

Diet quality during pre-laying and nestling periods influences growth and survival of Florida scrub-jay (*Aphelocoma coerulescens*) chicks

S. James Reynolds^{1*}, Stephan J. Schoech¹ and Reed Bowman²

¹Department of Biology, University of Memphis, Memphis, Tennessee 38152-3540, U.S.A.

²Archbold Biological Station, P.O. Box 2057, Lake Placid, Florida 33862, U.S.A.

(Accepted 31 March 2003)

Abstract

Food availability is one of the most important determinants of successful reproduction in birds. In a previous study, it was shown that Florida scrub-jays *Aphelocoma coerulescens* maintained a third egg mass when supplemented with a high fat and high protein diet during pre-breeding, as opposed to birds that were not supplemented that laid third eggs markedly lighter in mass than first- and second-laid eggs. Increases in egg quality promote chick growth and survival in many avian species. In this study, scrub-jays were provided with supplements throughout the pre-laying and nestling periods of 2001 and 2002 to investigate whether diet quality influenced growth and survival of chicks. Fledging success and survival to independence of unsupplemented chicks were higher for 2002 compared with 2001 indicating that breeding conditions (e.g. natural food availability) for jays were probably improved in the former year. Consistent growth patterns were found during the first 11 days post-hatch between chicks on supplemented and those on unsupplemented territories. Of the three growth measures, only seventh primary feather growth tended to be greater for third-hatched chicks on supplemented territories compared with third-hatched chicks on control territories. Food supplementation influenced survival of chicks. Compared with chicks hatching on unsupplemented territories, fledging success of chicks hatching from second-laid eggs was significantly greater in 2001, but not in 2002. Chicks from third-laid eggs on supplemented territories also tended to survive better in 2001 compared with chicks from unsupplemented territories, but, again, no such effect was found in 2002. We conclude that food supplementation in the pre-laying and nestling periods results in little measurable improvement in chick growth. However, improvements were found in survival of chicks that may be mediated through improvements in egg quality, but also may be the result of changes in foraging strategies of provisioning birds on supplemented territories. Chicks on supplemented territories might be in better body condition than those on unsupplemented ones. Methods other than morphometrics may be required to detect elevations in body condition of chicks raised on supplemented territories.

Key words: *Aphelocoma coerulescens*, growth, nutrients, reproduction, survival

INTRODUCTION

For most organisms, reproduction is a nutrient-demanding process and many animals accumulate endogenous nutrient reserves in preparation for breeding. In many avian species, however, especially in passerines, the capacity for nutrient storage before breeding is limited (see review by Reynolds & Perrins, in press) and exogenous supplies of nutrients are fundamental for successful breeding. Consequently, food availability during the pre-laying period can have a marked

influence on egg production (see review by Martin, 1987). Supplementary feeding provides a powerful tool to investigate the effects of food availability and diet quality on the breeding performance of birds (see review by Boutin, 1990). Previous work has typically focused on the effects of supplementary food on proximate measures such as laying date (e.g. Kelly & van Horne, 1997), clutch size (e.g. Bolton, Monaghan & Houston, 1993), egg size (see review by Christians, 2002) and composition (e.g. Bolton, Houston & Monaghan, 1992), and to a lesser extent on ultimate measures of breeding performance such as fledging success (e.g. Gill, Hatch & Lanctot, 2002).

The efficacy of food supplementation in investigations of the role of pre-breeding diet on breeding performance of birds relies upon a number of factors. Food

*All correspondence to: S. J. Reynolds, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, U.K.
E-mail: j.reynolds.2@bham.ac.uk

supplementation is less effective in years when natural food availability is high compared with years when natural foods are more limiting (e.g. Korpimäki, 1989). Different measures of breeding performance of birds vary in their sensitivity to timing of food provisioning (reviewed in Meijer & Drent, 1999). For example, Wiebe & Bortolotti (1995) found that providing food supplements to American kestrels *Falco sparverius* only 2 weeks before laying did not influence the timing of clutch initiation but it had a positive effect on egg size. Furthermore, some species are more suited to food supplementation than others. The best candidates for food supplementation are those species that are year-round residents, are strongly territorial, excluding other birds from their territories and thereby from established feeders, and use novel food sources exhaustively. The Florida scrub-jay *Aphelocoma coerulescens* is a prime candidate for food supplementation. Reynolds, Schoech & Bowman (2003) provided food supplements *c.* 2 months before the start of laying, and showed that the nutritional quality of the pre-breeding diet affected proximate measures of breeding performance in Florida scrub-jays. They found that birds with access to high fat and high protein food supplements showed significant advancements in laying date, laid significantly heavier third eggs and produced significantly larger clutches than controls without access to supplementary food. Particularly pertinent to this report is the increased mass of third eggs, a finding upon which this present study is founded. The study of Reynolds *et al.* (2003) was the first to demonstrate for any avian species that the nutritional quality of the pre-breeding diet can simultaneously influence laying date, clutch size and egg size.

For many non-avian organisms, a positive relationship exists between the size of eggs or propagules and the survival, growth and productivity of offspring produced from them (e.g. Sinervo & Huey, 1990). (Note: throughout this paper we treat increases in *size* and *mass* of eggs as being synonymous with an increase in egg quality.) This relationship holds for many taxa but unequivocal evidence for its support in birds is scarce (Williams, 1994). To date this relationship holds for offspring survival immediately post-hatching and during chick rearing (e.g. Risch & Rohwer, 2000), but, as Christians (2002) states, rarely are data available on the long-term effects of egg size on more ultimate measures of offspring fitness such as survival to nutritional independence and recruitment to the breeding population (e.g. Cooke, Rockwell & Lank, 1995).

Reynolds *et al.* (2003) found that the effect of high fat and high protein supplementation on egg size was consistent over 2 years that differed dramatically in rainfall and therefore in predicted food availability. Here, the results of a 2-year investigation in which the growth of chicks hatching from eggs laid by females on high fat and high protein supplements was compared with that of chicks hatching from eggs laid by unsupplemented females are reported. The long-term effects of pre-breeding diet are also assessed by measuring survival to fledging and to nutritional independence.

METHODS

Study population and general methods

A population of Florida scrub-jays was studied at Archbold Biological Station, Highlands County, Florida (27°10'N, 81°21'W, elevation 38–68 m). The population and study area have been described in detail in other studies (see Schoech, Mumme & Moore, 1991; Mumme, 1992; Schoech, Mumme & Wingfield, 1996). All birds were colour-ringed with unique colour combinations to facilitate identification, and sex, age, breeding status and group membership were known for each bird in the study population (see Schoech *et al.*, 1996 and references therein). Nests were located by observing the breeding pair carrying building materials and all nests were subsequently monitored throughout the breeding season.

