

Why is brood reduction in Florida scrub-jays higher in suburban than in wildland habitats?

Matthew D. Shawkey, Reed Bowman, and Glen E. Woolfenden

Abstract: In a population of Florida scrub-jays, *Aphelocoma coerulescens* (Bosc, 1795), in a suburban scrub habitat, partial brood loss is much more common (averaging about 30% of nestlings from successful nests) than in a natural habitat (averaging about 5%). We hypothesized that this partial brood loss was attributable to starvation of last-hatched nestlings (i.e., brood reduction), and that large differences in partial brood loss were caused by differences in arthropod food abundance between the two sites. To test these hypotheses, we closely monitored nests in suburban scrub in 1999 and performed arthropod surveys and focal-nest observations in both habitats in 1998 and 1999. In suburban scrub, later hatched nestlings were three times more likely to die before fledging than earlier hatched nestlings, suggesting that brood reduction occurred. In both years, arthropod abundance in the suburban scrub was less than half that of the natural scrub. However, patterns of food delivery by parents were not significantly different between sites, suggesting that lower food abundance does not in itself explain higher partial brood loss in suburban habitat. Differences in the number of helpers, a greater degree of hatching asynchrony or the delivery of lower quality food throughout the nestling period may increase the probability that later hatched nestlings starve in suburban scrub.

Résumé : Au sein d'une population du geai à gorge blanche, *Aphelocoma coerulescens* (Bosc, 1795), dans un habitat suburbain, le taux de réduction de la couvée (en moyenne 30 % des oisillons provenant de nidifications réussies) est beaucoup plus élevé que dans un habitat naturel (en moyenne 5 % des oisillons). Nous proposons deux hypothèses pour expliquer ce phénomène. Nous suggérons premièrement que la mort par famine des oisillons qui sont les derniers à éclore est responsable de la réduction des couvées et deuxièmement que cette famine est causée par une différence dans l'abondance de nourriture provenant d'arthropodes entre ces deux habitats. Afin d'examiner ces hypothèses, nous avons méticuleusement surveillé plusieurs nids dans un habitat suburbain de buissons en 1999 et nous avons conduit des inventaires d'arthropodes ainsi que des observations focales des nids dans un habitat suburbain et un habitat naturel en 1998 et 1999. Dans l'habitat suburbain, les oisillons les derniers à éclore sont trois fois plus susceptibles de mourir avant l'envol que les oisillons les premiers à éclore; il y a donc une réduction des couvées. Pendant ces deux années, l'abondance d'arthropodes était deux fois plus élevée dans l'habitat naturel que dans l'habitat suburbain. Cependant, il n'y avait pas de différence significative entre les deux sites en ce qui concerne le nombre de livraisons de nourriture au nid par les parents ou ni la quantité de nourriture livrée au nid. Ces résultats laissent croire que la réduction d'abondance de nourriture n'est pas seule responsable du plus haut taux de réduction de la couvée dans l'habitat suburbain. La plus haute probabilité de mort par famine des oisillons les derniers à éclore dans l'habitat suburbain pourrait plutôt être causée par une différence dans le nombre d'assistants au nid, par un taux plus élevé d'éclosions asynchrones des oeufs, ou par la livraison de nourriture de plus basse qualité par les parents.

Introduction

The loss of some nestlings prior to fledging occurs frequently in many bird species (reviewed in Mock and Forbes 1995). When this loss occurs nonrandomly relative to nestling size or hatching sequence, it is termed brood reduction (Lack 1954, 1968), and when it is random it is termed partial brood loss. Brood reduction typically occurs when the later hatched, smaller nestlings starve (Stoleson and Beissinger 1995). Many birds lay clutches of eggs that hatch asynchronously and earlier hatched nestlings may be fed before

their siblings hatch. This leads to within-brood asymmetry in nestling mass in which earlier hatched nestlings weigh more than their later hatched siblings at hatch completion. In years of high food abundance parents are able to feed the entire brood. When food abundance is low, parents can bring only enough food to meet the demands of some of the nestlings. Whether by parental preference or sibling competition, the larger nestlings get most of this food and the smaller ones starve (Lack 1954, 1968).

Many studies have shown that food abundance influences nestling growth and survival in birds. Nestling tree swal-

Received 4 December 2003. Accepted 17 August 2004. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 18 November 2004.

M.D. Shawkey,^{1,2} R. Bowman, and G.E. Woolfenden. Archbold Biological Station, 123 Main Drive, Venus, FL 33960, USA, and Department of Biology, University of South Florida, Tampa, FL 33613, USA.

¹Corresponding author (e-mail: shawkmd@auburn.edu).

²Present address: Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36849, USA.

lows, *Tachycineta bicolor* (Vieillot, 1808), grew and survived better in habitats with higher food abundance, and brood reduction occurred only in habitats with low food abundance (Quinney et al. 1986). The mass of nestling red-winged blackbirds, *Agelaius phoeniceus* (L., 1766), increased and starvation decreased during periodic cicada emergences (Strehl and White 1986). During years of low food abundance, European blackbirds (*Turdus merula* L., 1758) could raise their marginal nestling only when provided with supplemental food (Magrath 1989). Thus, low food abundance appears to be associated with low nestling mass and increased starvation and brood reduction.

Some studies have shown that arthropod abundance is relatively low in urbanized areas (reviewed in McIntyre 2000). This decrease in abundance may be caused by habitat fragmentation and loss (Pyle et al. 1981), pollution (McIntyre 2000), fire suppression (Deyrup and Franz 1994; Chambers and Samways 1998), or pesticide use. Arthropods are a critical part of the nestling diet in many bird species (O'Connor 1984). Thus, brood reduction in insectivorous birds is likely to increase along a gradient of increasing urbanization and decreasing arthropod abundance.

Only a few studies have looked for differences in brood reduction between urban or suburban and wildland habitats. In England, great tit (*Parus major* L., 1758) nestlings reared in suburban gardens and hedgerows were lighter on day 15 post hatching than those reared in woodlands (Van Balen 1973). European blackbird nestlings in suburban habitats weighed less at fledging than those in woodland habitats (Snow 1958); however, Chamberlain et al. (1999) found that rates of brood reduction in blackbirds were similar between rural and woodland habitats, even though earthworms were less abundant in the rural habitat. In Switzerland, carrion crow (*Corvus corone* L., 1758) nestlings reared in urban habitats were lighter at fledging than those reared in rural habitats (Richner 1989). Thus, the young of birds in urban or suburban habitats appear to be lighter at fledging than those of birds in rural or wildland habitats, but the association between food abundance and brood reduction is not clear and has not been explicitly addressed in these studies.

