a) was to be eaten by a predator, and the rapidity of renesting was a significant determinant of annual reproductive success (Zanette *et al.* 2006a,b). 'Over-investing' in any given nest could thus reduce annual reproductive success if this delays renesting (Slagsvold 1982, 1984), which could explain why fed and unfed mothers both invested equally in total egg and brood biomass, per nest.

The high risk of nest predation may also explain the greater asymmetry within fed broods (figure 2). Just as over-investing resources should be avoided where the risk of nest predation is high, so should over-investing time (Slagsvold 1982). Laying a larger clutch, as fed mothers did, takes more time. Sockman *et al.* (2006) suggested that birds that lay larger clutches may avoid extending the total time between laying and fledging by shortening the period between the onset of laying and onset of incubation (e.g. by initiating incubation on the third-to-last laid egg rather than the second-to-last laid egg). An earlier onset of incubation is almost certain to increase hatching asynchrony, because earlier laid eggs will begin to be incubated sooner than later ones (Sockman *et al.* 2006). Increased hatching asynchrony may then be expected to 'automatically' increase developmental asymmetry within the brood

(since some nestlings are older), which may be exaggerated if parents provide more care to larger nestlings (Forbes *et al.* 2002; Sockman *et al.* 2006). In a separate experiment on song sparrows in which we added 2-day-old nestlings to just-hatched 'host' nests, the added nestlings demonstrated increased growth and the host nestlings reduced growth, consistent with parents exaggerating initial asymmetries (R. DeCaire *et al.* 2008, unpublished data), as our results here suggest (figure 2). Several authors have argued that a larger, more asymmetrical brood increases the likelihood that at least one young will fledge (the 'core' nestling) if resources run short, while providing the prospect of fledging more young than otherwise if conditions remain favourable (Forbes *et al.* 2002; Sockman *et al.* 2006).

Laying more, lighter eggs significantly contributed to fed mothers fledging more young (Zanette *et al.* 2006*a*,*b*), and hence presumably producing more recruits (accepting that fed and unfed fledglings were equally likely to recruit; see Material and Methods). Russell *et al.* (2007) reported that fairy-wren (*Malurus cyaneus*) mothers reduce the size of the eggs they lay when conditions are favourable, to lessen the burden on themselves. Sinervo *et al.* (2000) similarly showed that, as song sparrows evidently do, female side-blotched lizards (*Uta stansburiana*) always produce the same clutch mass, but when conditions are favourable (in low-density 'boom' years) they produce more, smaller propagules (eggs). Bernardo (1996) reviewed comparable instances in many other taxa of parents reducing propagule size when conditions are favourable.

Wagner & Williams (2007) recently demonstrated experimentally that compensatory growth after hatching from a lighter egg can have adverse effects on the development of zebra finches. Fisher *et al.* (2006) showed that compensatory growth can adversely affect the development of learning abilities, which could presumably include song learning, and Arnold *et al.* (2007) subsequently showed such effects can stem from a deficit in just the first 15 days post-hatch. Current research thus suggests song learning ability in our fed recruits could have been impaired by accelerated growth during the first 6 days post-hatch (figure 2). Alternatively, hatching from a lighter egg in itself may have affected repertoire size (Garamszegi *et al.* 2007).

Our results suggest the benefits of food supplementation may attenuate over time if food-supplemented parents produce offspring of poorer quality than themselves. Schoech *et al.* (2008) recently reported the findings from a 7-year food supplementation experiment aimed at increasing the reproductive output of US federally threatened Florida scrub-jay (*Aphelocoma coerulescens*) populations. Whereas food supplementation was clearly beneficial, the effect was greatest during the first 2 years and declined thereafter. This decline was not due to changes in density, and Schoech *et al.* (2008) suggested several other mechanisms but did not consider intergenerational effects. Following from Lindström's (1999) arguments, intergenerational consequences of food supplementation are probably commonplace. Consequently, more effort aimed at measuring the intergenerational effects of food supplementation would undoubtedly prove productive, particularly as regards conservation programmes.

REFERENCES

Arnold, K. E., Blount, J. D., Metcalfe, N. B., Orr, K. J., Adam, A., Houston, D. & Monaghan, P. 2007 Sex-specific differences in compensation for poor neonatal nutrition in the zebra finch *Taeniopygia guttata*. *J. Avian Biol.* **38**, 356–366.

