

# Super size me: an experimental test of the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European Starlings

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## Summary

1. Lipids are a major source of energy storage in vertebrates. A cross-fostering brood manipulation was conducted to assess the role of rearing environment *vs* common origin on lipid stores.

2. Rearing conditions, especially nest temperatures, explained more variation in lipid levels than did nest of origin. As nest temperatures increased, lipid levels in nestlings also increased. Larger individuals, reflected in both wet and lean dry mass, tended to store more lipids.

3. There was no trade-off between structural growth and lipid stores. However, body mass growth was linked with lipids. In addition, nestlings raised early in the season tended to maintain greater lipid levels, suggesting a role of individual quality.

4. Because the assessment of lipid stores is difficult, it is common to use residual body mass (RBM) as a surrogate. Multiple methods of calculating RBM were compared with actual lipid mass in nestling European Starlings (*Sturnus vulgaris*). RBM was correlated with lipid levels ( $R^2$  up to 0.66); models calculated using ordinary least squares regression predicted lipid stores better than reduced major axis regression.

5. These results indicate that RBM can be a non-invasive predictor of lipid levels in nestling birds and that studies examining variation in physiological stores should consider development conditions and individual quality.

*Key-words:* Body condition, individual variation, nest temperatures, offspring quality, *Sturnus vulgaris*

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## Introduction

Physiological stores have been found to be a critical influence on fitness in many animals, such as mammals (Wade & Schneider 1992; Schneider 2004), lizards (Svensson *et al.* 2002), amphipods (Glazier 2000) and birds (Smith & Moore 2003). One common store in vertebrates is lipids, hydrophobic molecules commonly stored in vertebrates as fats and oil (Griminger 1986). They are the major form of energy storage in birds, and the first stores mobilized in times of energy need (Blem 1990). Empirical studies examining lipid storage have found that variation in lipid levels can greatly influence migration strategies (Pierce & McWilliams 2004), overwinter survival (Rogers & Reed 2003) and clutch size (Christians 2000), among other factors. Lipids, as

resource stores, would be expected to fluctuate with resource availability and demands and thus should be quite sensitive to environmental conditions, while at the same time being influenced by parental quality.

To investigate factors affecting variation in lipid stores among offspring, a split-nest cross-fostering brood manipulation was conducted to compare the role of common origin (genetic relatedness) and common rearing environment. Previous cross-fostering studies have found that body condition has both genetic and environmental components, but with more variance explained by environmental conditions (Smith & Wettermark 1995; Merilä, Przybylo & Sheldon 1999; Jensen *et al.* 2003); if lipid stores are indeed reflected in body condition, then there should be a stronger environmental component to lipid stores as well. To help minimize unexplained environmental variance, nest temperatures were measured, as body condition can be sensitive to temperatures during development (Visser 1998; Massemin *et al.* 2002).

The trade-off between growth rate and lipid levels was also assessed, as nestlings are under conflicting pressure

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both to increase size and to fledge as early as possible (Hochachka & Smith 1991). In many species there is strong selection on rapid growth in order to fledge as early as possible (Winkler & Allen 1996; Monrós, Belda & Barba 2002), while at the same time larger fledglings have a higher probability of survival (Tinbergen & Boerlijst 1990; Hochachka & Smith 1991). I tested whether individuals with high growth rates have lower lipid reserves or if some individuals gain both body size and lipid stores concurrently. Larger individuals do not always have the highest lipid stores (Thompson, Flux & Tetzlaff 1993), and the overall importance of body mass varies depending on the time of the breeding season, with earlier heavier birds having the highest probability of survival (Thompson & Flux 1991; Both, Visser & Verboven 1999). Indeed, previous work conducted at the same research site as this study found that large body mass enhanced survival early in the breeding season (Thompson & Flux 1991); the causal mechanism for this pattern is unknown. Accordingly, how timing of breeding influences lipid stores was explicitly tested as a possible explanation for why earlier-fledged nestlings might have higher recruitment rates.

