Nutritional bias as a new mode of adjusting sex allocation

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Sex biases in the allocation of resources to offspring occur in a broad range of taxa. Parents have been shown to achieve such biases either by producing numerically more of one sex or by providing the individuals of one sex with a greater *quantity* of resources. In addition, skews in allocation could occur if the offspring of one sex receive resources of higher *quality* (greater nutritional or energetic value by weight or volume), although this mode of adjustment has, to our knowledge, never been demonstrated. We compared the types of prey and the metabolizable energy provisioned to male and female nestlings in one of the most sexually size dimorphic of all birds, the brown songlark, *Cinclorhamphus cruralis*. Within broods, we found that males not only received more prey than their smaller sisters, but also prey of apparently higher quality. This dietary disparity could result either from mothers actively discriminating between the sexes when providing prey or from competition among siblings. We suggest that sex differences in offspring diet quality may occur in a wide range of other taxa and function as an additional mechanism of sex allocation adjustment.

Keywords: sex allocation; sex-biased provisioning; sexual size dimorphism; avian nutrition

1. INTRODUCTION

Sex allocation describes how parents distribute resources between the production of sons and daughters (Charnov 1982; Frank 1990). Typically, resources are divided approximately equally between the sexes, but there is a range of scenarios where the parents of some animals and plants may profit from the ability to bias allocation (Charnov 1982; Hardy 2002).

In some taxa, resource distribution can be adjusted by producing numerically more of one sex. Such sex-ratio skews are well documented among many invertebrates (Charnov 1982), but are also evident in a range of birds, mammals and reptiles (Hardy 2002). Skewed allocation may also be achieved by providing the individuals of one sex with a greater quantity of resources (Charnov 1982; Stamps 1990). Among size-dimorphic birds, for example, chicks of the larger sex commonly receive a greater proportion of delivered prey items (Anderson *et al.* 1993).

A sex bias in allocation could also occur if one sex received resources of higher *quality* (Teather & Weatherhead 1988), such as milk or prey items of greater energetic or nutritional value by weight or volume. However, to our knowledge, qualitative differences in parental provisioning of the sexes have never been reported in vertebrates. In several insect taxa, including some parasitoid wasps, male and female eggs are often allocated to different host types, but even in these cases there is no evidence that host specialization has evolved to afford one sex a nutritional advantage (Hunter & Wooley 2001).

We examine parental provisioning in one of the most sexually size-dimorphic of all birds (Andersson 1994), the brown songlark, *Cinclorhamphus cruralis*, to determine whether male offspring receive a different diet of higher quality than their (smaller) sisters. We investigated this question by comparing both the prey consumption and energy intake of male and female nestlings in mixed-sex broods.

2. METHODS

We studied brown songlarks between September and December over three consecutive years (1998–2000) in semi-arid grasslands near the towns of Hillston and Hay in southeastern Australia. These populations were highly polygynous, with males defending territories on which an average of more than five females nested over the course of the breeding season (Magrath *et al.* 2003). Females provided almost all parental care: males were never observed to incubate, and contributed to nestling feeding at only 6% of 66 broods, and even at these broods contributed less than 20% of feeds (Magrath *et al.* 2003). Following the discovery of a nest, each egg or chick was individually marked, and the nest was monitored until the brood either failed or fledged successfully.

We sampled the number, type and size of invertebrate prey delivered to each chick in 54 broods (45 were of mixed sex) that were between 7 and 11 days old, using a miniature CCD camera connected to a Sony Handycam (TR840). Each recording lasted for 3 h. Some broods ($n = 14$) were recorded on several occasions, and the data for these nests were pooled. Prey were identified at least to the level of order and categorized as small, medium or large using the bill length of the female as a reference. The mass of chicks in 51 of these broods was recorded when the broods were 10 days old.

The content of indigestible chitin in several of the most common prey types was determined by first desiccating *ca.* 10 g of each prey type in an oven for 3 days at 60 °C to gain their dry weight. These samples were then dissolved in 3 M NaOH for 2 days before the remaining chitinous material was flushed with water, dried and weighed (Kaspari & Joern 1993). The chitin content of these prey types was then expressed as a percentage of the total dry weight of the sample.

In addition, we determined the daily energy expenditure (DEE) of a male and female sibling in each of ten, 10-day-old broods using the doubly labelled water technique (Speakman 1997). We also estimated the amount of energy each of these chicks assimilated as new body tissue calculated from their mass change over the same 24 h period and the function derived for the conversion of energy to mass in growing chicks (Visser & Schekkerman 1999). Summing the DEE and assimilated energy then provided the total metabolizable energy intake (MEI) for each of these 20 chicks.