The Florida scrub-jay, *Aphelocoma coerulescens* (Bosc, 1795), is restricted to xeric oak–scrub habitats in peninsular Florida. These habitats occur on relatively high, well-drained sandy ridges that often are preferred for human residential developments because of the relatively low risk of flooding. Over 30% of extant Florida scrub-jays range-wide occur in scrub habitat patches surrounded by suburban development (Breininger 1999). Among scrub-jays in wildland habitats, brood reduction or partial brood loss is relatively rare; about 5% of nestlings from nests that fledge at least one young die prior to fledging (Woolfenden and Fitzpatrick 1996). However, in scrub-jay populations surrounded by suburban habitats, brood reduction or partial brood loss is much more frequent, averaging 30% of all nestlings from otherwise successful nests (Bowman and Woolfenden 2001).

We hypothesized that partial brood loss in suburban habitats is nonrandom and is thus appropriately termed brood reduction. We hypothesized that high levels of brood reduction among scrub-jays in suburban scrub is associated with reduced arthropod abundance in those habitats. Although scrub-jays are omnivorous (Woolfenden and Fitzpatrick

1996), the primary food provided to nestling scrub-jays is arthropods, especially lepidopteran larvae and orthopteran (Stallcup and Woolfenden 1978). If arthropods are less abundant in suburban habitats, then parents would have to exert more effort to feed similar numbers of nestlings or feed nestlings less food than parents in wildland scrub. If the latter were true, this could lead to higher levels of brood reduction in suburban habitats. In this study, we examine variation in arthropod abundance in xeric oak scrub at a natural preserve, hereinafter referred to as wildland scrub, and in oak-scrub patches surrounded by suburban development, hereinafter referred to as suburban scrub. We predicted that arthropod populations, especially orthopterans and lepidopteran larvae, would be lower in suburban scrub than in wildland scrub, and that nestlings would be fed less food, resulting in higher rates of brood reduction and decreased mass prior to fledging. We distinguish between partial brood loss and brood reduction, but we do not test the potential adaptive value of brood reduction in the suburban jay population. Rather, we seek to explain the differences in rates of brood reduction between a population in suburban habitat and one in wildlands.

Methods

Study organism

Florida scrub-jays are cooperative breeders that occupy large, permanently defended all-purpose territories in oak-scrub habitat. Adult scrub-jays live in family units consisting of a monogamous breeding pair and sometimes one or more nonbreeding helpers. Helpers provide some food to nestlings and fledglings, and assist in nest defense (Woolfenden and Fitzpatrick 1996).

Study sites

Oak scrub is a xeric, pyrogenic, shrubby plant community dominated by low-growing (<3 m high) oaks (species of the genus *Quercus* L.) and several other species of woody shrubs (e.g., species of the genera *Ilex* L. and *Lyonia* Nutt., *Befaria racemosa* Mutix ex L., *Ceratiola ericoides* Michx.), palmettos (*Serenoa repens* (Bartr.) Small and *Sabal etonia* Swingle ex Nash) and many endemic herbaceous plants (for a further description of wildland scrub see Abrahamson et al. 1984).

Of the two scrub-jay populations in this study, one occurs in natural scrub (wildlands) at Archbold Biological Station (27°10'N, 81°21'W) in Lake Placid, Florida, where the scrub-jays have been studied extensively over the past 30 years (Woolfenden and Fitzpatrick 1996). At Archbold Biological Station, prescribed fire management maintains scrub as habitat suitable for scrub-jays (for further details of the study tract see Woolfenden and Fitzpatrick 1984). The other scrub-jay population occurs in fragmented patches of scrub embedded in a matrix of residential suburban development (suburbs) (27°16'N, 81°24'W), 8 km north of Archbold Biological Station. This population has been studied over the past 10 years (Bowman et al. 1998; Bowman and Woolfenden 2001). As a result of fire suppression, oaks are taller, pine density is greater, and open sand patches are fewer in the suburban scrub patches than in wildland habitat (Bowman and Woolfenden 2001). In general, vital rates for scrub-jays such as adult and juvenile survival and nesting

and hatching success decline under these fire-suppressed conditions (Woolfenden and Fitzpatrick 1996; Bowman and Woolfenden 2001). Pesticides are commonly used both on residential lawns and in adjacent orange groves. Fire suppression, habitat fragmentation, and pesticide use may decrease the population sizes of many arthropods (McIntyre 2000).

In the suburbs, virtually all scrub-jays have access to human-provided food from bird feeders, pet foods, garbage, and neighborhood residents who feed peanuts and other foods to these social birds. Although these foods are available essentially *ad libitum*, many (seeds, bread) may have lower protein content than natural foods (orthopterans, lepidopteran larvae) (Bell 1990; Karasov 1990) and thus may be of relatively lower quality as food for growing nestlings.

Definition of terms

We define successful nests as those that fledge at least one young and brood reduction as nonrandom loss of nestlings from successful nests. Following Woolfenden and Fitzpatrick (1996), we define a dilling as the last-hatched nestling in a brood.

Patterns of brood reduction

In 1999, we distinguished brood reduction from partial brood loss in the suburbs by determining whether later hatched nestlings were more likely to die than their siblings. We did so by frequently checking nests in the suburbs during the hatching and nestling stage. Florida scrub-jays have an 18-day incubation period (Woolfenden and Fitzpatrick 1996). On day 17 of incubation, we checked nests once, between 1000 and 1400, to determine if hatching had started. Beginning on day 18, we checked nests three times daily: at approximately 0900, 1200, and 1600. At each visit, we weighed each nestling and marked each newly hatched nestling on a different toe using nail polish. We continued daily visits at the same time intervals until all eggs hatched or until 1600 on the third day after the first egg had hatched. We assumed that all viable eggs had hatched by this time. Once we determined that hatch completion had occurred, we did not revisit the nest until day 3 of the nestling stage. On days 3 and 8 post hatching (i.e., after the hatching of the final egg), we checked each nest for loss of nestlings. On day 11 we weighed and individually banded each nestling.