Beckerman, A., Benton, T. G., Ranta, E., Kaitala, V. & Lundberg, P. 2002 Population dynamic consequences of delayed life-history effects. *Trends Ecol. Evol.* **17**, 263–269. (doi:10.1016/S0169-5347(02)02469-2)

Benton, T. G., Plaistow, S. J., Beckerman, A. P., Lapsley, C. T. & Littlejohns, S. 2005 Changes in maternal investment in eggs can affect population dynamics. *Proc. R. Soc. B* **272**, 1351–1356. (doi:10.1098/rspb.2005.3081)

Bernardo, J. 1996 The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* 216–236.

Boutin, S. 1990 Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* **68**, 203–220. (doi:10.1139/z90-031)

Buchanan, K. L., Catchpole, C. K., Lewis, J. W. & Lodge, A. 1999 Song as an indicator of parasitism in the sedge warbler. *Anim. Behav.* **57**, 307–314. (doi:10.1006/anbe.1998.0969)

Cassidy, A. L. E. V. 1993 Song variation and learning in island populations of song sparrows. PhD thesis, University of British Columbia, Canada.

Clinchy, M., Zanette, L., Boonstra, R., Wingfield, J. C. & Smith, J. N. M. 2004 Balancing food and predator pressure induces chronic stress in songbirds. *Proc. R. Soc. Lond. B* **271**, 2473–2479. (doi:10.1098/rspb.2004.2913)

Doutrelant, C., Blondel, J., Perret, P. & Lambrechts, M. M. 2000 Blue tit song repertoire size, male quality and interspecific competition. *J. Avian Biol.* **31**, 360–366. (doi:10.1034/j.1600-048X.2000.310312.x)

Duncan-Rastogi, A., Zanette, L. & Clinchy, M. 2006 Food availability affects diurnal nest predation and adult antipredator behaviour in song sparrows, *Melospiza melodia*. *Anim. Behav.* **72**, 933–940. (doi:10.1016/j.anbehav.2006.03.006)

Fisher, M. O., Nager, R. G. & Monaghan, P. 2006 Compensatory growth impairs adult cognitive performance. *PLoS Biol.* **4**, 1462–1466. (doi:10.1371/journal.pbio.0040251)

Forbes, S., Grosshans, R. & Glassey, B. 2002 Multiple incentives for parental optimism and brood reduction in blackbirds. *Ecology* **83**, 2529–2541.

Garamszegi, L. Z., Biard, C., Eens, M., Moller, A. P., Saino, N. & Surai, P. 2007 Maternal effects and the evolution of brain size in birds: overlooked developmental constraints. *Neurosci. Biobehav. Rev.* **31**, 498–515. (doi:10.1016/j.neubiorev.2006.11.008)

Ginsburg, L. R. & Taneyhill, D. T. 1994 Population cycles of forest Lepidoptera: a maternal effect hypothesis. *J. Anim. Ecol.* **63**, 79–92. (doi:10.2307/5585)

Kempster, B., Zanette, L., Longstaffe, F. J., MacDougall-Shackleton, S. A., Wingfield, J. C. & Clinchy, M. 2007

Do stable isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. *Oecologia* **151**, 365–371. (doi:10.1007/s00442-006-0597-7)

Krebs, C. J. 1999 *Ecological methodology*, 2nd edn. Menlo Park, CA: Benjamin Cummings.

Lindström, J. 1999 Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**, 343–348. (doi:10.1016/S0169-5347(99)01639-0)

MacDonald, I. F., Kempster, B., Zanette, L. & MacDougall-Shackleton, S. A. 2006 Nutritional stress impairs development of song-control brain regions in juvenile male and female song sparrows (*Melospiza melodia*). *Proc. R. Soc. B* **273**, 2559–2564. (doi:10.1098/rspb.2006.3547)

Metcalfe, N. B. & Monaghan, P. 2001 Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**, 254–260. (doi:10.1016/S0169-5347(01)02124-3)

Monaghan, P. & Nager, R. G. 1997 Why don't birds lay more eggs? *Trends Ecol. Evol.* **12**, 270–274. (doi:10.1016/S0169-5347(97)01094-X)

Monaghan, P., Nager, R. G. & Houston, D. C. 1998 The price of eggs: increased egg production reduces offspring rearing capacity. *Proc. R. Soc. Lond. B* **265**, 1731–1735. (doi:10.1098/rspb.1998.0495)

Mousseau, T. A. & Fox, C. W. 1998 The adaptive significance of maternal effects. *Trends Ecol. Evol.* **13**, 403–407. (doi:10.1016/S0169-5347(98)01472-4)

Newton, I. 1998 *Population limitation in birds*. London, UK: Academic Press.