Food supplementation

In 2001 and 2002, birds were provided with a custom-made high fat and high protein supplement (19.3% fat and 34.5% protein by mass; Research Diets Inc., New Brunswick, NJ) from the middle of January until chicks had reached 11 days of age. In 2001, territories were randomly assigned to either supplemented or unsupplemented (control) groups. In 2002, territories were again randomly assigned to a dietary treatment but reassignment was carried out to assure that territories were not allocated the same diet as the previous year. The supplement was provided to birds as custom-made pellets (10 mm long × 5 mm diameter) dispensed from bird feeders placed at the centre of breeding territories (see Reynolds *et al.*, 2003 for further details). Feeders were replenished every 2 days with 2 handfuls (*c.* 100 g) of pellets. Feeders were never completely empty when they were revisited and, therefore, it was assumed that birds were provided with *ad libitum* food. From direct observations, it was determined that only resident birds on a supplemented territory fed at the feeder, excluding birds from neighbouring territories. The following numbers of territories were supplemented in 2001 and 2002, respectively: 9 and 9; control: 19 and 18.

Growth

Nests were checked every few days after clutch completion. Modal incubation time for the Florida scrub-jay is 18 days (Woolfenden & Fitzpatrick, 1996) and, therefore, from 16 days of incubation nests were visited every day until the first chick hatched, this day being designated day 0. Nest visits were made between 10:00 and 14:00 when diurnal predators were least active (Schaub, Mumme & Woolfenden, 1992). Once the first chick had hatched, nests were not visited again until day 3. Hatching usually occurs over 24 h for this species (Woolfenden & Fitzpatrick, 1996) and eggs that had not hatched by

day 3 were not viable and were invariably removed by parents during brooding. Each chick within a brood was marked for future identification by painting a specific claw with dark red nail varnish. Nail varnish was applied on each nest visit. No brood contained > 5 chicks during the 2 years of the study.

Growth measures were taken from chicks on days 3, 5, 8 and 11, and chicks were ringed on the last visit. Jays can fledge as early as day 15 (Woolfenden, 1978) and nest visits after day 11 can cause premature fledging (Woolfenden & Fitzpatrick, 1984). Chicks were categorized as the first, second, third, etc., of the brood from the heaviest to the lightest chick as measured on day 3. Hereafter they will be designated as chick 1, 2 or 3. Intra-clutch egg-size hierarchies have been shown to reflect intra-brood chick-size hierarchies for a number of species (e.g. lesser snow goose *Anser caerulescens caerulescens*, Cargill & Cooke, 1981; tree swallow *Tachycineta bicolor*, Clotfelter, Whittingham & Dunn, 2000; green-rumped parrotlet *Forpus passerinus*, Beissinger & Waltman, 1991; see review by Stoleson & Beissinger, 1995).

On each nest visit, all chicks were removed and taken at least 50 m away from the nest before they were measured, thus minimizing disturbance at the nest site. Each chick was weighed (to 0.05 g) with a 100-g Pesola spring balance and lengths of the left tarsus and the seventh primary feather were measured (to 0.05 mm) with dial callipers. Tarsus length was measured on the bent left leg as the diagonal from the joint with the tibiotarsus, where there is a distinct notch, to the joint with the middle toe when the foot is bent. The seventh primary feather was always measured on the left wing from the point of attachment with the skin to the tip of the papilla. SJR took all growth measurements from all chicks during the 2 years of the study.

Survival

Breeding performance was measured by continuing to monitor the population after ringing of chicks on day 11. At this time, each chick was given a uniquely numbered aluminium U. S. Fish and Wildlife Service (USFWS) ring and 1 of the 3 colour rings that constitute the unique combination of colour rings by which an individual jay can be identified (see Woolfenden & Fitzpatrick, 1984 for further details).

Fledging success was determined as the percentage of hatched chicks that fledged. Nests were visited 4 (day 15) and 9 (day 20) days after chicks were ringed. Visits to the nest vicinity were brief (< 1 min) and nests were never approached closer than 10 m. Usually, chicks were still in the nest on day 15 and they could be observed directly through binoculars. However, when direct observation of chicks was problematic (e.g. nests > 2 m high or those obscured by dense vegetation), adults were provided with mealworms *Tenebrio molitor* to observe whether birds delivered them to nestlings or to fledglings on the ground.

Fledglings seek refuge in dense cover for the first few days post-fledging (Woolfenden & Fitzpatrick, 1996) but they can be readily heard begging for food. Chicks had usually fledged by the second visit on day 20. Successful fledging was confirmed by hearing chicks begging out of the nest and by inspection of the nest. After successful fledging, the nest-lining material usually remains tucked and appears flattened. Depredation of nestlings is evident from disturbance of the nest platform (e.g. snake, mammal predators) and/or by disturbance of the nest cup (e.g. avian predators). Usually, predation of nestlings results in loss of the entire brood (but see Schoech, 1999). Following successful fledging, each territory was visited every day until each fledgling had been identified from the specific colour ring that it carried.

Survival to independence was determined as the percentage of hatched jays that survived until *c.* 85 days of age when they are nutritionally independent (McGowan & Woolfenden, 1990; Woolfenden & Fitzpatrick, 1996). All independent young were trapped and ringed with the full complement of colour rings. Independent young were identified from the USFWS rings that they received as nestlings.

Statistical analysis

All statistical tests were performed using SAS (SAS Institute, 1999). Only first broods were considered but, because some chicks hatched from second- and later-laid clutches, as a result of earlier clutches being lost to predation, hatch date was used as a covariate in statistical tests to control for potential time-of-breeding effects. Sample sizes for analyses of fledging success were greater than those for analyses of survival to independence because at some nests chicks survived to fledging but were depredated before reaching nutritional independence.

Growth measures were tested only for chicks 1, 2 and 3 because so few fourth and fifth chicks were hatched. All growth data were log-transformed to reduce heteroscedasticity between successive measures from the nestling period and 1 was added to all feather measures before transformation to avoid negative characteristics of calculated values (Sokal & Rohlf, 1995). Since we were interested in how chick growth measures varied between successive nest visits in the nestling period (i.e. in chick-growth trajectories), 2-way repeated-measures ANOVA (PROC GLM; SAS Institute Inc., 1999) was used with dietary treatment (supplemented and unsupplemented) and year (2001 and 2002) as the factors, performing a polynomial analysis (von Ende, 2001; also referred to as trend analysis, Winer, Brown & Michaels, 1991) to construct independent contrasts between successive measurements in the nestling period to detect significant first-order (linear) and second-order (quadratic) trends in data. Predominantly quadratic responses (except where stated otherwise) of chick growth across the nestling period were examined between dietary treatments and