Lastly, assessing lipid stores normally requires collecting individuals or using techniques logistically difficult enough to preclude universal use. Consequently, it is common to use a surrogate predictor of 'body condition', normally residual body mass (hereafter RBM), which is calculated from a regression of body mass vs a measure of structural size (Brown 1996). Positive residuals are assumed to represent excess mass relative to body size and therefore more physiological stores. RBM has been used to assess many questions in ecology, evolution and behaviour, especially in birds, including but not limited to variation in offspring quality (Altwegg, Ringsby & Saether 2000), survival (Brown & Roth 2004), life-history trade-offs (Sedinger, Flint & Lindberg 1995) and sexual selection (Jawor & Breitwisch 2004). In most cases, physiological stores are believed to be lipids, but only one previous study in birds has examined the ability of RBM to predict actual lipid stores (Conway, Eddleman & Simpson 1994). In comparing the ability of RBM to predict lipid stores, Conway *et al.* (1994) found that RBM explained about 50% of variation in lipid stores. In this paper, the relationship between RBM and lipid stores in nestling European Starlings (*Sturnus vulgaris*) was re-examined through a brood manipulation, as well as by increasing the sample size of individuals examined (102 vs 21 used in Conway *et al.* 1994). In addition, the ability of multiple methods of calculating RBM to predict lipids was compared. In particular, reduced major axis (RMA) regression was compared with ordinary least squares (OLS) regression, as the use of OLS regression to compare structural size and body mass has been criticized (Green 2001).

Overall, the objectives of this study were to: (1) assess the role of common origin and common rearing environment through a cross-fostering brood manipulation; (2) test for a trade-off between growth and lipid stores;

(3) examine whether individuals with the largest body mass also have the larger lipid stores; and (4) compare whether residual body mass estimates of body condition predict actual lipid stores.

## Methods

Research took place on a 1000-ha (2500-acre) sheep and cattle farm in the Belmont Hills, Lower Hutt, New Zealand (41°10' S, 88°53' W) from October to December 2000. The European Starling (*Sturnus vulgaris*) is a cavity-nesting passerine native to Europe and Central Asia, but starlings were introduced to New Zealand in the early 20th century (Thompson & Flux 1988). New Zealand starlings commonly lay between four and six eggs and have incubation periods of 11–13 days and nestling periods of 19–21 days, with hatching occurring over a 24–36-h period.

Nests were checked daily to determine date of clutch initiation and clutch size and were revisited daily at the end of incubation to determine hatching date. To manipulate nest conditions, nests with the same hatching date were randomly assigned to one of three treatments: (1) enlarged ( $n = 7$ ); (2) reduced ( $n = 8$ ); or (3) control ( $n = 8$ ) to create broods that were roughly 40% larger or smaller than original clutch size (e.g. on average, 3, 5 and 7 nestlings on day 4) for a total of 102 nestlings that survived to be collected. Chicks were individually marked with small dabs of nail polish on their claws and swapped for all treatments on day 3 of the nestling period (all days are referred to by days from hatch of first nestling). Each nest contained a mix of nestlings hatched in the nest and nestlings hatched in other nests. When more than one new egg was found in a nest over a 24-h cycle ( $N = 25$ ), one egg was always markedly different in colour and shape (suggesting that it was laid by another starling) and it was then removed, ensuring that only eggs laid by the attending females remained in the nest (Brown & Sherman 1989).

Nests were visited on days 4, 8, 12, 16, 19 and 20 to measure nestlings and lipid levels were assessed on day 20. During each visit, body mass (to the nearest 0.1 g with a digital balance), head-bill (distance from back of skull to tip of bill) and tarsus length (to the nearest 0.05 mm with callipers) and flattened straightened primary wing length (to the nearest 0.1 mm with a ruler) were recorded. Nestling quality was characterized using two variables: (1) growth rate and (2) residual body mass. Growth rate from day 4 to day 20 was calculated as the growth rate constant  $K$  of a logistic growth function (Starck & Ricklefs 1998). Body mass, head-bill length and tarsus reach their maximum by days 12–14, and by day 20 feather growth has reached its maximum length (Cabe 1993). Nest temperatures were measured to the nearest 0.1 °C with a thermocouple thermometer. Occupied nest temperature was measured by placing the temperature probe at the base of the nest cup to measure the external temperature of the brood in the nest.