Nordby, J. C., Campbell, S. E. & Beecher, M. D. 2002 Adult song sparrows do not alter their song repertoires. *Ethology* **108**, 39–50. (doi:10.1046/j.1439-0310.2002.00752.x)

Nowicki, S., Peters, S. & Podos, J. 1998 Song learning, early nutrition and sexual selection in songbirds. *Am. Zool.* **38**, 179–190.

Nowicki, S., Searcy, W. A. & Peters, S. 2002 Brain development, song learning and mate choice in birds: a review and experimental test of the 'nutritional stress hypothesis'. *J. Comp. Physiol. A* **188**, 1003–1014. (doi:10.1007/s00359-002-0361-3)

Pfaff, J. A., Zanette, L., MacDougall-Shackleton, S. A. & MacDougall-Shackleton, E. A. 2007 Song repertoire size varies with HVC volume and is indicative of male quality in song sparrows (*Melospiza melodia*). *Proc. R. Soc. B* **274**, 2035–2040. (doi:10.1098/rspb.2007.0170)

Plaistow, S. J., Lapsley, C. T. & Benton, T. G. 2006 Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. *Am. Nat.* **167**, 206–215. (doi:10.1086/499380)

Pravosudov, V. V. & Kitaysky, A. S. 2006 Effects of nutritional restriction during post-hatching development on adreno-cortical function in western scrub-jays (*Aphelocoma californica*). *Gen. Comp. Endocrinol.* **145**, 25–31. (doi:10.1016/j.ygcen.2005.06.011)

Reid, J. M., Arcese, P., Cassidy, A. L. E. V., Hiebert, S. M., Smith, J. N. M., Stoddard, P. K., Marr, A. B. & Keller, L. F. 2004 Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia. Anim. Behav.* **68**, 1055–1063. (doi:10.1016/j.anbehav.2004.07.003)

Reid, J. M., Arcese, P., Cassidy, A. L. E. V., Hiebert, S. L., Smith, J. N. M., Stoddard, P. K., Marr, A. B. & Keller, L. F. 2005 Fitness correlates of song repertoire size in free-living song sparrows (*Melospiza melodia*). *Am. Nat.* **165**, 299–310. (doi:10.1086/428299)

Russell, A. F., Langmore, N. E., Cockburn, A., Astheimer, L. B. & Kilner, R. M. 2007 Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science* **317**, 941–944. (doi:10.1126/science.1146037)

Schoech, S. J., Bridge, E. S., Boughton, R. K., Reynolds, J., Atwell, J. W. & Bowman, R. 2008 Food supplementation: a tool to increase reproductive output? A case study in the threatened Florida Scrub-Jay. *Biol. Conserv.* **141**, 162–173. (doi:10.1016/j.biocon.2007.09.009)

Sinervo, B., Svensson, E. & Comendant, T. 2000 Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**, 985–988. (doi:10.1038/35023149)

Slagsvold, T. 1982 Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* **54**, 159–169. (doi:10.1007/BF00378388)

Slagsvold, T. 1984 Clutch size variation in birds in relation to nest predation: on the cost of reproduction. *J. Anim. Ecol.* **53**, 945–953. (doi:10.2307/4669)

Sockman, K. W., Sharp, P. J. & Schwabl, H. 2006 Orchestration of avian reproductive effort: an integration of the ultimate and proximate bases for flexibility in clutch size, incubation behaviour, and yolk androgen deposition. *Biol. Rev.* **81**, 629–666. (doi:10.1017/S1464793106007147)

Wagner, E. C. & Williams, T. D. 2007 Experimental (antiestrogen-mediated) reduction in egg size negatively affects offspring growth and survival. *Physiol. Biochem. Zool.* **80**, 293–305. (doi:10.1086/512586)

Wingfield, J. C., Vleck, C. M. & Moore, M. C. 1992 Seasonal changes in the adrenocotriocal response to stress in birds of the Sonoran Desert. *J. Exp. Zool.* **264**, 419–428. (doi:10.1002/jez.1402640407)

Zanette, L., Clinchy, M. & Smith, J. N. M. 2006a Combined food and predator effects on songbird nest survival and annual reproductive success: results from a bi-factorial experiment. *Oecologia* **147**, 632–640. (doi:10.1007/s00442-005-0330-y)

Zanette, L., Clinchy, M. & Smith, J. N. M. 2006b Food and predators affect egg production in song sparrows. *Ecology* **87**, 2459–2467. (doi:10.1890/0012-9658(2006)87[2459:FAPAEP]2.0.CO;2)