In the suburbs during 1998 and in the wildlands in both 1998 and 1999, we collected nesting data using slightly less intensive methods than those described above. Nest visitation was slightly more frequent at the wildland site than at the suburban site. Virtually all nests were found prior to the laying of the final egg. Nests were checked every 3 days during incubation in the wildlands and on days 9 and 18 of incubation in the suburbs. During the nestling stage, nests were checked every 3 days in the wildlands and on days 6 and 11 post hatching in the suburbs. At both sites on day 11, nestlings were weighed, their tarsi were measured, and they were banded with one metal US Fish and Wildlife Service band and one plastic color band.

All nests at both sites in both years were visited on days 16 and 18 post hatching to determine fledging. We considered brood reduction to have occurred if a nestling disappeared before fledging from any nest that fledged at least

one young. We measured brood reduction as both the percentage of nestlings lost per successful nest and the proportion of successful nests experiencing brood reduction.

Differences in arthropod abundance and feeding patterns

To address the hypothesis that relatively high rates of brood reduction in the suburban scrub-jay population are associated with reduced arthropod availability, we determined for both the suburban and wildland study sites (*i*) the number of arthropods found per hour, (*ii*) the number of food deliveries by adult scrub-jays to nestlings, and (*iii*) nestling mass gain on day 5.

To determine the number and types of arthropods available, we selected random points in oak-scrub habitat at both sites. We used a grid and random number generator to place 21 points throughout scrub patches at the suburban site. Points had previously been placed using similar techniques in wildland scrub. Only points within oak-scrub patches were used, and all points at both sites were spaced sufficiently to avoid repeated sampling in any one scrub-jay territory. From March to June we measured arthropod abundance once a month at each of these points by searching, for 1 h, as much vegetation as possible within a 10-m radius of the point. We recorded all vegetation searched, as well as all orthopterans and lepidopteran larvae found. We used the total number of orthopterans and lepidopteran larvae found per month as our estimate of arthropod abundance because these arthropods are the most common food items fed to nestling scrub-jays (Woolfenden and Fitzpatrick 1996). Different observers performed arthropod counts in suburban and wildland scrub; however, to reduce the possibility of observer bias, we performed two test counts 1 week apart at each other's sites prior to the breeding season in both years. Counts of both orthopterans and lepidopteran larvae by different observers differed only by about $\pm 5\%$ in each year, therefore we concluded that our data were comparable.

To determine nestling feeding rates, we observed active nests for 1 h, beginning 1 h after sunrise on day 5 of the nestling period at both sites. We performed observations from a blind 10 m from the nest after waiting 10 min following weighing of nestlings (see below). Most scrub-jays resumed feeding either during or soon after this 10-min period. Using a spotting scope, we observed the number of food deliveries made to the nest by each parent. To control for the effects of group size, we observed only nests without helpers.

To determine the average mass gain of nestlings, we weighed each nestling and marked it individually by painting a toe with nail polish immediately prior to our observation period. At the end of the observation, we again weighed all nestlings. By subtracting the initial mass of each nestling from its postobservation mass, we calculated how much mass each nestling gained. Because we could not directly measure the size of boluses delivered to nestlings, we used average mass gain as a measure of the total amount of food delivered to each nestling. We were unable to obtain feeding-rate data for some broods, mostly because we could not easily observe the nest without disturbance, but we still used the nestling-mass data from these nests.

Analyses

We measured partial brood loss as the average percentage of nestlings lost from successful nests of each brood size and as the proportion of all successful nests at each site experiencing some brood reduction. The first is a measure of the intensity of brood reduction and the second is a measure of its occurrence in the population. We compared the former using univariate ANOVA (SPSS Inc. 1999) with site, year, presence of helpers (when applicable), and brood size as fixed factors. We compared the latter between sites and, within sites, between years, using χ^2 analysis. For analyses of arthropod abundance, food deliveries, and nestling mass we used ANOVA. Percentage data were arcsine transformed. Data lacking normality or homogeneity of variance were appropriately transformed.

Results

Patterns of partial brood loss

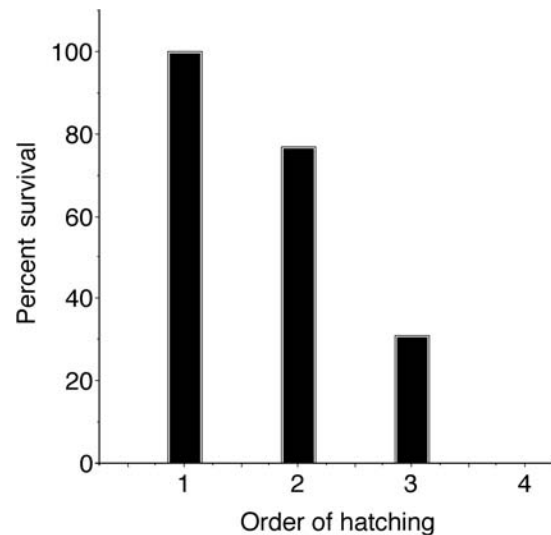
In suburban scrub in 1999, dillings fledged least often and first-hatched nestlings fledged most often (Fig. 1). For broods of three and four, 100% (13/13) of first-hatched nestlings fledged. For broods of three, 87.5% (7/8) of second-hatched nestlings, and 37.5% (3/8) of third-hatched nestlings fledged. For broods of four, 60% (3/5) of second-hatched nestlings, 20% (1/5) of third-hatched nestlings, and 0% (0/5) of fourth-hatched nestlings fledged. Thus, partial brood loss in the suburbs was nonrandom and is appropriately termed brood reduction. Dillings in wildland habitat do not experience higher levels of mortality as nestlings (Woolfenden and Fitzpatrick 1996), suggesting that partial brood loss there is random; however, for consistency we subsequently refer to all partial brood loss as brood reduction in both habitats.

