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BODY MASS, COMPOSITION, AND SURVIVAL OF NESTLING AND FLEDGLING STARLINGS *(STURNUS VULGARIS)* AT BELMONT, NEW ZEALAND

Summary: Earlier studies of the starling *(Sturnus vulgaris)* population at Belmont, Lower Hutt, New Zealand, showed that nest productivity was low compared with other populations in New Zealand and elsewhere. Therefore, we investigated possible trade-offs between offspring number and quality (as measured by body mass and composition). We also compared these measures of offspring condition with pre- and post-fledging survival. Nestling mass did not significantly differ with clutch size or brood size at any age. In starlings about to leave the nest, lean (i.e., fat-free) dry mass and water mass increased with body mass, but lipid mass increased approximately twice as much. When the effects of the other variables were controlled in a partial correlation analysis, lean dry mass, water mass, lipid mass, and mass of stomach contents were positively correlated with mass at nest-leaving; brood size was not correlated with mass at nest-leaving. Nest success was independent of clutch size and brood size, but lighter broods were more likely to fail totally than were heavier broods early in the nestling period. Nestling survival early, but not late, in the nestling period was positively correlated with nestling mass. The likelihood that a nestling raised in 1973-1979 would be recruited as a breeder was independent of its mass at brood-day 12. Thus, unlike some other passerines, larger, heavier starling nestlings did not seem to survive better than average ones. Low productivity was not accompanied by a decrease in body condition of those nestlings that survived the nestling period. Therefore, starlings at Belmont reduced offspring number rather than offspring quality when they encountered unfavourable conditions.

Keywords: starling; *Sturnus vulgaris;* nestling growth; nestling survival; fledgling survival; body mass; body composition; lipid stores.

Introduction

The successful establishment and expansion of starling *(Sturnus vulgaris* L.) populations following introductions in both the northern and southern hemispheres provides an excellent opportunity for comparative studies of avian breeding biology in different environments. Starlings were introduced to New Zealand in about 1862, and became widespread by the end of the 1880s (Thomson, 1922). They now occur throughout New Zealand (Bull, Gaze, and Robertson,1985).

Previous studies of a population of starlings at Belmont, Lower Hutt, New Zealand, showed that adult survival there, as elsewhere in New Zealand, was considerably higher than that in other countries (Aux and Aux, 1981). Productivity of nests, in contrast, was lower at Belmont than at other localities both in New Zealand and overseas. Aux and Aux (1981) attributed this low productivity to wet, windy conditions which make Belmont a marginal breeding habitat for starlings.

Low productivity may represent a trade-off between number and quality (i.e., body condition) of offspring produced (Smith and Fretwell, 1974; Brockelman, 1975; Winkler and Wallin, 1987). Because quality of those starlings that survive to leave the nest at Belmont has not been investigated, we analysed variation in chick mass and composition to determine if the low productivity was accompanied by poor body condition of those chicks that did survive to leave the nest. We also investigated the relationship between body mass and both nestling survival and subsequent recruitment of nestlings to the breeding population at Belmont.

Methods

The 1500 ha study area at Belmont (41°10 'S, 174°54 'E) ranges in altitude from 250 to 400 m a.s.l. and is entirely covered in pasture closely grazed by sheep. Starlings nested in some of the 500 boxes built into ventilation shafts of abandoned ordnance storage bunkers. Aux and Aux (1981; 1982) and Flux {l987) describe the study area and the history of the Belmont starling population.

After egg-laying began on 20 October 1984, nests were checked daily until laying of first clutches was completed on 2 November. Brood-day 0 was the day on which the first nestling hatched in a brood.

Nestlings were weighed on a Pesola spring scale accurate to 0.5 g and their mass (= wet mass) recorded to the nearest 1.0 g on brood-days 6, 12, and 20-23. Toenails of nestlings were clipped to allow individuals to be distinguished after brood-day 6. All nestlings (n=373) were collected on brood-days 20-23 (hereafter brood-day 20+) between 1000 hr and 1400 hr, weighed, killed with ether, and immediately frozen. Stomach contents were subsequently removed from thawed carcasses and weighed and the carcasses refrozen for drying in a freeze-drier. Procedures used to extract lipids and to determine body composition are described in Thompson and Flux (1988). Variables recorded for each nestling or nest are listed in the legend of Table 3. Data on nestling mass and subsequent survival were obtained from 3252 starlings raised during the 1973-1979 breeding seasons.