On day 20, following measurements, nestlings were collected via over-etherization and weighed after digestive tract contents were removed. Nestlings were freeze-dried at  $-40^{\circ}\text{C}$  until dry mass stabilized, weighed to obtain dry mass and then ground in a mixer. Two 2.5-g samples of homogenate was analysed in duplicate via a semicontinuous Soxhlet extraction using petroleum ether for 16 h (Dobush, Ankney & Kremenz 1985). Following extraction, samples were placed in a fume hood to evaporate remaining solvent, oven-dried at  $40^{\circ}\text{C}$  and then reweighed. Feathers were not removed from carcasses. The difference between the pre-extraction and postextraction mass was considered the lipid mass. The proportion of lipids lost from the 5-g samples was used to calculate the total quantity of lipids in each individual based on total dry mass. Lean dry mass was calculated as the total dry mass – lipid content.

#### STATISTICAL ANALYSES

To compare the relationship between different methods of computing residual body mass (often called ‘body condition index’) and lipid content, a series of linear regressions were conducted. All residual body masses were computed as the residuals of a regression of a structural measure *vs* body mass on nestling day 20. For structural measures, the following were used: untransformed tarsus length,  $\log_{10}$  tarsus length, (tarsus length)<sup>3</sup> and the first principal component of a principal component analysis (PCA) of tarsus, head-bill and primary wing feather length. Body mass used either untransformed or  $\log_{10}$  body mass. Regression analyses were either standard ordinary least square regressions or reduced major axis regression (RMA). RMA regressions were calculated using the computer program RMA (Bohanak & van der Linde 2004).

Factors predicting lipid content of nestlings were analysed using a mixed model ANOVA (SAS PROC MIXED, Littell *et al.* 1996), with nest of origin and nest of rearing as random factors and the following fixed effects: lean dry mass, clutch initiation date, clutch size, nest temperature and brood manipulation treatment (reduced, control, enlarged). All pairwise interaction terms were entered into the model and then removed sequentially when not significant. No interaction terms remained in the model. Random effects were tested by subtracting the  $-2$  log-likelihood scores of a model containing all random effects from the  $-2$  log likelihood score of the model minus the effect being tested (Littell *et al.* 1996). Log-likelihood scores are generated to derive estimators of parameters in a model. The difference in the  $-2$  log-likelihood scores between the full model and the model minus the variable of concern is computed as a  $\chi^2$  value ( $df = 1$ ). To compare the relative contribution of each random effect in explaining variance not explained by fixed effects, covariate parameter estimates are reported.

Nest temperatures were grouped into three periods of the nesting cycle (early days 4–8, mid days 12–16

and late days 19–20). To produce partial regression plots describing the relationship between continuous variables and lipid content, a multiple linear regression model was constructed containing clutch initiation date, clutch size, nest temperatures, number of nest-mates on day 20 and lean dry mass. Partial regression plots are the best method of examining the relationship between two variables while accounting for covariation with other independent variables in a model (Neter *et al.* 1996). Partial regression plots for a pair of variables are created by regressing the first variable of interest against the other independent variables minus the second variable of interest and plotting the residual of this regression against the residuals of a regression of the first variable of interest against all other variables including the second variable.