In suburban scrub, the nestling-mass asymmetry at hatch completion (i.e., mass of first-hatched nestling minus mass of dilling) was 1.96 ± 0.17 g (mean \pm SE; $N = 38$). Dillings weighed 30% less than first-hatched nestlings at hatch completion. On day 5, this asymmetry was 7.01 ± 0.59 g ($N = 28$), and dillings weighed 38% less than first-hatched nestlings. On day 11, asymmetry was 13.05 ± 1.63 g ($N = 13$), but dillings weighed about 33% less than first-hatched nestlings. This leveling of asymmetry between days 5 and 11 may have been caused by the disappearance of 54% of dillings during that period.

Mass asymmetry at both hatch completion (Mann-Whitney test, $U = 17.5$, $P = 0.022$) and at day 5 (ANOVA, $F_{[1,23]} = 7.14$, $P = 0.016$) was significantly greater in broods that experienced loss of dillings by day 11 than in those that did not. Mass asymmetry at both hatch completion and day 5 was not significantly different between broods that did and did not experience loss of dillings by fledging (all $P > 0.20$), but only 23% (3/13) of dillings from successful nests fledged.

The percentage of nestlings lost per successful nest was significantly higher in suburban scrub than in wildland scrub ($F_{[1,123]} = 16.5$, $P < 0.001$; Fig. 2) and significantly higher for groups without helpers than for groups with helpers ($F_{[1,123]} = 5.2$, $P < 0.05$; Fig. 2). Brood reduction was almost significantly greater in larger broods ($F_{[3,123]} = 2.6$, $P = 0.058$; Fig. 2). A significant interaction existed between the two habitat types and brood size ($F_{[2,123]} = 3.6$, $P < 0.05$; Fig. 2); brood reduction was greater in large broods in sub-

Fig. 1. Hatch sequence of Florida scrub-jay (*Aphelocoma coerulescens*) nestlings and percent fledging in suburban scrub in central Florida in 1999 ($N = 13$ nests in total: 8 broods of three and 5 broods of four).



urban scrub but not in wildland scrub. No other differences or interactions were significant (all $P > 0.08$).

For the 2 years combined, the proportion of nests experiencing brood reduction was significantly higher in suburban scrub than in wildland scrub ($\chi^2 = 9.5$, $P < 0.01$). In suburban scrub, the proportion of nests experiencing brood reduction did not differ between 1998 and 1999 ($\chi^2 = 0.2$, $P = 0.6$), but in wildland scrub, brood reduction was higher in 1999 than in 1998 ($\chi^2 = 4.4$, $P = 0.04$).

Differences in arthropod abundance

Total arthropod abundance was significantly lower in suburban scrub than in wildland scrub ($F_{[1,310]} = 45.3$, $P < 0.001$; Fig. 3a), and was almost significantly lower in 1999 than in 1998 ($F_{[1,310]} = 3.2$, $P = 0.072$). These differences greatly exceed the 5% difference associated with observer error. No other differences or interactions were significant (all $P > 0.08$).

Focal-nest observations

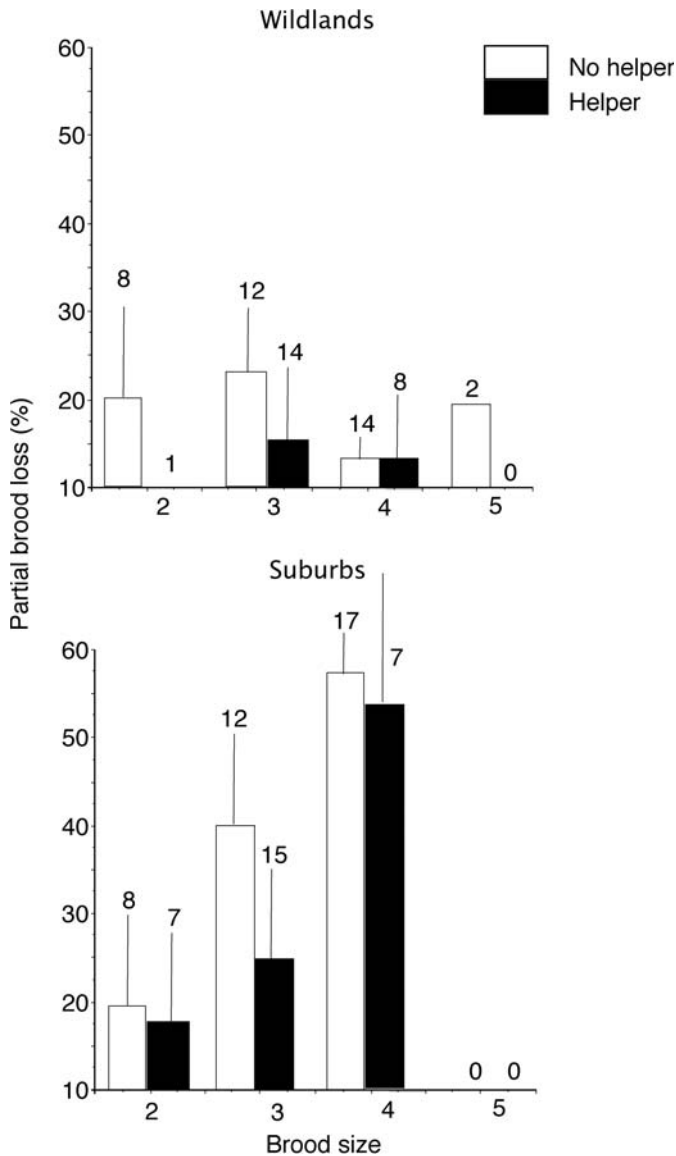
Adults made significantly fewer trips to the nest in 1999 than in 1998 ($F_{[1,41]} = 4.3$, $P < 0.05$; Fig. 3b). A significant interaction existed between year and site ($F_{[1,41]} = 4.7$, $P < 0.05$; Fig. 3b); in 1998, adults in suburban scrub made fewer trips to the nest than those in wildland scrub, but no difference existed in 1999. No other differences or interactions were significant (all $P > 0.08$).

Nestling mass gain per hour was significantly lower in 1999 than in 1998 ($F_{[1,41]} = 13.5$, $P < 0.01$; Fig. 3c). No other differences or interactions were significant (all $P > 0.08$).