Statistical analyses were performed using subprograms of the Statistical Analysis System (SAS Institute, 1985; 1986). Where appropriate, values for individual nestlings were used (e.g., hierarchical ANOVA), but for other analyses we used the means of each brood. SAS's MRANK procedure was used for non-parametric ANOVA.

Results

Nestling mass

The relationships between nestling wet mass and clutch and brood size on brood-days 6, 12, and 20+ are presented in Fig. 1. On each of the three brood days an hierarchical ANOVA showed that neither clutch size nor brood size significantly affected variation in nestling mass (Table 1). Regardless of age, variance in nestling mass was divided approximately equally between variation among broods of different clutch or brood sizes and variation within broods of different clutch or brood sizes.

Table 1: *Hierarchial analysis of variance of the effect of clutch size and brood size (within clutches), against the residual variance of chick size (within broods), on the wet body mass of starling chicks on brood-days 6, 12, and 20+. (***=p<0.001.*

	Sum of squares	d.f.	Mean squares	F	% variance explained
		---Clutch size---			
Brood-day 6					
Clutch size	618.7	5	123.7	0.92	0
Brood size	17597.8	131	134.3	4.26.***	47.4
Chick size	11316.7	359	31.5		52.6
Total	29533.1	495	59.7		100.0
Brood-day 12					
Clutch size	948.4	5	189.7	0.77	0
Brood size	31 858.0	129	247.0	6.08***	59.1
Chick size	13 804.3	340	40.6		40.9
Total	46 610.6	474	98.3		100.0
Brood-day 20 +					
Clutch size	126.9	5	25.4	0.46	0
Brood size	6236.3	114	54.7	3.99***	49.2
Chick size	3462.5	253	13.7		50.8
Total	9825.7	372	26.4		100.0
		---Broodsize---			
Brood-day 6					
Brood size	441.3	4	110.3	0.82	0
Brood size	17775.1	132	134.7	4.28***	47.6
Chick size	11316.7	359	31.5		52.4
Total	29533.1	495	59.7		100.0
Brood-day 12					
Brood size	959.4	5	191.9	0.78	0
Brood size	31847.0	129	246.9	6.08.***	59.1
Chick size	13804.3	340	40.6		40.9
Total	46610.6	474	98.3		100.0
Brood-day 20 +					
Brood size	334.9	5	67.0	1.27	0.7
Brood size	6028.4	114	52.9	3.86***	47.8
Chick size	3462.5	253	13.7		51.5
Total	9825.7	372	26.4		100.0

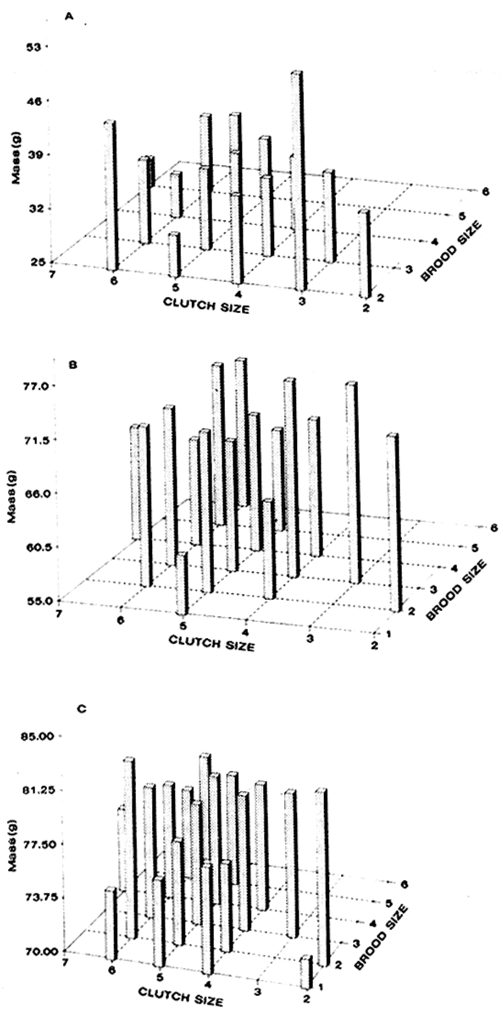

Figure 1: *Wet body mass of starling nestlings in relation to clutch size and brood size on (a) brood-day 6, (b) brood-day 12, and (c) brood-day 20+.*