3. RESULTS

The most common invertebrate types received by songlark chicks were orthopterans (43%; mostly grasshoppers), lepidopteran larvae (22%), arachnids (12%; mostly lycosid spiders) and hemipterans (4%; mostly cicadas). Across all 54 broods, the proportions of these four prey types did not vary with brood size or sex ratio (logistic regression; $p > 0.2$ for all). However, comparing the distribution of prey within the 45 mixed-sex broods revealed that sons

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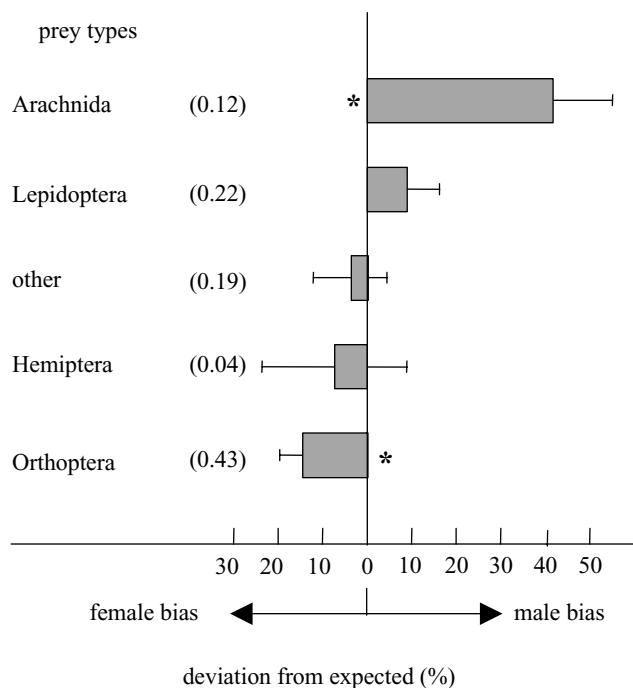DOI 10.1098/rsbl.2004.0187

S347

Figure 1. Distribution of major prey types provided to male and female siblings in 7–11-day-old, mixed-sex broods of brown songlarks. Deviations were calculated by deriving the mean of the difference in the proportion of the male and female diet that was comprised of each prey type for the 45 broods. Mean differences between male and female siblings were compared, for each prey type, using a paired *t*-test ($^*p < 0.01$). This mean difference is displayed as a percentage of the mean proportion of each prey type in the diet of these 45 broods (mean proportion shown in brackets). The category 'other' combines additional prey taxa that each represented less than 1% of the overall diet together with prey that could not be identified from the videotapes.

received significantly more arachnids and fewer orthopterans than expected by chance (figure 1). Moreover, the analysis of chitin composition in our samples of these prey types revealed that the arachnids contained only about half as much chitin as the orthopterans (9% versus 17%).

Relating the mass of chicks in 10-day-old broods to the proportion of each of these four main prey types in our sample of their diets revealed that the mean mass for both male and female chicks declined with the proportion of orthopterans (figure 2), but was not significantly related to the proportion of the other three prey types ($p > 0.2$ for each).

We then compared the rate and size of items fed to male versus female siblings in 10-day-old mixed-sex broods, and found that male chicks received an average of 34 ± 9% more prey items per hour (paired *t*-test; $t = 3.69$, $p = 0.001$, $n = 22$ broods), but that these items were not different in size from those provided to the females (paired *t*-test; $t = 1.04$, $p = 0.31$). At a subset of these broods, the total MEI was 52 ± 5% higher for males than for their sisters (paired *t*-test; $t = 9.58$, $p < 0.001$, $n = 10$ broods).