Nestling mass

The mean brood mass on day 11 post hatching was significantly lower in suburban scrub (37.1 ± 9.2 g) than in wildland scrub (41.8 ± 7.1 g; $F_{[1,179]} = 16.1$, $P < 0.001$). Mean brood masses also were lighter in 1999 than in 1998

Fig. 2. Partial brood loss among Florida scrub-jays in suburban and wildland scrub in central Florida, sorted by brood size, for groups with and without helpers. Partial brood loss was measured as the percentage of nestlings lost from successful nests (mean \pm 1 SE). The numbers above the bars show the number of successful nests.



($F_{[1,179]} = 10.2, P < 0.01$; Fig. 4). Mean brood mass was greater in groups with helpers than those without ($F_{[1,179]} = 5.9, P < 0.02$; Fig. 4). No significant interactions (all $P > 0.10$) existed among the three variables (site, year, helpers). The mean mass of the first-hatched nestling in the brood was significantly lower in suburban scrub than in wildland scrub (42.7 and 46.2 g, respectively; $F_{[1,145]} = 5.8, P < 0.02$), regardless of brood size. The mean mass of the smallest nestling in the brood (always the dilling, unless it had disappeared by day 11) also was significantly lower in suburban scrub than in wildland scrub (31.6 and 35.9 g, respectively; $F_{[1,145]} = 11.7, P < 0.001$). At each site, the smallest nestling was significantly larger in broods of two than in

broods of three or four (Duncan post-hoc comparisons, $P < 0.02$).

Discussion

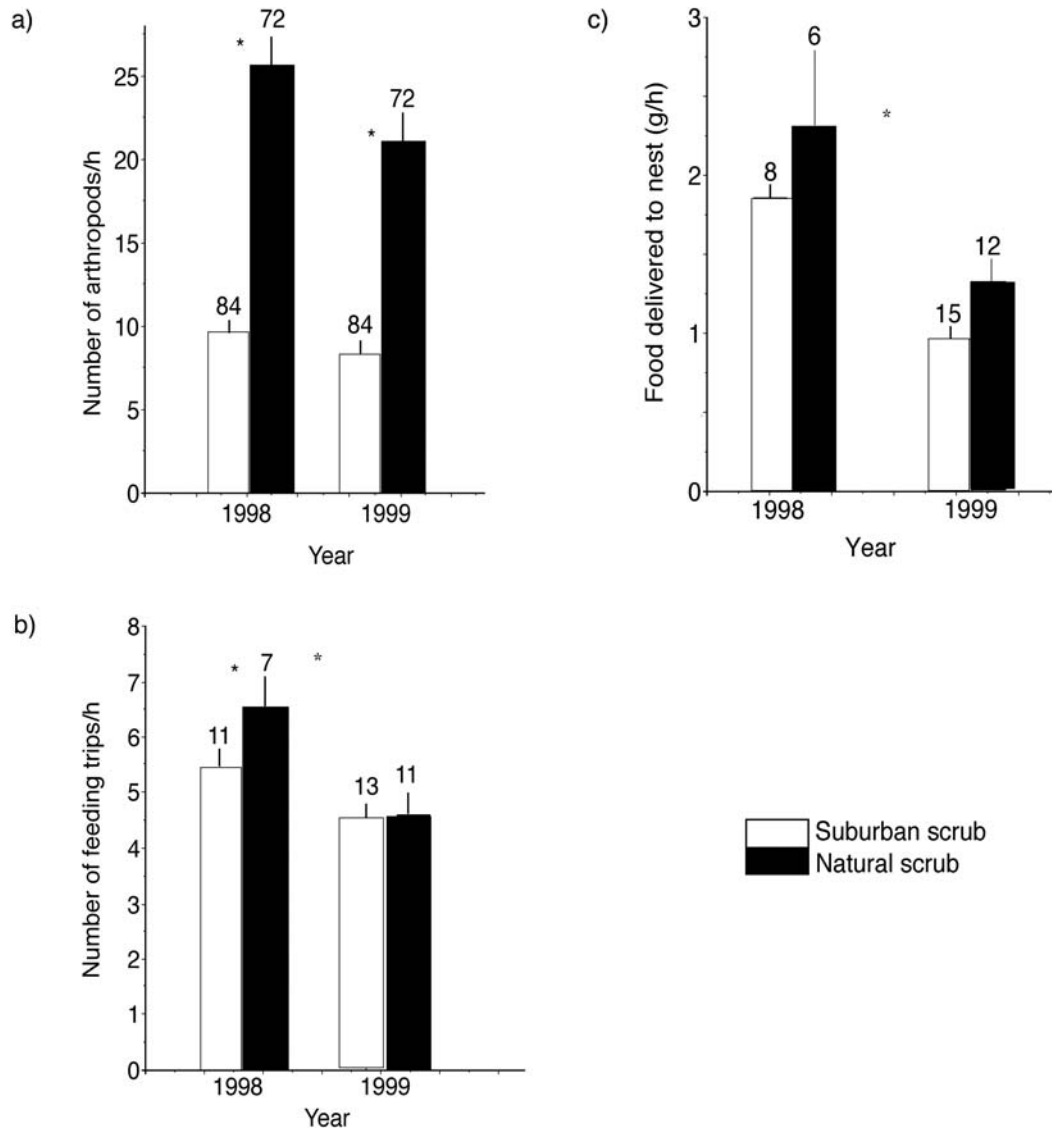
We found that partial brood loss in Florida scrub-jays in suburban habitats was nonrandom, occurring most often through the loss of later hatched, lighter weight nestlings. In wildland scrub, partial brood loss appears to be random (Woolfenden and Fitzpatrick 1996). In addition, nestlings, especially dillings, were smaller in suburban scrub than in wildland scrub. Arthropods were less abundant in the suburbs than in wildlands, but their abundance also varied between years. However, only in wildland scrub did more nests experience partial brood loss when arthropods were less abundant. Suburban scrub-jays made fewer trips to the nest in 1998, but nestlings gained as much mass as wildland jays.