Nestling mass and composition on brood-day 20+

The natural logarithm of the mass of each component - water, lipid, and lean dry (i.e., fat-free) mass - was regressed on the natural logarithm of wet mass on brood-day 20+ to determine if each component increased at the same rate as nestling mass, i.e., whether the slope of the regression is not significantly different from unity. The slope of the regression of lean dry mass on wet mass did not differ significantly from unity, but those of water mass and lipid mass did, with lipid mass increasing approximately twice as fast as did lean dry mass and water mass in relation to nestling mass (Table 2). Thus, heavier nestlings at brood-day 20+ had, on average, more lipid but less water than lighter nestlings in proportion to their body weight; but nestling lean dry mass varied directly with their wet mass.

Table 2: *Regression of the natural logarithm of the mass of body components (y) on the natural logarithm of wet body mass (x) of starling nestlings on brood-day 20+. Slopes significantly different (P<0.05) from unity indicate that the body component does not increase proportionately with wet body mass.*

Component	Slope	Standard error of slope	*P*
Lipid mass	2.531	0.272	<0.001
Lean dry mass	0.936	0.072	>0.05
Water mass	0.887	0.036.	<0.01

The nestling mass on brood-day 20+ was positively correlated with brood-day 12 mass and, not surprisingly, with its three constituents (lipid mass, water mass, and lean dry mass; Table 3). Because many of the II variables recorded for each nest were correlated with each other, we used partial correlation analysis to investigate the relationship between each of ten variables, excluding nestling mass change between brood-days 12 and 20+. When the effects of the nine other variables were controlled, only water mass, lipid mass, lean dry mass, and wet mass of stomach contents were positively correlated with brood-day 20+ nestling mass (Table 3).

Variation in nestling mass and body components was partitioned into within- and among-nest sources using an hierarchical ANOVA. Approximately half of the variation in nestling mass (48.4%), lipid mass (57.9%), lean dry mass (53.2%), and water mass (47.2%) on brood-day 20+ was attributable to variation among nests.

Nest success and productivity

Eggs were laid in 256 nests in 1984; 207 nests had completed clutches; 185 nests hatched young; and 162 nests (63.3%) contained nestlings at brood-day 6. Of the 162 nests, 25 (15.4%) failed between brood-day 6 and 12, and of the 137 remaining nests, 20 (14.6%) failed between brood-day 12 and 20+. The proportion failing to survive the interval was independent of clutch and brood size during both intervals (brood-day 6 to 12: clutch size, x^2=8.05, df=5, P=0.15; brood size, x^2=6.05, df=4, P=0.20) (brood-day 12 to 20+: clutch size, x^2=2.52, df=5, P=0.77; brood size, x^2=2.89, df=5, P=0.72). The 256 nests produced 371 nestlings (1.45 nest^{-1}) that

Table 3: *Simple and partial correlation coefficients (xl00) for 11 attributes of starling nestlings. Pearson correlation coefficients are given above the diagonal and partial correlation coefficients are given'below the diagonal. Variables: wet mass on brood-day 20+ (M20), wet mass on brood-day 12 (M12), wet mass change between brood-day 12 and 20+ (MC), lean dry mass on brood-day 20+ (LDM), water mass on brood-day 20+ (WM), lipid mass on brood-day 20+ (LM), primary length (PL), tarsus length (TL), stomach contents (SC), brood size (BS), clutch size (CS). The natural logarithm of the mean for each nest was used. The variable MC, a combination of M20 and M12, was not included in the partial correlation analysis. Sample sizes ranged from 115 to 135 nests. Individual tests were considered significant (*) if P 0.00I in order to achieve an overall alpha of ca. 0.05 using the Bonferroni method for multiple tests.*