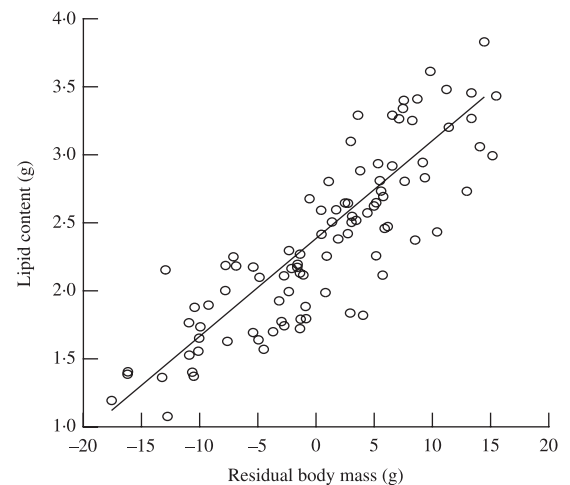
## Results

### IS RESIDUAL BODY MASS A MEASURE OF CONDITION?

Nestlings with high residual body mass (RBM) also had high lipid stores (Fig. 1), regardless of the method of calculating RBM (Table 1). Models using a single morphological measure (tarsus) explained much more variance than those using a principal component of structural size ( $R^2$  0.64–0.66 *vs* 0.44–0.45, Table 1). Interestingly, residuals calculated using ordinary least squares methods explained more variation in lipid stores ( $R^2$  up to 0.66) than did residuals calculated using reduced major axis regression ( $R^2$  up to 0.31). Overall, the models reported here explain more variation than found in previous studies ( $R^2 = 0.50$ , Conway *et al.* 1994).

### WHAT FACTORS PREDICT LIPID STORES?

There was a significant random effect of nest of rearing on lipid content ( $\chi^2 = 15.7$ ,  $P < 0.001$ ), but there was



**Fig. 1.** The relationship between residual body mass and lipid content in nestling European Starlings in New Zealand. Residual body mass was calculated from a regression of untransformed tarsus length *vs* untransformed body mass.

**Table 1.** Regression analyses comparing multiple methods of calculating body condition index to total lipid content of European Starling nestlings ( $N = 102$ ). All body condition indexes are residuals of a regression of a structural measure vs body mass. Principal component 1 is a combination of tarsus, head-bill length and primary feather length. Type refers to regression model: OLS = ordinary least squares, RMA = reduced major axis

Body condition index						
Structural measure	Body mass	Type	$\beta$	$F_{1,97}$	$P$	$R^2$
Tarsus	Mass vs lipid	OLS	0.071	13.45	<0.0001	0.65
Tarsus	Mass vs lipid	RMA	0.039	42.20	<0.0001	0.31
Log <sub>10</sub> tarsus	Mass vs lipid	OLS	0.072	13.64	<0.0001	0.66
Log <sub>10</sub> tarsus	Log <sub>10</sub> mass vs lipid	OLS	11.63	13.19	<0.0001	0.64
Log <sub>10</sub> tarsus	Log <sub>10</sub> mass vs lipid	RMA	6.36	41.92	<0.0001	0.29
(Tarsus) <sup>3</sup>	Mass vs lipid	OLS	0.072	13.62	<0.0001	0.66
(Tarsus) <sup>3</sup>	Log <sub>10</sub> mass vs lipid	OLS	11.62	13.17	<0.0001	0.64
Principal component 1	Mass vs lipid	OLS	0.072	8.93	<0.0001	0.45
Principal component 1	Log <sub>10</sub> mass vs lipid	OLS	11.57	8.69	<0.0001	0.44

no effect of nest of origin ( $\chi^2 = 0.09$ ,  $P > 0.05$ ). This was confirmed by a comparison of covariance parameter estimates (box of rearing 0.059, 51.3% of variation; box of birth 0.015, 13.0%; residual error 0.041, 35.6%).