In suburban scrub, nonrandom patterns of partial brood loss and the relatively low mass of nestlings, especially dillings, suggests that losses are brought on by starvation. The increase in the rate of partial brood loss with brood size further supports the idea that this loss is caused by starvation. The significantly greater nestling-mass asymmetry among broods that experienced loss of dillings by day 11 and the large increase in asymmetry by day 5 suggest that dillings are at a disadvantage relative to their earlier hatched nestmates. While brood reduction can occur through outright siblicide or infanticide (Mock and Forbes 1995), these two behaviors are not known to occur in this species (Woolfenden and Fitzpatrick 1996). These patterns together fit the definition of brood reduction provided by Clark and Wilson (1981), and we conclude that brood reduction, most likely by starvation of dillings, occurs in Florida scrub-jays in suburban habitats.

In contrast, partial brood loss occurs infrequently in wildland scrub with little apparent pattern (Woolfenden and Fitzpatrick 1996). Although dillings often are the lightest weight nestling in a brood, they do not experience higher rates of mortality as nestlings than do their heavier nestmates (Woolfenden and Fitzpatrick 1996). Thus, in wildland habitats, nestling loss from otherwise successful nests is appropriately termed partial brood loss, and may be attributed primarily to stochastic events such as predation rather than starvation (Schoech 1999). The differences between sites are consistent with our hypothesis that in suburban scrub, brood reduction is associated with lower overall availability of food. In wildlands, sufficient food may be available in most years that all nestlings, including dillings, have sufficient food to fledge. In some years, arthropods may be less abundant and more nests may have some partial brood loss. In suburban habitats, arthropod abundance always may be limiting enough that dillings frequently starve in most years.

Several studies have demonstrated that brood reduction occurs more frequently when food is limited (Quinney et al. 1986; Strehl and White 1986; Magrath 1989). Our observations in suburban and wildland habitats are consistent with these studies. When arthropod abundance was reduced in the wildland habitat in 1999, brood reduction increased (49% of nests in 1999 vs. 19% of nests in 1998). In the suburbs, where arthropod abundance is consistently low, little differ-

Fig. 3. (a) Arthropod abundance in suburban and wildland scrub in central Florida, calculated as the average number of orthopterans and lepidopteran larvae (± 1 SE) found per hour in 1998 and 1999. The numbers above the bars show the number of sampling hours for March–June. Asterisks indicate significant differences ($P < 0.05$) between sites. (b) Numbers of feeding trips (mean ± 1 SE) taken to the nest by Florida scrub-jays in suburban and wildland scrub in central Florida during 1-h focal-nest observations in 1998 and 1999. The numbers above the bars show the number of nests observed. Numbers of feeding trips differed significantly between sites in 1998 and between years for both sites combined (*, $P < 0.05$). (c) Nestling mass gain (mean ± 1 SE) for Florida scrub-jays in suburban and wildland scrub in central Florida during 1-h focal-nest observations in 1998 and 1999. The numbers above the bars show the number of nests observed. Mass gain differed significantly between years (*, $P < 0.05$) but not between habitat types ($P > 0.05$). Only nests without helpers were observed.



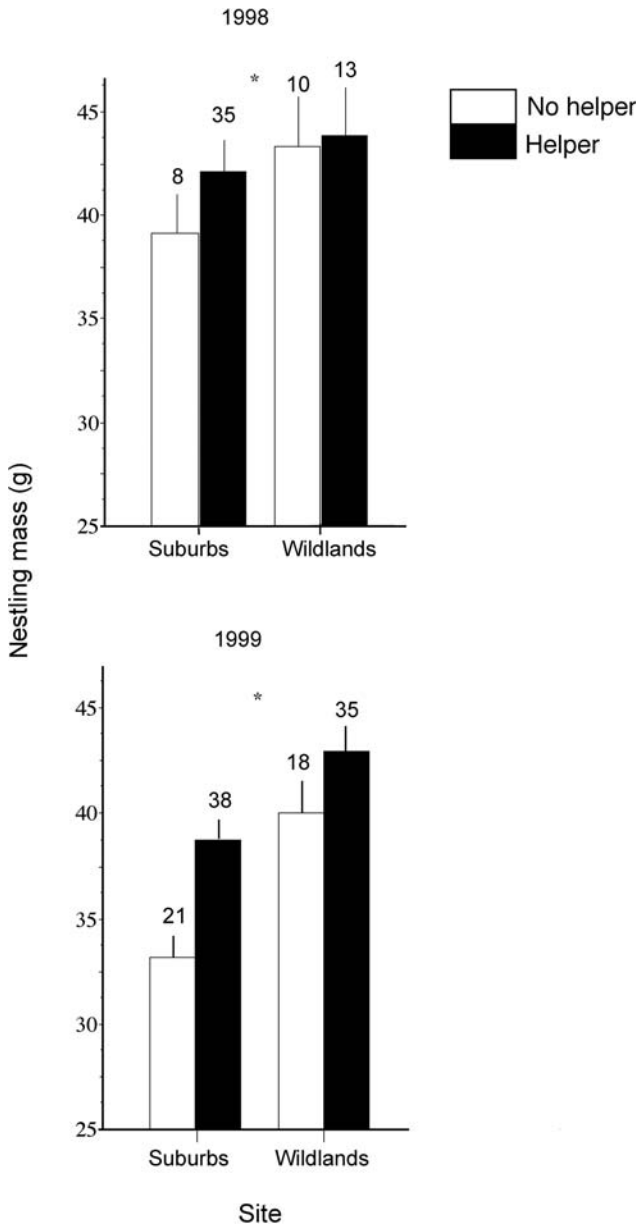
ence in the occurrence of brood reduction existed between the 2 years (71% of nests in 1999 vs. 65% of nests in 1998).

Although the apparent covariation between food abundance and brood reduction in our study supports our hypotheses, we found less convincing evidence when examining the effect of parental effort on brood reduction. In 1998, birds in the wildlands made more feeding trips per observation than did birds in the suburbs, while in 1999, these rates did not differ. However, brood reduction was still much higher in suburban scrub in 1999. At both sites, the mass gain of nestlings per observation was lower in 1999, but in neither year did the mass gain of nestlings differ between

suburban and wildland scrub. From these data it is difficult to conclude that differences in parental effort or food delivery per se caused the differences in brood reduction between the two sites.