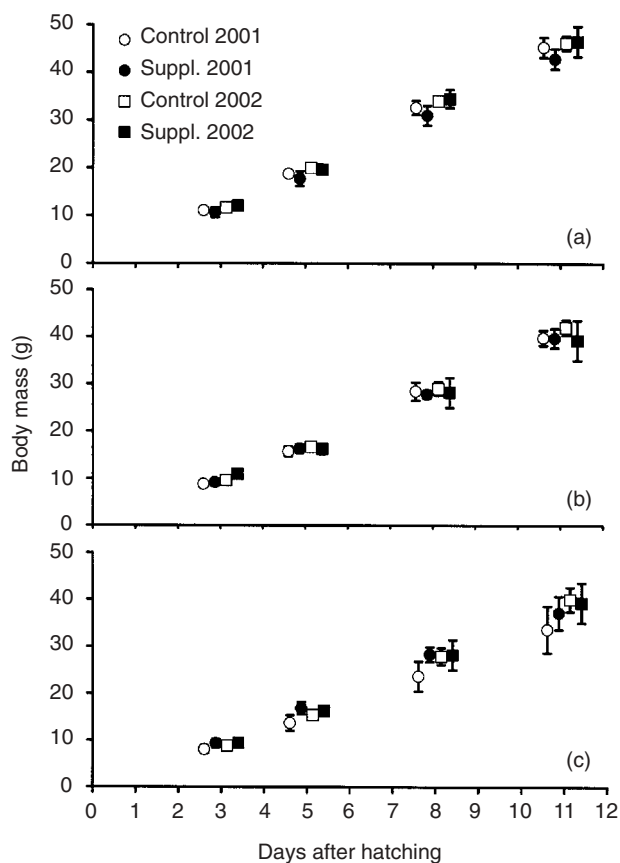


Fig. 1. Changes in body mass through the nestling period of chicks (a) 1, (b) 2 and (c) 3 (see Methods for definitions) hatching from eggs laid by Florida scrub-jays *Aphelocoma coerulescens* with access to high fat and high protein (Suppl.) food during pre-laying and nestling periods and those laid by females that were not supplemented (Control) during 2001 and 2002. Points, means; bars, standard errors. Data are separated slightly for clarity.

years. A separate analysis was carried out for chicks 1, 2 and 3. ANCOVA was also used with hatch date as the covariate to examine if hatch date had a significant influence on any of the growth parameters of chicks.

To examine further potential chick-growth responses to diet quality, untransformed data were analysed for each growth parameter at day 11. To avoid pseudoreplication, chicks 1, 2 and 3 were examined separately; 1-way ANOVA (PROC GLM; SAS Institute, 1999) was used to test for differences between years in the growth of chicks raised on unsupplemented territories. A 2-way ANOVA (PROC GLM; SAS Institute, 1999) was used with dietary treatment (supplemented and unsupplemented) and year (2001 and 2002) as the factors to contrast chick growth between supplemented and unsupplemented territories.

Fisher's exact tests were used to compare fledging successes and survival to independence between chicks. Survival data were analysed separately for each year of the study because it was suspected that local food availability was markedly different between 2001 and 2002 (see Results and Discussion below).

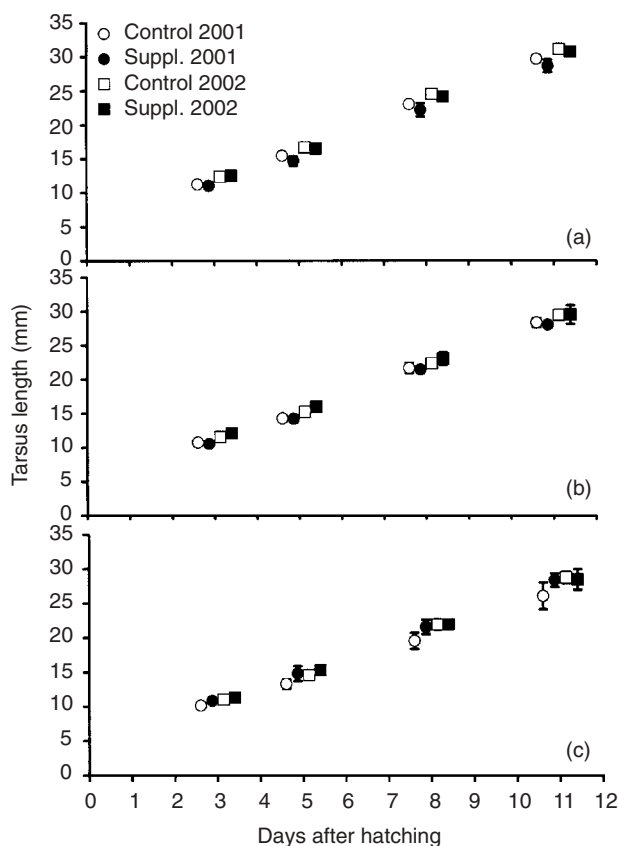


Fig. 2. Changes in tarsus length through the nestling period of chicks (a) 1, (b) 2 and (c) 3 (see Methods for definitions) hatching from eggs laid by Florida scrub-jays *Aphelocoma coerulescens* with access to high fat and high protein (Suppl.) food during pre-laying and nestling periods and those laid by females that were not supplemented (Control) during 2001 and 2002. Points, means; bars, standard errors. Data are separated slightly for clarity.

RESULTS

Growth and survival of chicks on unsupplemented territories

Growth parameters of chicks during the nestling period raised on unsupplemented territories did not differ significantly between 2001 and 2002 (Figs 1, 2 & 3). There were no significant differences between years for body mass (repeated-measures ANOVA: chick 1: $F_{1,26} = 0.70$, $P = 0.41$; chick 2: $F_{1,22} = 0.81$, $P = 0.38$; chick 3: $F_{1,11} = 1.96$, $P = 0.19$; Fig. 1), tarsus length (chick 1: $F_{1,26} = 1.55$, $P = 0.22$; chick 2: $F_{1,22} = 1.11$, $P = 0.30$; chick 3: $F_{1,11} = 0.65$, $P = 0.44$; Fig. 2) or length of the seventh primary (chick 1: $F_{1,26} = 1.02$, $P = 0.32$; chick 2: $F_{1,22} = 0.23$, $P = 0.64$; chick 3: $F_{1,11} = 0.59$, $P = 0.46$; Fig. 3).