The range of lipid stores found in nestlings was 1.07–4.12 g (mean  $2.38 \pm 0.68$  SD). Nestlings raised in enlarged broods did not have lower lipid reserves than did nestlings in control or reduced broods (least squares mean lipid mass (g)  $\pm$  SD: reduced  $2.54 \pm 0.78$ ,  $n = 21$ ; control  $2.45 \pm 0.81$ ,  $n = 41$ ; enlarged  $2.28 \pm 0.91$ ,  $n = 40$ , Table 2). However, brood manipulation led to nestlings in enlarged broods having lower body mass and lean dry mass (body mass  $F_{2,32} = 3.44$ ,  $P = 0.04$ , least squares mean body mass (g)  $\pm$  SD: reduced  $75.02 \pm 7.38$ ,  $n = 21$ ; control  $75.8 \pm 6.91$ ,  $n = 41$ ; enlarged  $67.91 \pm 8.31$ ,  $n = 40$ ; lean dry mass  $F_{2,32} = 3.98$ ,  $P = 0.02$ , least squares mean lean body mass (g)  $\pm$  SD: reduced  $23.25 \pm 2.21$ ,  $n = 21$ ; control  $24.78 \pm 1.79$ ,  $n = 41$ ; enlarged  $18.54 \pm 2.31$ ,  $n = 40$ ). Individuals with greater overall lean dry mass did maintain greater lipid levels (Table 2, Fig. 2a). Nestlings born to early breeding females had greater lipid content than later-laid nestlings ( $\beta = -0.06$ , Table 2).

Nest temperatures during the nestling period ranged from 4 °C to 21 °C (mean  $13.2^\circ \pm 3.97$  SD). Nest temperatures during the late nesting period were highly correlated with lipid levels; as nest temperatures increased, lipid levels in nestlings increased ( $\beta = 0.04$ ,

Table 2, Fig. 2b). However, the influence of nest temperatures in the early period on lipid levels was close to significance ( $P = 0.06$ ), but temperatures during the mid-nesting period had not effect on lipid levels (Table 2).

#### IS THERE A TRADE-OFF BETWEEN GROWTH AND LIPID CONTENT?

There was no relationship between growth rate of either tarsus or head-bill length on lipid stores ( $P > 0.2$ ). However, nestlings with faster rate of wet mass gain also had larger lipid stores (overall model:  $F_{2,96} = 104.54$ ,  $R^2 = 0.68$ ,  $P < 0.0001$ ; growth rate,  $\beta = 0.02$ ,  $F_{1,96} = 7.08$ ,  $P = 0.01$ ; body mass  $\beta = 0.06$ ,  $F_{1,96} = 13.07$ ,  $P < 0.0001$ , Fig. 2c).

#### ARE HEAVIER NESTLINGS FATTER?

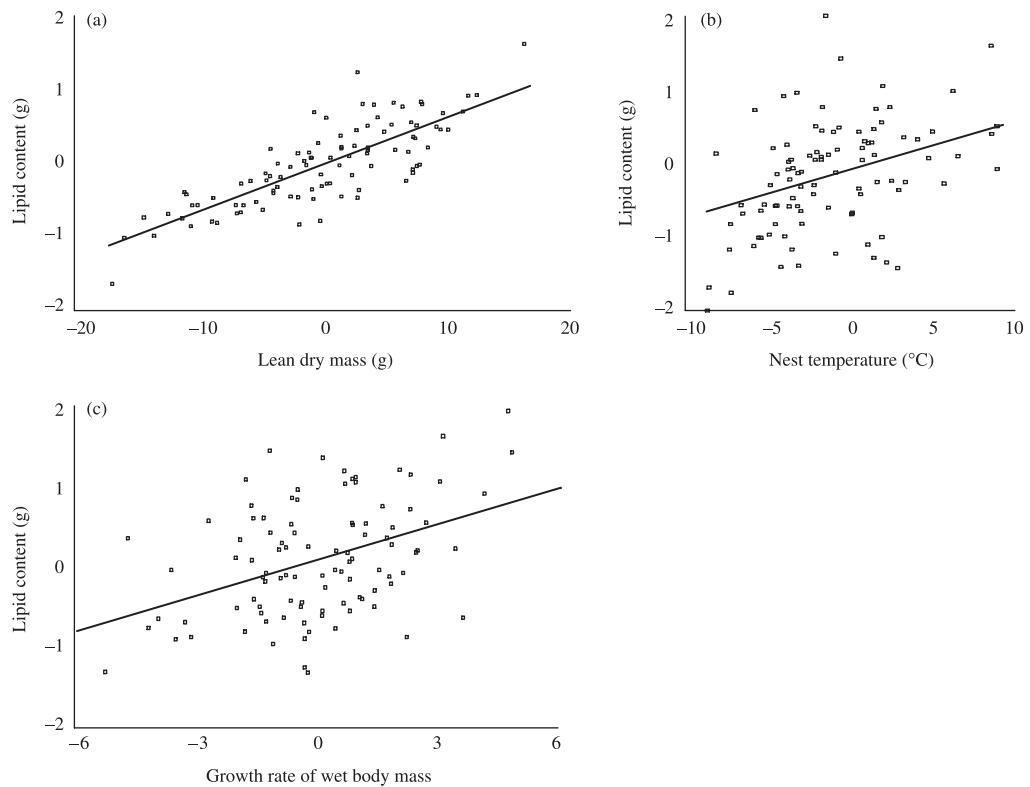
Heavier nestlings, on average, maintained greater lipid reserves (fat =  $0.069 \times$  body mass  $-2.76$ ,  $F_{1,97} = 209.88$ ,  $P < 0.0001$ ,  $R^2 = 0.68$ ; Fig. 3). However, examining the distribution of lipid stores in each quartile (Fig. 3) makes it clear that the nestlings with the largest lipid levels were not always in the largest quartile; the nestlings with the largest lipid stores were in the 3rd and 4th quartiles.