Variable									Variable		
	M20	M12	MC	LDM	WM	LM	PL	TL	SC	BS	CS
M20	-	33*	11	77*	92*	65*	20	23	15	21	-08
MI2	-14	-	-90*	66*	11	29	78*	68*	0	39*	-10
MC			-	-35*	31*	0	-73*	-62*	06	-32*	01
LDM	92*	21		-	57*	47*	60*	48*	-12	38*	-09
WM	99*	13		-87*	-	39*	-05	12	11	09	-05
LM	96*	16		-87*	-94*	-	27	06	0	13	-11
PL	04	48*		12	-12	-02	-	51*	-08	34*	01
TL	-03	46*		06	03	-04	-04	-	02	29*	-07
SC	87*	18		-87*	-84*	-84*	-02	03	-	14	06
BS	-26	04		32*	23	24	-02*	01	32*	-	11
CS	0	-03		-04	02	-03	12	-06	01	13	

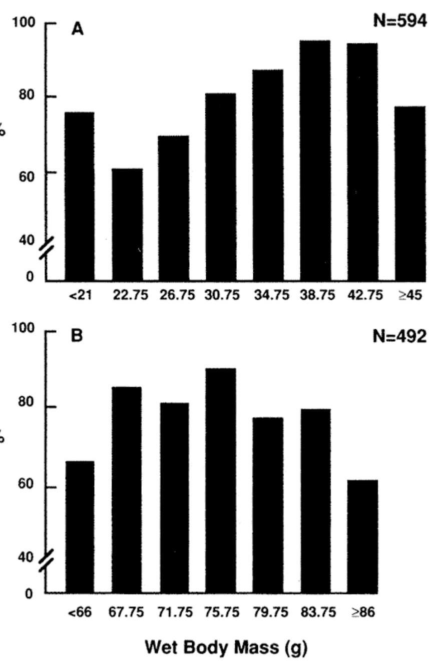

Figure 2: *Survival of starling nestlings (a) between brood-day 6 and brood-day 12 and (b) between brood-day 12 and brood-day 20+ in relation to wet body mass at the beginning of the interval. Body mass is given as the mid-point of each mass class.*

survived to brood-day 20+. These nestlings were in 117 nests (3.17 nest^{-1}). Broods that survived from brood-day 6 to 12 were slightly heavier ($\overline{X}$ =35.4 g) than those that did not survive ($\overline{X}$ =30.6 g; t=2.03, df=21, P=0.06). In contrast, the wet mass of broods on brood-day 12 did not differ significantly between those that survived to brood-day 20+ ($\overline{X}$ =69.8 g) and those that did not survive ($\overline{X}$ =68.6 g; t=0.42, df=22, P=0.68). Among successful broods (i.e., those with at least one nestling surviving to brood-day 20+), those losing nestlings between brood-day 6 and 12 were significantly lighter ($\overline{X}$ =31.5 g) than those not losing nestlings ($\overline{X}$ =35.7 g; t=3.19, df=98, P=0.0019). Similarly, broods losing nestlings between brood-day 12 and 20+ were lighter ($\overline{X}$ =62.1 g) on brood-day 12 than were those not losing nestlings ($\overline{X}$ =72.0 g; t=5.13, df=31, P=0.0001).

Nestling survival

The proportion of nestlings that survived from brood-day 6 to 12 increased as nestling mass increased, but this was not the case between brood-day 12 and 20+ (Fig. 2). Nestlings that died in successful nests between brood-day 6 and 12 were significantly lighter on brood-day 6 ($\overline{X}$ =27.5 g ± 1.6 S.E.) than were those that survived ($\overline{X}$ =35.3 g ± 0.3; MRANK: x^2=11.82, df=l, P=0.0006). In contrast nestlings that died in successful nests between brood-day 12 and 20+ were not significantly lighter on brood-day 12 ($\overline{X}$ =61.1 g:t 1.8) than were those that survived ($\overline{X}$ =70.9 g ± 0.4; MRANK: X^2=0.28, df=l, P=0.60), although the former were considerably more variable in mass than were the latter.