By day 11, first chicks had significantly longer tarsi (31.15 ± 0.35 (± 1 SE) mm, $n = 16$ vs 29.70 ± 0.55 mm, $n = 12$; $F_{1,26} = 5.25$, $P = 0.03$; Fig. 2) and seventh primary feathers (17.60 ± 0.60 mm, $n = 16$ vs 15.00 ± 0.65 mm, $n = 12$; $F_{1,26} = 8.25$, $P = 0.008$; Fig. 3) in 2002 compared

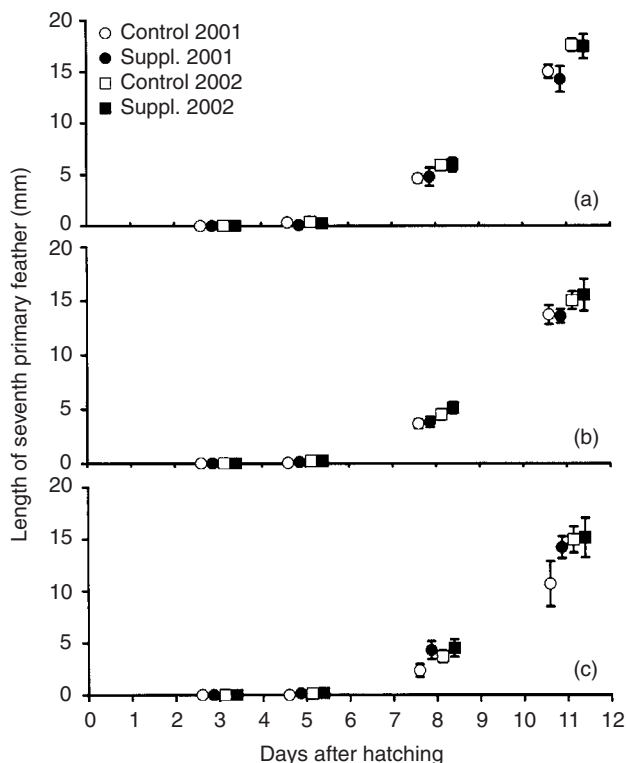


Fig. 3. Changes in the length of the seventh primary feather through the nestling period of chicks (a) 1, (b) 2 and (c) 3 (see Methods for definitions) hatching from eggs laid by Florida scrub-jays *Aphelocoma coerulescens* with access to high fat and high protein (Suppl.) food during pre-laying and nestling periods and those laid by females that were not supplemented (Control) during 2001 and 2002. Points, means; bars, standard errors. Data are separated slightly for clarity.

with 2001. There was no significant difference in their body masses between the 2 years ($F_{1,26} = 0.12$, $P = 0.73$). For chicks 2 and 3, body masses ($F_{1,22} = 0.87$, $P = 0.36$ and $F_{1,11} = 1.58$, $P = 0.23$, respectively), tarsus lengths ($F_{1,22} = 1.98$, $P = 0.17$ and $F_{1,11} = 2.01$, $P = 0.18$,

respectively) and lengths of seventh primaries ($F_{1,22} = 1.14$, $P = 0.30$ and $F_{1,11} = 3.35$, $P = 0.09$, respectively) did not differ significantly between 2001 and 2002.

Generally, of those chicks that hatched, a greater percentage survived to fledging and nutritional independence in 2002 compared with 2001 (Table 1). Fledging success had a tendency to be higher for chicks 1 ($P = 0.08$) and 2 ($P = 0.07$) in 2002, but similar percentages of third chicks fledged in both years ($P = 0.24$). A significantly greater percentage of first ($P = 0.05$) and second ($P = 0.04$) chicks that hatched survived to nutritional independence in 2002 compared with 2001, but similar percentages of third chicks survived to independence in both years ($P = 0.11$).

Growth and survival of chicks on supplemented territories

Body masses of all chicks increased significantly over the nestling period (repeated-measures ANOVA: chick 1: $F_{1,38} = 142.66$, $P = 0.0001$; chick 2: $F_{1,33} = 136.55$, $P = 0.0001$; chick 3: $F_{1,18} = 75.74$, $P = 0.0001$; Fig. 1). However, chick body masses did not differ significantly between dietary treatments (chick 1: $F_{1,38} = 0.03$, $P = 0.86$; chick 2: $F_{1,33} = 0.09$, $P = 0.77$; chick 3: $F_{1,18} = 2.90$, $P = 0.11$) and there was no significant difference in body masses between years for chick 1 ($F_{1,38} = 2.26$, $P = 0.14$), chick 2 ($F_{1,33} = 1.09$, $P = 0.30$) or chick 3 ($F_{1,18} = 1.17$, $P = 0.29$). The year \times treatment interaction was not significant for chicks 1 ($F_{1,38} = 0$, $P = 0.99$) and 3 ($F_{1,18} = 1.74$, $P = 0.20$), while it tended towards significance for chick 2 ($F_{1,33} = 3.46$, $P = 0.07$). Body-mass trajectories across the nestling period were not significantly influenced by hatch date for any of the three chicks (ANCOVA: chick 1: $F_{1,37} = 0.41$, $P = 0.53$; chick 2: $F_{1,32} = 1.41$, $P = 0.24$; chick 3: $F_{1,17} = 1.50$, $P = 0.24$).

By day 11, no significant difference was detected in body masses of first, second or third chicks between 2001 and 2002 ($F_{1,38} = 1.05$, $P = 0.31$, $F_{1,33} = 0.50$, $P = 0.49$ and $F_{1,18} = 1.21$, $P = 0.29$, respectively) or between

Table 1. Survival to fledging and nutritional independence of Florida scrub-jay *Aphelocoma coerulescens* chicks 1, 2, and 3 (see Methods for definitions) hatching from eggs laid by females either on high fat and high protein (Supplemented) supplementary food or on no supplementary food (Control) during the pre-laying and nestling periods of 2001 and 2002. Numbers in parentheses represent the number of chicks hatching from supplementation and control treatments, respectively

	Fledging success (%)		Survival to independence (%)	
	Dietary treatment		Dietary treatment	
	Supplemented	Control	Supplemented	Control
2001				
Chick 1 (9, 19)	66.7	52.6	33.3	26.3
Chick 2 (7, 17)	100.0	52.9	42.9	11.8
Chick 3 (4, 10)	100.0	40.0	50.0	0
2002				
Chick 1 (9, 18)	77.8	77.8	77.8	55.6
Chick 2 (8, 16)	62.5	81.3	37.5	43.8
Chick 3 (7, 10)	71.4	60.0	42.9	30.0

dietary treatments ($F_{1,38} = 0.23$, $P = 0.64$, $F_{1,33} = 0.05$, $P = 0.83$ and $F_{1,18} = 0.13$, $P = 0.72$, respectively). The year \times treatment interaction was not significant for chicks 1 ($F_{1,38} = 0.40$, $P = 0.53$), 2 ($F_{1,33} = 0.04$, $P = 0.85$) or 3 ($F_{1,18} = 0.30$, $P = 0.59$).