The presence of helpers also had a significant effect on both brood-reduction rates and nestling mass. Scrub-jay helpers feed nestlings (Woolfenden and Fitzpatrick 1996); thus, we might expect groups with helpers to be better able to compensate for large broods. Although we found no significant interaction between the presence of helpers and site, group size is generally lower in the suburban scrub-jay population than in the wildland population (R. Bowman, unpub-

Fig. 4. Mass (mean \pm 1 SE) of Florida scrub-jay nestlings in suburban and wildland scrub in central Florida in 1998 and 1999, sorted by presence or absence of a helper. The numbers above the bars show the number of broods. Mean brood mass was significantly lower in suburban than in wildland habitats (*, $P < 0.05$), and in nests without helpers than in nests with helpers (*, $P < 0.05$).



lished data). If helpers provide additional food, then groups with helpers are more likely to be able to obtain and deliver adequate food when either food abundance is low or brood size is large. Few studies of brood reduction in cooperative breeding birds have been conducted. Bryant and Tatner (1990) did not consider the effect of group size on rates of brood reduction in blue-throated bee-eaters (*Merops viridis* L., 1758). Legge (2000) found that helpers did not affect brood reduction in laughing kookaburras, *Dacelo novaeguineae* (Hermann, 1783). However, most brood reduction in both of these species is caused by siblicide, which is ab-

sent in Florida scrub-jays (Woolfenden and Fitzpatrick 1996). Helpers could probably alleviate brood reduction caused by starvation more easily than that caused by siblicide. We used only groups without helpers for our observation of food deliveries, thus we were unable to assess the direct effects of helpers on the amount and rate of food deliveries. However, the greater brood loss and lower nestling mass in nests without helpers than in nests with helpers suggest that they may alleviate brood reduction in this species.

The appropriate amount of food delivered to nestlings is determined, in part, by their food demands, i.e., larger broods require more food. However, it is possible, but unlikely, that the food demands of nestlings in the suburbs are higher than those of nestlings in wildland scrub because their metabolic rates differ. Adult scrub-jays in the suburbs, especially males, have higher field metabolic rates than scrub-jays in wildland scrub (Ellis et al. 1999), but nothing is known about the energetic demands of nestlings in the two habitats.

It also is possible that the relative quality of the food delivered to nestlings differed between the suburbs and wildlands. Food quality, especially protein content, can influence the growth and survival of nestlings (Johnson 1960; Johnston 1993; Birkhead et al. 1999). Although we did not determine the types and amounts of different foods delivered to nestlings in the suburbs, on many occasions we observed parents feeding nestlings human-provided foods (millet, peanuts, bread crumbs, pet foods). Recent experimental work suggests that adult scrub-jays show a preference for lepidopteran larvae when they are feeding nestlings, but if the handling costs associated with lepidopteran larvae are increased, their preference switches to more easily available human-provided foods (A. Sauter and R. Bowman, unpublished data). Thus, if the handling and searching costs for arthropods in suburban habitats are high because their relative abundance is low, parents may prefer to feed nestlings easily available foods, even if they are relatively low-quality human-provided foods. Fleischer et al. (2003) found that the diet of adult suburban scrub-jays consists of 30% human-provided food, 70% of which consists of foods such as millet seed and bread crumbs, which have less protein than arthropods. In addition, the assimilation efficiency of protein in these foods may be much lower. Effective digestion of low-quality foods may require longer gut retention times (Hilton et al. 2000), potentially imposing a processing constraint on growing nestlings.

Finally, differences in the rates of brood reduction between suburban and wildland habitats might be caused by differences in hatch spread and the resulting size hierarchy among nestlings. Some studies have shown that brood reduction increases with nestling mass asymmetry (Sydesman and Emslie 1992; Haydock and Ligon 1986), while others have shown no effect (Gibbons 1987; Skagen 1988; Wiebe and Bortolotti 1995). Clutch size is significantly larger in the suburbs and it may take slightly longer for all eggs in larger clutches to hatch. If this led to an increase in nestling-mass asymmetry, it could represent a greater competitive disadvantage for later hatched chicks and hence lead to their rapid starvation. Mass asymmetry at hatch completion at the suburban site was substantial, and was larger in broods that lost dillings by day 11. However, we were not able to collect

these data at the wildland site, making comparisons impossible. Ideally we would have collected mass-asymmetry data throughout the nestling period at both sites, but this was logistically unfeasible. We found no difference in nestling-mass asymmetries at day 11 between sites, in part because all nestlings in the suburbs were lighter, regardless of within-brood mass rank.

In summary, an association between food availability and brood reduction appears to exist in Florida scrub-jays. Brood reduction is highest in years and in the habitat in which food is less available. Food availability also appears to influence the rate at which adults deliver food to nestlings, but not the mass gain of nestlings; thus, the potential links between food availability, parental care, and brood reduction remain ambiguous. Variation in food deliveries to nestlings could be influenced by helpers and variation in diet quality could influence the potential value of that food for nestling growth and survival. Both of these possibilities should be addressed in further studies examining variation in the reproductive ecology of this species across urban gradients.

Acknowledgments

We thank A.L. Fleischer, Jr. for collecting the arthropod data at Archbold Biological Station. The manuscript benefited from discussions with K.B. Brand, C. Brand, T.L. Fleischer, A.V. Badyaev, A.M. Estes, and G.E. Hill and his laboratory personnel, as well as comments from two anonymous reviewers. L.K. Estep and S.M. Doucet made valuable comments on the manuscript and translated the abstract. Archbold Biological Station provided a graduate research assistantship and the University of South Florida provided a teaching assistantship for M.D.S. Research at the suburban and wildland study sites was supported by National Science Foundation grants IBN-00777469 to R.B. and DEB-9707622 to G.E.W.