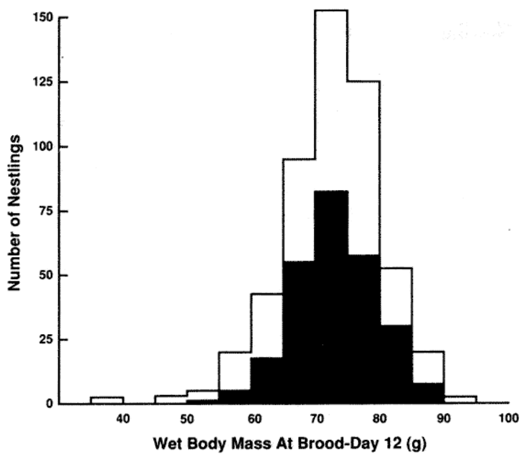

Figure 3: *Frequency distribution of wet body mass of starling nestlings (n =258) on brood-day 12 in 1973-1979 which were recruited as breeders at Belmont (filled) and their siblings (n=521) which did not return as breeders (open). Body mass categories are in 5g increments.*

Nestling mass and subsequent survival
Between 1973 and 1979, nestlings were weighed and banded on approximately brood-day 12. As nestling mass on brood-day 12 was positively correlated with mass on brood-day 20+ in 1984 (Table 3) and in 1973 to 1979 with their adult body mass on returning to nest in subsequent breeding seasons (r=0.33, n=207, P=0.00001), we compared the mass of brood-day 12 nestlings that were subsequently recruited as breeders at Belmont (n=258) with that of their siblings not recruited (n=521) (Fig. 3). Nestling mass on brood-day 12 did not differ significantly between recruited (72.3 g) and non-recruited (72.0 g) nestlings (t=0.81, P=0.42).

To check for differential return to the study area of heavier chicks within broods, we ranked the 161 returning chicks (from all broods of more than 2 in which only one chick returned) by mass in relation to their siblings. The three categories: heaviest chick (or heaviest equal), middle mass, and lightest (or lightest equal) comprised 51, 56, and 60 chicks, respectively. Chicks that returned from broods in which two or three chicks returned were ranked in a similar way, giving 23, 23, and 28 chicks, respectively. To obtain the maximum contrast, all brood sizes are included except broodsize 1, and those in which all chicks returned, which cannot be compared with any siblings. Use of the heaviest equal and lightest equal categories depletes the number of "middle" chicks, so there is no expected distribution. Summing all broods, 74 heaviest chicks returned compared with 88 lightest chicks. This indicates that a chick's mass at brood-day 12 relative to its siblings had no positive effect on its subsequent recruitment.

Regardless of mass, there could be a tendency for some broods to produce relatively more recruits that return to the study area than others (if only, for example, by having a central position in the study area). The observed and expected distributions of number of recruits per brood were significantly different (Grouped data: x^2=13.09, df=l, P=0.001), showing that some broods did indeed contribute more recruits (Table 4). Small broods, of course, do not have the opportunity of contributing the maximum number of recruits, causing a bias in the opposite direction to that found; hence the difference from expected is a minimum value.

Table 4: *Observed and expected number of recruits from starling broods.*

No. of recruits per brood	0	1	3	4
No. of observed broods	870	170	4	1
Expected Poisson distribution	852	202	2	0.1

Discussion

The low productivity of the Belmont starling population, which averaged 1.92 chicks per nest from 1970 to 1979 (range 1.2-2.7) as documented earlier by Flux and Flux (1981), prevailed again in 1984. Only 1.45 nestlings per nest survived, on average, to near the end of the nestling period. Observer activity was minimal compared with other studies of starlings, and mortality seems to be largely a result of environmental factors. To determine if this low productivity was accompanied by poor body condition of the surviving nestlings, we examined body mass and composition of chicks about to leave the nest.

Body mass and composition

Starling body mass on brood-day 20+ was not correlated with tarsus length, a linear body dimension, confirming that the two variables measure different aspects of body size (c.f., Richner, Schneiter and Stirnimann, 1989). This contrasts with Ricklefs' (1984) report of a positive correlation between tarsus length and both maximum and asymptotic (estimated mass at the asymptote) mass in a North American starling population.