The linear growth of tarsi of all chicks increased significantly over the nestling period (repeated-measures ANOVA: chick 1: $F_{1,38} = 7108.06$, $P = 0.0001$; chick 2: $F_{1,33} = 4715.05$, $P = 0.0001$; chick 3: $F_{1,18} = 2572.87$, $P = 0.0001$; Fig. 2). Over the nestling period, tarsus length did not differ significantly between dietary treatments (chick 1: $F_{1,38} = 0.18$, $P = 0.67$; chick 2: $F_{1,33} = 0.81$, $P = 0.37$; chick 3: $F_{1,17} = 0.03$, $P = 0.87$) and for chicks 1 and 3 it did not differ significantly between years ($F_{1,38} = 1.64$, $P = 0.21$ and $F_{1,17} = 0$, $P = 0.97$, respectively). However, tarsus length was significantly longer in 2002 than in 2001 for second chicks from both dietary treatment groups combined ($F_{1,33} = 5.57$, $P = 0.02$). The year \times treatment interaction was not significant for chick 1 ($F_{1,38} = 0.47$, $P = 0.50$), 2 ($F_{1,33} = 0.69$, $P = 0.41$) or 3 ($F_{1,17} = 0.05$, $P = 0.83$). Hatch date did not significantly influence the linear growth of tarsus lengths for chick 1 ($F_{1,37} = 0.26$, $P = 0.61$), chick 2 ($F_{1,32} = 2.32$, $P = 0.14$) or chick 3 ($F_{1,17} = 0.05$, $P = 0.83$).

Tarsus length of first chicks by day 11 differed significantly between years ($F_{1,38} = 9.11$, $P = 0.005$) with chicks in 2002 having tarsi that were *c.* 1.7 mm longer than those in 2001. However, tarsus length did not differ between dietary treatments ($F_{1,38} = 1.53$, $P = 0.23$). The year \times treatment interaction was not significant for chick 1 ($F_{1,38} = 0.30$, $P = 0.58$). For second chicks, tarsus lengths tended to be significantly longer by *c.* 1.25 mm in 2002 compared with 2001 ($F_{1,33} = 3.23$, $P = 0.08$), but there was no significant difference between dietary treatments ($F_{1,33} = 0.02$, $P = 0.89$). The year \times treatment interaction was not significant ($F_{1,33} = 0.06$, $P = 0.81$). Finally, tarsus lengths of third chicks did not differ significantly between years ($F_{1,18} = 1.74$, $P = 0.20$) or dietary treatments ($F_{1,18} = 1.05$, $P = 0.32$), and the year \times treatment interaction was not significant ($F_{1,18} = 0.48$, $P = 0.50$).

Seventh primary feathers only began to emerge by day 5 of the nestling period and therefore their growth was only compared from day 5 to day 11 (Fig. 3). It was found that feather growth increased significantly over the 6-day period for all chicks (repeated-measures ANOVA: chick 1: $F_{1,38} = 58.34$, $P = 0.0001$; chick 2: $F_{1,33} = 27.33$, $P = 0.0001$; chick 3: $F_{1,18} = 5.88$, $P = 0.03$). Feather growth did not differ significantly between dietary treatments for chicks 1 and 2 ($F_{1,38} = 0.39$, $P = 0.53$ and $F_{1,33} = 0.36$, $P = 0.55$, respectively), but growth of seventh primary feathers was significantly higher for third chicks from the supplementation treatment compared with controls ($F_{1,18} = 4.29$, $P = 0.05$). Seventh primary feather growth was elevated in 2002 compared with 2001 for chick 1 ($F_{1,38} = 5.09$, $P = 0.03$), but not for chick 2 ($F_{1,33} = 2.51$, $P = 0.12$) or chick 3 ($F_{1,18} = 0.20$, $P = 0.66$). The year \times treatment interaction was not significant for chicks 1 ($F_{1,38} = 0.43$, $P = 0.51$),

2 ($F_{1,33} = 1.30$, $P = 0.26$) or 3 ($F_{1,18} = 0.37$, $P = 0.55$). Similar to mass and tarsus measures, it was found that the dates of hatching of chicks had no significant influence on the growth of feathers of chick 1 ($F_{1,37} = 3.03$, $P = 0.09$), chick 2 ($F_{1,32} = 3.09$, $P = 0.09$) or chick 3 ($F_{1,17} = 0.44$, $P = 0.51$).

By day 11, first chicks had seventh primaries that were 2.85 mm longer in 2002 compared with 2001 ($F_{1,38} = 10.95$, $P = 0.002$), but feather length did not differ significantly between dietary treatments ($F_{1,38} = 0.27$, $P = 0.61$) and the year \times treatment interaction was not significant ($F_{1,38} = 0.12$, $P = 0.73$). For neither chick 2 nor 3 did seventh primary length differ significantly between years ($F_{1,33} = 3.12$, $P = 0.09$ and $F_{1,18} = 2.33$, $P = 0.14$, respectively) or between dietary treatments ($F_{1,33} = 0$, $P = 0.99$ and $F_{1,18} = 1.18$, $P = 0.29$, respectively). The year \times treatment interaction was not significant for either chick 2 ($F_{1,33} = 0.24$, $P = 0.63$) or chick 3 ($F_{1,18} = 0.96$, $P = 0.34$).

Over 50% of all chicks that hatched survived to fledging in both years (Table 1). Fledging success of first chicks was not significantly different between dietary treatments for either 2001 ($P = 0.26$) or 2002 ($P = 0.37$). Fledging success was significantly greater for second chicks hatching from eggs laid by supplemented females *vs* controls in 2001 ($P = 0.03$) but not in 2002 ($P = 0.23$, Table 1). Fledging success had a tendency to be greater for third chicks hatching from eggs laid by supplemented females than those hatching from controls in 2001 ($P = 0.07$) but this was not the case in 2002 ($P = 0.36$, Table 1).

Dietary treatment had less effect on survival of chicks to nutritional independence than it did on their fledging success. No significant difference was found in survival to independence between treatments within years for chicks 1 (2001: $P = 0.31$; 2002: $P = 0.19$) and 2 (2001: $P = 0.11$; 2002: $P = 0.33$). However, in 2001 the survival to independence of third chicks from eggs laid by supplemented females had a tendency to be higher than controls (50% *vs* 0%; $P = 0.07$, Table 1). This was not the case in 2002 when 42.9% of third chicks from eggs of supplemented females survived to independence compared with 30% of controls ($P = 0.34$, Table 1).

DISCUSSION

This is the first experimental study to investigate how diet quality during pre-breeding and nestling periods might influence proximate (chick growth) and ultimate (fledging success and survival to nutritional independence) measures of breeding performance for this threatened and declining species. Providing a dietary supplement high in fat and protein to females early in pre-laying until day 11 of the nestling period in 2 consecutive years resulted in small improvements in growth of chicks between hatching and day 11. Fledging success of second chicks was significantly improved by supplementation in 2001, but not in 2002. Both fledging success and survival to nutritional independence tended to be higher for third

chicks as a result of supplementation in 2001, but not in 2002.