## Discussion

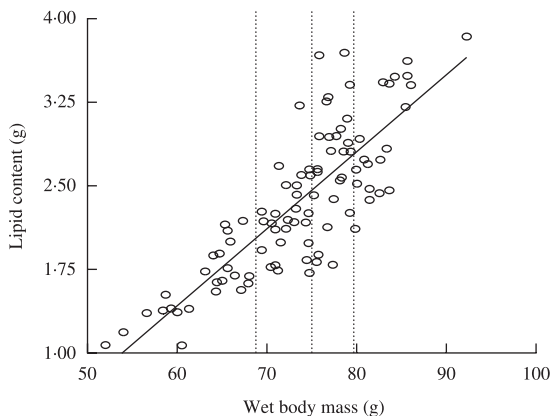
Nestling lipid stores, an important measure of physiological stores, were strongly affected by environmental conditions, as the cross-fostering experiment conducted here revealed a stronger influence of rearing environment than nest of origin. A common rearing environment probably exerts an influence through similar food intake (quality and quantity of food) and common development conditions. Here, one important rearing condition, nest temperature, helped explain much of the variance among nests, but there was still considerable unexplained variance related to rearing environment. The effect of

**Table 2.** Factors predicting lipid content of nestling European Starlings from a cross-fostering brood manipulation ( $N = 102$ ). Output from a mixed model with nest of origin and nest of rearing as random factors. Significant effects are shown in bold

Fixed effect	df	$F$	$P$
<b>Clutch initiation date</b>	<b>1, 26</b>	<b>3.74</b>	<b>0.03</b>
Clutch size	1, 31	0.58	0.45
<b>Lean dry mass</b>	<b>1, 90.4</b>	<b>130.51</b>	<b>&lt;0.0001</b>
Nest temperature – early nesting period	1, 33.9	3.12	0.06
Nest temperature – mid nesting period	1, 32.8	0.35	0.55
<b>Nest temperature – late nesting period</b>	<b>1, 33.5</b>	<b>11.20</b>	<b>0.0024</b>
Brood manipulation treatment	2, 30.3	2.38	0.11



**Fig. 2.** Partial regression plots of factors affecting lipid content of nestling European Starlings. Values on axes are the residuals from a regression of axis label vs all other variables in the model minus the variable on the other axis. For more information on partial regression plots see text: (a) lean dry mass; (b) nest temperature; (c) rate of growth in wet body mass (PC1).