Neither clutch size nor brood size was correlated with wet body mass on brood-day 20+. Although Lack (1948) suggested that nestling mass may be inversely related to brood size in starlings, this has not been found to be the case in most subsequent studies (Dunnet, 1955; Delvingt, 1962; Feare, 1984). Westerterp (1973) suggested that a negative correlation between body mass and brood size occurs only when starlings experience poor feeding conditions. However, final wet body mass of Belmont starlings in 1984 (78.4 g; Thompson and Flux, 1988) was well within the range of maximum or asymptotic masses reported for other populations. For example, Ricklefs and Peters (1979) and Ricklefs (1984) report mean asymptotic masses ranging from 72.1 to 85.3 g from early broods in Pennsylvania, USA, and Ricklefs and Peters (1979) summarized results from five localities in the northern hemisphere in which final mass ranged from 76 to 84 g. In contrast, Westerterp (1973) reported lower mean plateau masses (62-74 g) from a population in the Netherlands, and concluded that the population was experiencing a food shortage. The 21-day-old nestlings of Myrcha, Pinowski and Tomek (1973) weighed 70.4 g. Their 12-day-old nestlings weighed 69.3 g, almost identical to the 69.5-g mean of brood-day 12 nestlings in 1984 and similar to the seven-year average of 70.5 g at Belmont (Thompson and Flux, 1988). Feare (1984, p. 155) points out that comparison of masses from different localities is hampered by annual differences that are likely to be related to variations in weather conditions. However, despite the apparently suboptimal breeding conditions at Belmont (Flux and Flux, 1981), nestlings 'on brood-day 12 and on brood-day 20+, shortly to be leaving the nest, were similar in mass to those of many populations in the northern hemisphere.

Consideration of the body composition of chicks about to leave the nest also failed to detect any evidence that chicks were in poor condition. Lipid stores were adequate in all but the lightest nestlings (Thompson and Flux, 1988). These lipid reserves, however, resulted in similar average estimated fasting tolerances for all but the lightest chicks (Thompson and Flux, 1988). Consequently, low productivity was not accompanied by poor body condition of fledglings, either in the form of low total body mass or of low lipid stores and estimated fasting tolerance. The proportion of the variance in body mass that was explained by brood size did not increase during the nestling period, suggesting that brood size changed throughout the nestling period in such a way as to minimize effects on nestlings. Belmont starlings apparently responded, in this average year, to poor environmental conditions for nesting by reducing the number of offspring through brood reduction rather than by producing more offspring of low quality. Both brood reduction and lower fledging weights were found when food was apparently scarce in other years and in second broods (Flux and Flux, 1981), as also reported overseas (Feare, 1984).

Nestling mass and survival

Nestling body mass was positively related to survival during the early stages of the nestling interval, as would be expected if brood-reduction was taking place. Dunnet (1955) also reported that the lightest nestlings were the most likely to disappear from broods in Scotland. About brood-day 12 nestling. survival improved and was not linearly related to mass.

In 1973-1979 there was no relationship between mass on brood-day 12 and the likelihood that a nestling would be recruited to subsequent breeding populations. Brood-day 12 mass was positively correlated with brood-day 20+ mass in 1984; and a similar relationship held for earlier years, to judge from the positive correlation between brood-day 12 mass and mass as an adult returning to nest. Body mass at nest-leaving and survival after leaving the nest may therefore not be correlated as they are in some species (e.g., Perrins, 1965; Garnett, 1981; Nur, 1984) or even in other starling populations (Krementz, Nichols and Hines, 1989). In the latter study, heavy nestlings from early nests (which they define as fledged before 4 June) were more likely to be resighted than were light nestlings during the nine weeks following nest-leaving. In earlier work on the same study area, however, Stromborg *et al.* (1988) found no relationship between body mass at fledging and post-fledging survival. These conflicting results may be reconciled by differences in the time of hatching, or differences between years.

At Belmont some broods raised in 1973-1979 contributed more recruits than did others to subsequent breeding populations. The reason for this is unknown, but does not apparently involve chick quality as judged by body mass. It closely reflects the skewed pattern of recruits produced per female lifetime (Flux, *in prep.)* and hence is likely to be a function of parental, rather than chick, quality.

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