Year effects

Although growth trajectories of unsupplemented chicks were similar in 2001 and in 2002, we found marked differences in other measures between 2001 and 2002. By day 11, unsupplemented first chicks had longer tarsi and feathers in 2002 compared with 2001. Fledging success and survival to independence of unsupplemented chicks were generally improved in 2002 compared with 2001. Supplementation improved feather growth of third chicks compared with unsupplemented chicks. Furthermore, supplementation differentially improved fledging success and survival to independence of chicks in 2001 compared with 2002. Taken collectively, these results suggest that underlying breeding conditions were better for scrub-jays in 2002 compared with 2001. Emergence of herpetological fauna and insects that are important foods for birds may be delayed by low rainfall (Pianka, 1988; Wingfield & Kenagy, 1991) and shortage of food for breeding birds, when they are recrudescing reproductive tissues and engaged in courtship behaviour, may limit their nutrient intake and thereby delay breeding (Wingfield & Kenagy, 1991; Hahn *et al.*, 1995; Morrison & Bolger, 2002). In 1992, scrub-jays bred extremely late and this was attributed to low rainfall (and reduced food availability) in the 3-month period (November to January) preceding the breeding season (Schoech, 1996). Woolfenden & Fitzpatrick (1984) found that mean annual first-clutch size was highly correlated with total rainfall in the preceding summer (June to September). Although we lack data on natural food availability, we know that rainfall differed markedly between the 2 years of the present study (Fig. 4). The study population of scrub-jays has been characterized since 1987. In most years, researchers have studied birds throughout the breeding season (January–May) and the study site has been revisited later in the year (usually July or August) to make up full colour-ring complements for all independent young. Nest charts from the study site compiled over the last 16 years (R. L. Mumme & S. J. Schoech, pers. obs.) were consulted and they highlighted the marked contrast between the 2 years of this study. In terms of independent-young production per breeding territory, 2002 was the best year on record while 2001 was one of the worst (Table 2).

Chick growth

Woolfenden (1978) provided a detailed description of the growth of Florida scrub-jay chicks for the first 16 days post-hatch. Our data are not directly comparable with his because he presents growth data as overall means collected from the majority of 73 chicks produced from 47 nests during 1973. However, a crude comparison between our study (SJR) (for first chicks regardless of treatment and year – see above) and his (GEW) revealed that our

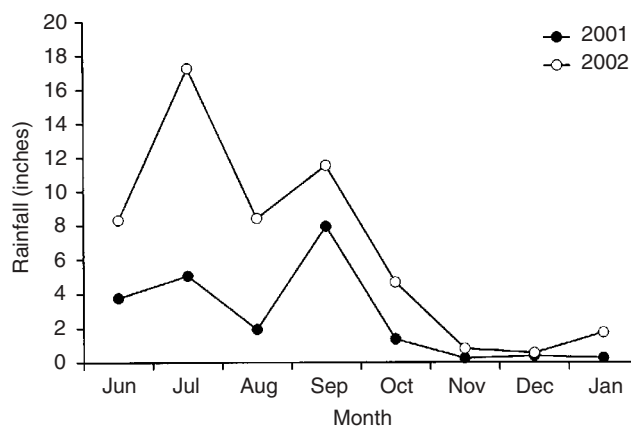


Fig. 4. Total monthly rainfall at Archbold Biological Station in Florida for the summer (June–September) and the pre-breeding (November–January) periods preceding the breeding season of Florida scrub-jays *Aphelocoma coerulescens* in 2001 and 2002. See Discussion for the rationale for considering rainfall during these periods.

Table 2. Production of fledgling and nutritionally independent Florida scrub-jays *Aphelocoma coerulescens* in the study population at Archbold Biological Station in south-central Florida. Only years where complete breeding records were available are presented. Production is expressed per territory because the number of breeding territories fluctuates between years. Data for the years in which the present study was carried out are in bold

Year	No. of fledglings per territory	No. of nutritionally independent young per territory
1987	1.56	0.73
1988	1.52	0.73
1989	1.29	0.42
1990	1.18	0.48
1992	1.36	0.64
1993	2.11	1.17
1994	1.60	1.00
1997	1.31	0.91
1998	0.98	0.57
1999	2.04	1.05
2000	1.67	0.84
2001	1.67	0.70
2002	2.03	1.22

measures of chicks at day 11 were similar: SJR vs GEW for: body mass: 45.50 ± 1.05 g vs 47.25 ± 1.00 g; tarsus length: 30.25 ± 0.30 mm vs 30.35 ± 0.30 mm; seventh primary length: 16.25 ± 0.45 mm vs 16.60 ± 0.45 mm.

Food supplementation had little effect on the growth of chicks in terms of body mass through the nestling period (Fig. 1), despite our suspicions of markedly different natural food availabilities between the 2 years of study (see above). Our findings concur with those of some other investigations. For example, Lepczyk & Karasov (2000) found that growth rates of house sparrow *Passer domesticus* chicks were not altered by changes in local food availability. Furthermore, Massemin *et al.* (2002) found that fledging mass of Eurasian kestrels

Falco tinnunculus was similar between supplemented and unsupplemented birds, even in years when natural food availability was low. The above findings contrast markedly with those from other investigations. For example, in seabirds, chick growth is very sensitive to natural food availability (e.g. Monaghan *et al.*, 1989) and food supplementation can result in marked improvements (e.g. Gill *et al.*, 2002). Such differential growth responses of chicks of different species to food supplementation suggest that experimental approaches may be inappropriate to test the importance of food availability to chick development. Alternatively, breeding conditions (e.g. climate) other than food availability may limit chick growth.

In this study, few differences were found in the growth trajectories of tarsi and feathers between chicks 1, 2 or 3 hatching from eggs laid by supplemented *vs* unsupplemented females (Figs 2 & 3). Seventh primary feathers of third chicks tended to grow significantly longer in chicks hatching from eggs laid by supplemented females than those laid by control females in both years of the study. In comparison with tarsus growth, which may be more strongly under genetic control (e.g. Gard & Bird, 1992), feather growth may be more sensitive to epigenetic factors. For example, Massemin *et al.* (2002) found that supplemented kestrel chicks had similar tarsus lengths but longer feathers than unsupplemented chicks.

When growth measures were compared between chicks 1, 2 and 3 at day 11, there was no evidence that the dietary treatment was differentially affecting growth of different brood members. First chicks were always heavier with longer tarsi and seventh primary feathers than second and third chicks, regardless of whether chicks hatched from eggs laid by supplemented or unsupplemented females.

Chick survival

We believe that the enhanced survival of third chicks (and that of second chicks in one of the 2 years of the study) hatching from eggs laid by supplemented females relative to control chicks did not result because chicks on supplemented territories were fed the supplementary food. Adult scrub-jays were never observed feeding supplementary food to chicks (S. J. Reynolds, pers. obs.). Chicks are fed only animal food (Woolfenden & Fitzpatrick, 1996), primarily lepidopteran larvae and orthopterans. Florida scrub-jay helpers also increase the reproductive success of breeding birds (Woolfenden, 1975); however, no more helpers occurred on supplemented than on control territories (2001: 0.78 ± 0.32 *vs* 1.05 ± 0.26 , respectively; $t_{26} = -0.63$, $P = 0.54$; 2002: 1.11 ± 0.39 *vs* 1.00 ± 0.32 , respectively; $t_{25} = 0.21$, $P = 0.84$).