**Fig. 3.** Relationship between wet body mass and lipid content of nestling European Starlings in New Zealand ( $N = 102$ ). Lipid content was determined via a Soxhlet extraction. Vertical lines denote quartiles for body mass.

nest temperatures varied depending on the age of nestlings. There was a strong effect late in the nesting period (days 19 and 20), suggesting that conditions late in development exert the strongest influence on lipid stores at time of fledging. The site where this research was conducted is cold and wet with frequent storms (Thompson & Flux 1988); greater thermoregulatory demands in colder nests may result in reduced nestling condition. There was only a weak effect of temperatures earlier in development (days 4–8). Adult females

may ameliorate colder conditions through brooding, thus minimizing thermoregulatory demand in offspring. In addition, 4-day-old nestlings are not yet thermoregulating, so energy costs to nestlings should be minimal, at least within a larger bound of temperatures (Visser 1998). In addition, the effect of temperatures on younger chicks may be minimized by day 20, the time of measure of lipid stores in this study. Conclusions regarding the effects of temperature on lipid stores are only suggestive, because I did not explicitly manipulate temperature and thus temperature conditions could be correlated with a factor that was not measured. Future studies should consider the role of developmental conditions on physiological stores. By including nest temperatures in analyses it was possible to reduce the amount of unexplained variance attributed to the rearing environment.

Nestlings do not appear to trade-off growth in structural size for lipid stores, as there was no relationship between structural growth and lipid levels. However, chicks that gained wet body mass rapidly also had greater lipid levels. This may be due in part to heavier nestlings tending to have greater lipid levels. However, independent of final body mass, rapid growth rate in body mass was linked with high lipid content, suggesting that factors benefiting growth rate also benefit storage of lipid reserves.

Thus the quality of parents may affect which individuals are better able to grow rapidly *and* to increase

lipid stores. Individual lipid stores may be explained in part by variation in quality, expressed as timing of breeding. Chicks raised later in the breeding season had lower average levels of lipid stores. The fact that early nestlings had larger stores may explain, in part, why early fledglings at this site have higher recruitment rates (Thompson & Flux 1991). Larger lipid levels in early chicks may be due to seasonal changes in food availability, but starlings are highly synchronous and, thus, many of the later chicks were at most 5–7 days younger than the earliest nestlings. Thus, it is more likely that timing of breeding reflects differences in individual quality among parents (Christians, Evanson & Aiken 2001; Smith 2004), where higher-quality females breed earlier and are better able to produce offspring with high lipid levels. The split-nest cross-fostering experiment here helped to break the correlation between maternal effects and genetic quality. Inclusion of timing of breeding and clutch size, another measure of quality in starlings (Christians *et al.* 2001; Smith 2004) may explain the lack of an effect of common origin on lipid stores.

Brood manipulation *per se* did not appear to have a direct effect on lipid stores, rather, it appear to exerted an effect on lipids through influencing the size of nestlings, as nestlings in larger broods tended to be smaller, which in turn affected lipid levels. The overall relationship between size and lipid levels was not clear. On average, larger nestlings (by wet mass) had greater stores, but many of the individuals with the highest lipid reserves were not the heaviest. There was also a very strong relationship between lean dry mass (a measure of size independent of lipid levels) and lipids. Thus the proper relative comparison of size and lipid stores should be independent of lipids, which may explain why  $R^2$  values for regressions of RBM calculated from wet body mass and lipids do not explain all variation. However, it is difficult to measure lean dry mass non-invasively (but see Conway *et al.* 1994), so using wet body mass, at least in this case, is an acceptable alternative.

Finally, the use of RBM to predict actual lipid stores appears to be supported in European Starling nestlings. Positive residuals are assumed to represent excess body mass for an individual's body size; the results reported here support this contention. The effectiveness of RBM as a predictor of lipid stores varied depending on the method of calculating RBM. Here the best fit models were those calculated from a single structural measure (in this case tarsus length) *vs* body mass, regardless of the method of transformation. Ordinary least squares regressions (OLS) predicted the relationship between RBM and lipid stores better than reduced major axis regression (RMA). This is surprising, given the criticisms mounted against OLS regression (Green 2001). However, at least for this population, residuals calculated using OLS methods are much more effective at predicting lipid stores than is RMA. Overall, the results reported here make it clear that residual body mass can be a good predictor of lipid stores and that especially when other factors affecting offspring quality, such as

individual quality, are considered it is possible to use non-invasive measures to reliably predict physiological stores in nestling birds.

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