4. DISCUSSION

During the late nestling period, male songlarks not only received substantially more prey items than their sisters,
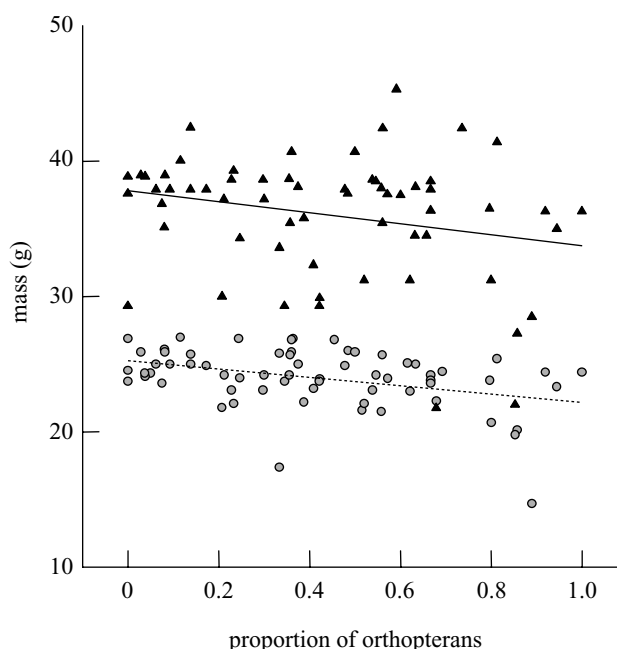
Figure 2. Mean mass of male (triangles) and female (circles) brown songlark nestlings in 10-day-old broods in relation to the proportion of orthopterans in our sample of their diet. Data represent the average masses of male and female nestlings in each nest. Nestling mass declined with the proportion of orthopterans, and this relationship was similar for both sexes (ANCOVA; $F_{1,98} = 13.0$, $p = 0.001$, $n = 51$ broods; interaction between 'sex' and 'proportion of orthopterans', $F_{1,97} = 0.39$, $p = 0.53$; model also included the independent variables 'brood size' and 'day of the breeding season').

but also a different composition of prey types. Disparities in the quantity of prey received by the sexes have been reported in a range of sexually size-dimorphic birds (Anderson *et al.* 1993) and many other vertebrate and invertebrate taxa (Charnov 1982; Hardy 2002). However, the finding that their diets differed in composition is apparently unique among vertebrates.

Furthermore, we suggest that the observed asymmetric distribution of prey types equated to sons receiving a superior diet. First, our comparison of MEI with prey intake found that sons had a 52% higher MEI than their sisters at 10 days of age and yet only received 34% more prey items, a discrepancy that suggests males received items of higher average energy content. Furthermore, this disparity was apparently not explained by differences in prey size, though our measure of prey size was quite approximate.

Moreover, the relative energetic value to birds of different arthropods is largely determined by their chitin content, as this carbohydrate is largely indigestible (Karasov 1990; Klasing 1998). Indeed, the adults of some birds remove chitinous body parts before swallowing some insects (Zach & Falls 1978; Grundel & Dahlsten 1991; Kaspari 1991), although this was not evident among the prey fed to songlark nestlings. Comparing the chitin content of spiders and grasshoppers collected at our field sites revealed that the grasshoppers contained almost twice the level of chitin as the spiders. This difference is consistent with previous studies (e.g Zach & Falls 1978; Kaspari 1991) that show orthopterans to have a much higher

percentage of chitin than either spiders or lepidopteran larvae, which in our study also tended to be fed more commonly to male nestlings.

Previous studies on the diets of altricial nestlings have also concluded that spiders are among the most preferred prey items because of their relatively low chitin content (Cowie & Hinsley 1988; Grundel & Dahlsten 1991), but also because of their high content of certain amino acids (Ramsay & Houston 2003). Relative to other arthropods, spiders have a high concentration of the amino acids cysteine, essential for feather development, and especially taurine, which appears to be important in early growth and development (Ramsay & Houston 2003). Consequently, the male diet of more spiders and fewer orthopterans relative to their sisters is likely to be both energetically and nutritionally superior.

This conclusion is also supported by our data on nestling growth, which revealed that chick mass at day 10, for both sexes, declined markedly with the proportion of orthopterans in their diet. Indeed, the rapid growth rate observed in male chicks (males were already heavier than their mothers at 10 days of age) may only be sustainable on a high-quality diet that minimizes the potential for digestive (Karasov 1990) or nutritional (Pulliam 1975) bottlenecks to inhibit their growth rate. As we argue that spiders are high-quality prey, a positive relationship between the proportion of spiders and nestling mass may also have been expected. However, spiders comprised an average of only 12% of the nestling diet, so our limited diet sampling may have lacked the resolution to detect this relationship.

This disparity in diet composition must result either from mothers actively discriminating between the sexes when providing prey or from competition among siblings. There are several potential cues that mothers could use to distinguish the sexes, including begging calls or morphological differences (males already weighed over 50% more than their sisters by 10 days of age), and these will be assessed in a future study. Provisioning sons with a superior diet may be favoured in strongly polygynous animals because body size is often a more important determinant of lifetime reproductive success in males than in females (Andersson 1994). We suggest that similar skews in diet quality may function as a means of adjusting sex allocation in other dimorphic species, and more generally in any taxa where selection favours the ability facultatively to skew resource allocation.

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