Previously, Reynolds *et al.* (2003) showed that supplemented females laid significantly heavier third eggs than controls and that this was consistent across 2 consecutive years. Similar to previous studies investigating the effects of egg size and composition on offspring fitness (e.g. Moss *et al.*, 1981; Galbraith, 1988; Amundsen, 1995; but see Magrath, 1992), we believe that elevated egg mass

is a robust effect of food supplementation of the Florida scrub-jay and that this benefits chicks immediately post-hatching and until fledging. A sustained positive effect of egg size on offspring survival during chick-rearing is rarely reported in birds (e.g. Blomqvist, Johansson & Götmark, 1997; Risch & Rohwer, 2000). It was found that effects of supplementation persisted until nutritional independence in third chicks in 2001, but not in 2002, a year in which natural food availability was relatively high (see earlier) compared with 2001.

Unlike other studies that have shown an increase in egg size with food supplementation (e.g. egg volume; Ramsay & Houston, 1997), Reynolds *et al.* (2003) found no significant increase in the absolute dimensions of eggs. Instead, third eggs laid by females on high fat and high protein supplement in 2001 were significantly heavier than those laid by unsupplemented birds, containing an extra 0.27 g of water and 0.06 g of protein (Reynolds *et al.*, 2003). As fresh egg mass increased, water content increased isometrically whereas protein constituted an ever-decreasing fraction of total egg mass. A positive relationship exists between egg size and offspring survival in similar species to Florida scrub-jays where variation in egg size can be attributed to changes in wet albumen or water fractions of eggs (e.g. Bolton, 1991) rather than to the protein fraction *per se* (e.g. Meathrel & Ryder, 1987). Williams (1994) suggested that increases in the water content of eggs (whether they be isometric with or disproportionate to egg size or mass) might be adaptive if hatchlings from larger eggs retain more water than those from smaller or lighter eggs. Furthermore, the lack of investment in the protein fraction of eggs suggests that supplemented females do not facultatively modify the protein content of their eggs to promote the structural development of chicks hatching from them. While we found few differences in the growth of the tarsus and the gain in body mass over the first 11 days of the nestling period between chicks from supplementation *vs* control treatments, our results suggest that the quality of the diet during pre-breeding and nestling periods can influence long-term survival of Florida scrub-jay chicks and this may be mediated partially through egg quality. Amelioration of chick survival through such an egg effect is probably most profound in years when natural food availability is low.

Enhanced chick survival resulting from food supplementation may also be mediated through increased investment in foraging effort by supplemented parents and helpers. Birds on supplemented territories were observed using supplements intensely and, consequently, they may have provisioned chicks with significantly more animal prey than unsupplemented birds that probably consumed such prey themselves. No empirical data are available to test whether supplementary food elevates body condition of provisioning birds during chick-rearing, allowing them to invest more in the smaller brood members compared with unsupplemented birds. Extended parental care (especially applicable in the Florida scrub-jay; Stallcup & Woolfenden, 1978; McGowan & Woolfenden, 1990) probably allows chicks that hatch from smaller eggs to

improve their survival probability (but see Metcalfe & Monaghan, 2001). In comparison with precocial species, where little post-natal feeding of chicks occurs, altricial chicks, such as the Florida scrub-jay, are dependent on adults and helpers for both food and protection during the nestling period and any extended benefits from elevated egg quality are probably small in comparison with this post-natal investment.

Future research should investigate whether supplementation promotes survival of chicks through improvements of health (e.g. blood chemistry, immunocompetence), subtle condition measures that are not detectable from gross morphometrics. Future work should also test whether food supplementation results in improved body condition of adult birds (both parents and helpers), but catching birds to collect such data may be problematic. Parents particularly are wary when they have chicks in the nest. Furthermore, catching birds at this critical time would be ill-advised given the conservation concerns for this species and the increased likelihood of abandonment as a result of trapping.

Acknowledgements

We are grateful to Kim Fernie and Gail Weems for statistical advice. We thank Ed Ulman at Research Diets, Inc. and Kirk Klasing at the University of California at Davis for nutritional information. We also thank our team of field assistants: Raoul Boughton, Michel Duguay, Kate Eldridge, Julie Garvin, Alicia Korpach and Dan Levitis. We thank staff of Archbold Biological Station for continuous support during fieldwork. We are grateful to Nancy Deyrup for providing precipitation data and Ron Mumme for providing long-term breeding records for the study site. We thank Andrew McAdam and an anonymous referee for invaluable comments on the manuscript. SJR was financially supported by the Department of Biology at the University of Memphis, SJS and SJR by National Science Foundation (NSF) Grant IBN-9983201 and RB by NSF Grant IBN-0077469.