References

- Abrahamson, W.G., Johnson, A.F., Layne, J.N., and Peroni, P.A. 1984. Vegetation of the Archbold Biological Station: an example of the southern Lake Wales Ridge. *Fla. Sci.* **47**: 209–250.
- Bell, G.P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. *Stud. Avian Biol.* **13**: 416–422.
- Birkhead, T.R., Fletcher, F., and Pellatt, E.J. 1999. Nestling diet, secondary sexual traits and fitness in the Zebra Finch. *Proc. R. Soc. Lond. B Biol. Sci.* **266**: 385–390.
- Bowman, R., and Woolfenden, G.E. 2001. Nest success and the timing of nest failure of Florida Scrub-Jays in suburban and wildland habitats. In *Avian ecology and conservation in an urbanizing world*. Edited by J.M. Marzluff, R. Bowman, and R. Donnelly. Kluwer Academic Publishers, Norwell, Mass. pp. 383–402.
- Bowman, R., Woolfenden, G.E., and Fitzpatrick, J.W. 1998. Timing of breeding and clutch size in Florida Scrub-Jays *Aphelocoma coerulescens*. *Ostrich*, **69**: 316.
- Breining, D.R. 1999. Florida scrub-jay demography and dispersal in a fragmented landscape. *Auk*, **116**: 520–527.
- Bryant, D.M., and Tatner, P. 1990. Hatching asynchrony, sibling competition and siblicide in nestling birds: studies of swiftlets and bee-eaters. *Anim. Behav.* **39**: 657–671.
- Chamberlain, D.E., Hatchwell, B.J., and Perrins, C.M. 1999. Importance of feeding ecology to the reproductive success of Blackbirds *Turdus merula* nesting in rural habitats. *Ibis*, **141**: 415–427.
- Chambers, B.Q., and Samways, M.J. 1998. Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management. *Biodiversity Conserv.* **7**: 985–1012.
- Clark, A.B., and Wilson, D.S. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.* **56**: 253–277.
- Deyrup, M., and Franz, R. 1994. Rare and endangered biota of Florida. Vol. IV. Invertebrates. University Press of Florida, Gainesville.
- Ellis, H.I., Woolfenden, G.E., and Bowman, R. 1999. Field metabolism of Florida Scrub-Jays during breeding. *Ostrich*, **69**: 371.
- Fleischer, A.L., Jr., Bowman, R., and Woolfenden, G.E. 2003. Variation in foraging behavior, diet, and time of breeding of Florida Scrub-Jays in suburban and wildland habitats. *Condor*, **105**: 515–527.
- Gibbons, D.W. 1987. Hatching asynchrony reduces parental investment in the jackdaw. *J. Anim. Ecol.* **56**: 403–414.
- Haydock, J., and Ligon, J.D. 1986. Brood reduction in the Chihuahuan Raven: an experimental study. *Ecology*, **67**: 1194–1205.
- Hilton, G.M., Furness, R.W., and Houston, D.C. 2000. A comparative study of digestion in North Atlantic seabirds. *J. Avian Biol.* **31**: 36–46.
- Johnson, N.F. 1960. Effects of levels of dietary protein on Wood Duck growth. *J. Wildl. Manag.* **35**: 798–802.
- Johnston, R.D. 1993. Effects of diet quality on the nestling growth of a wild insectivorous passerine, the House Martin *Delichon urbica*. *Funct. Ecol.* **7**: 255–266.
- Karasov, W.H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. *Stud. Avian Biol.* **13**: 391–415.
- Lack, D. 1954. The natural regulation of animal numbers, Oxford University Press, New York.
- Lack, D. 1968. Ecological adaptations for breeding in birds, Chapman and Hall, London.
- Legge, S. 2000. The effect of helpers on reproductive success in the laughing kookaburra. *J. Anim. Ecol.* **69**: 714–724.
- Magrath, R. 1989. Hatching asynchrony and reproductive success in the blackbird. *Nature (Lond.)*, **339**: 536–538.
- McIntyre, N.E. 2000. Ecology of urban arthropods: a review and a call to action. *Ann. Entomol. Soc. Am.* **94**: 825–835.
- Mock, D.W., and Forbes, L.S. 1995. The evolution of parental optimism. *Trends Ecol. Evol.* **10**: 120–134.
- O'Connor, R.J. 1984. The growth and development of birds. John Wiley and Sons, New York.
- Pyle, R., Gendzient, M., and Opler, P. 1981. Insect conservation. *Annu. Rev. Entomol.* **26**: 233–245.
- Quinney, T.E., Hessel, D.J.T., and Ankney, C.D. 1986. Sources of variation in growth of Tree Swallows. *Auk*, **99**: 389–400.
- Richner, H. 1989. Habitat-specific growth and fitness in Carrion Crows (*Corvus corone corone*). *J. Anim. Ecol.* **58**: 427–440.
- Schoech, S.J. 1999. Florida Scrub-Jay nestlings preyed upon by an eastern coachwhip. *Fla. Field Nat.* **27**: 57–58.
- Skagen, S.K. 1988. Asynchronous hatching and food limitation: a test of Lack's hypothesis. *Auk*, **105**: 78–88.
- Snow, D.W. 1958. The breeding of Blackbirds *Turdus merula* at Oxford. *Ibis*, **100**: 1–30.
- SPSS Inc. 1999. SPSS®. Version 10.0 [computer program]. SPSS Inc., Chicago.

- Stallcup, J.A., and Woolfenden, G.E. 1978. Family status and contributions to breeding by Florida Scrub-Jays. *Anim. Behav.* **26**: 1144–1156.
- Stoleson, S.H., and Beissinger, S.R. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? *In Current ornithology. Edited by D.M. Power.* Plenum Press, New York. pp. 191–270.
- Strehl, C.E., and White, J. 1986. Effects of superabundant food on breeding success and behavior of the Red-winged Blackbird. *Oecologia*, **70**: 178–186.
- Sydeman, W.J., and Emslie, S.D. 1992. Effects of hatching asynchrony, egg size, and third-chick disadvantage in western gulls. *Auk*, **109**: 242–249.
- Van Balen, J.H. 1973. A comparative study of the breeding ecology of the Great Tit (*Parus major*) in different habitats. *Ardea*, **61**: 1–93.
- Wiebe, K.L., and Bortolotti, G.R. 1995. Food dependent benefits of hatching asynchrony in American Kestrels *Falco sparverius*. *Behav. Ecol. Sociobiol.* **36**: 49–57.
- Woolfenden, G.E., and Fitzpatrick, J.W. 1984. The Florida Scrub-Jay: demography of a cooperative-breeding bird. *Monogr. Popul. Biol.* No. 20.
- Woolfenden, G.E., and Fitzpatrick, J.W. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*). *In The birds of North America.* Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.