REFERENCES

- Amundsen, T. (1995). Egg size and early nestling growth in the snow petrel. *Condor* **97**: 345–351.
- Beissinger, S. R. & Waltman, J. R. (1991). Extraordinary clutch size and hatching asynchrony of a neotropical parrot. *Auk* **108**: 863–871.
- Blomqvist, D., Johansson, O. C. & Götmark, F. (1997). Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia (Berl.)* **110**: 18–24.
- Bolton, M. (1991). Determinants of chick survival in the lesser black-backed gull: relative contributions of egg-size and parental quality. *J. Anim. Ecol.* **60**: 949–960.
- Bolton, M., Houston, D. C. & Monaghan, P. (1992). Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *J. Anim. Ecol.* **61**: 521–532.
- Bolton, M., Monaghan, P. & Houston, D. C. (1993). Proximate determination of clutch size in lesser black-backed gulls: the roles of food supply and body condition. *Can. J. Zool.* **71**: 273–279.
- Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Can. J. Zool.* **68**: 203–220.
- Cargill, S. M. & Cooke, F. (1981). Correlation of laying and hatching sequences in clutches of the lesser snow goose (*Anser caerulescens caerulescens*). *Can. J. Zool.* **59**: 1201–1204.
- Christians, J. K. (2002). Avian egg size: variation within species and inflexibility within individuals. *Biol. Rev. Camb. Philos. Soc.* **77**: 1–26.
- Clotfelter, E. D., Whittingham, L. A. & Dunn, P. O. (2000). Laying order, hatching asynchrony and nestling body mass in tree swallows *Tachycineta bicolor*. *J. Avian Biol.* **31**: 329–334.
- Cooke, F., Rockwell, R. F. & Lank, D. B. (1995). *The snow geese of La Pérouse Bay: natural selection in the wild*. Oxford: Oxford University Press.
- Galbraith, H. (1988). Effects of egg size and composition on the size, quality and survival of lapwing *Vanellus vanellus* chicks. *J. Zool. (Lond.)* **214**: 383–398.
- Gard, N. W. & Bird, D. M. (1992). Nestling growth and fledging success in manipulated American kestrel broods. *Can. J. Zool.* **70**: 2421–2425.
- Gill, V. A., Hatch, S. A. & Lanctot, R. B. (2002). Sensitivity of breeding parameters to food supply in black-legged kittiwakes *Rissa tridactyla*. *Ibis* **144**: 268–283.
- Hahn, T. P., Wingfield, J. C., Mullen, R. & Deviche, P. (1995). Endocrine bases of spatial and temporal opportunism in Arctic-breeding birds. *Am. Zool.* **35**: 259–273.
- Kelly, J. F. & van Horne, B. (1997). Effects of food supplementation on the timing of nest initiation in belted kingfishers. *Ecology* **78**: 2504–2511.
- Korpimäki, E. (1989). Breeding performance of Tengmalm's owl *Aegolius funereus*: effects of supplementary feeding in a peak vole year. *Ibis* **131**: 51–56.
- Lepczyk, C. A. & Karasov, W. H. (2000). Effect of ephemeral food restriction on growth of house sparrows. *Auk* **117**: 164–174.
- Magrath, R. D. (1992). The effect of egg mass on the growth and survival of blackbirds: a field experiment. *J. Zool. (Lond.)* **227**: 639–653.
- Martin, T. E. (1987). Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* **18**: 453–487.
- Massemin, S., Korpimäki, E., Pöyri, V. & Zorn, T. (2002). Influence of hatching order on growth rate and resting metabolism of kestrel nestlings. *J. Avian Biol.* **33**: 235–244.
- McGowan, K. J. & Woolfenden, G. E. (1990). Contributions to fledgling feeding in the Florida scrub jay. *J. Anim. Ecol.* **59**: 691–707.
- Meathrel, C. E. & Ryder, J. P. (1987). Intraclutch variation in the size, mass and composition of ring-billed gull eggs. *Condor* **89**: 364–368.
- Meijer, T. & Drent, R. (1999). Re-examination of the capital and income dichotomy in breeding birds. *Ibis* **141**: 399–414.
- Metcalfe, N. B. & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later. *Trends Ecol. Evol.* **16**: 254–260.
- Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C. & Blackwood, J. (1989). The relationship between food supply, reproductive performance and breeding success in Arctic terns *Sterna paradisaea*. *J. Anim. Ecol.* **58**: 261–274.
- Morrison, S. A. & Bolger, D. T. (2002). Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia (Berl.)* **133**: 315–324.
- Moss, R., Watson, A., Rothery, P. & Glennie, W. W. (1981). Clutch size, egg size, hatch weight and laying date in relation to early mortality in red grouse *Lagopus lagopus scoticus* chicks. *Ibis* **123**: 450–462.
- Mumme, R. L. (1992). Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behav. Ecol. Sociobiol.* **31**: 319–328.

- Pianka, E. R. (1988). *Evolutionary ecology*. New York: Harper and Row.
- Ramsay, S. L. & Houston, D. C. (1997). Nutritional constraints on egg production in the blue tit: a supplementary feeding study. *J. Anim. Ecol.* **66**: 649–657.
- Reynolds, S. J. & Perrins, C. M. (In press). Dietary calcium availability and reproduction in birds. *Curr. Ornithol.*
- Reynolds, S. J., Schoech, S. J. & Bowman, R. (2003). Nutritional quality of pre-breeding diet influences breeding performance of the Florida scrub-jay. *Oecologia (Berl.)* **134**: 308–316.
- Risch, T. S. & Rohwer, F. C. (2000). Effects of parental quality and egg size on growth and survival of herring gull chicks. *Can. J. Zool.* **73**: 967–973.
- SAS Institute (1999). *SAS/STAT User's Guide*. (Release 8. 1 edn). Cary, NC: SAS Institute.
- Schaub, R., Mumme, R. L. & Woolfenden, G. E. (1992). Predation on the eggs and nestlings of Florida scrub jays. *Auk* **109**: 585–593.
- Schoech, S. J. (1996). The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida scrub-jay. *Condor* **98**: 234–244.
- Schoech, S. J. (1999). Florida scrub-jay nestlings preyed upon by an eastern coachwhip. *Fla Field Nat.* **27**: 57–58.
- Schoech, S. J., Mumme, R. L. & Moore, M. C. (1991). Reproductive endocrinology and mechanisms of breeding inhibition in cooperatively breeding Florida scrub jays (*Aphelocoma c. coerulescens*). *Condor* **93**: 354–364.
- Schoech, S. J., Mumme, R. L. & Wingfield, J. C. (1996). Prolactin and helping behaviour in the cooperatively breeding Florida scrub-jay, *Aphelocoma c. coerulescens*. *Anim. Behav.* **52**: 445–456.
- Sinervo, B. & Huey, R. B. (1990). Allometric engineering: an experimental test of the causes of interpopulational differences in performance. *Science* **248**: 1106–1109.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. New York: W. H. Freeman.
- Stallcup, J. A. & Woolfenden, G. E. (1978). Family status and contribution to breeding by Florida scrub jays. *Anim. Behav.* **26**: 1144–1156.
- Stoleson, S. H. & Beissinger, S. R. (1995). Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? *Curr. Ornithol.* **12**: 191–270.
- von Ende, C. N. (2001). Repeated-measures analysis: growth and other time-dependent measures. In *Design and analysis of ecological experiments*: 134–157. Scheiner, S. M. & Gurevitch, J. (Eds). Oxford: Oxford University Press.
- Wiebe, K. & Bortolotti, G. R. (1995). Egg size and clutch size in the reproductive investment of American kestrels. *J. Zool. (Lond.)* **237**: 285–302.
- Williams, T. D. (1994). Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Rev. Camb. Philos. Soc.* **68**: 35–59.
- Winer, B. J., Brown, D. R. & Michaels, K. M. (1991). *Statistical principles in experimental design*. New York: McGraw-Hill.
- Wingfield, J. C. & Kenagy, G. J. (1991). Natural regulation of reproductive cycles. In *Vertebrate endocrinology: fundamentals and biomedical implications*: 181–241. Screibman, M. P. & Jones, R. E. (Eds). New York: Academic Press.
- Woolfenden, G. E. (1975). Florida scrub jay helpers at the nest. *Auk* **92**: 1–15.
- Woolfenden, G. E. (1978). Growth and survival of young Florida scrub jays. *Wilson Bull.* **90**: 1–18.
- Woolfenden, G. E. & Fitzpatrick, J. W. (1984). *The Florida scrub jay: demography of a cooperative-breeding bird*. Princeton, NJ: Princeton University Press.
- Woolfenden, G. E. & Fitzpatrick, J. W. (1996). Florida scrub-jay (*Aphelocoma coerulescens*). In *The birds of North America*: 228. Poole, A. & Gill, F. (Eds). Philadelphia, PA: Academy of Natural Sciences, and Washington, DC: American Ornithologists' Union.