



Pair bond duration influences paternal provisioning and the primary sex ratio of brown thornbill broods

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Parents should vary their level of investment in sons and daughters in response to the fitness costs and benefits accrued through male and female offspring. I investigated brood sex ratio biases and parental provisioning behaviour in the brown thornbill, *Acanthiza pusilla*, a sexually dimorphic Australian passerine. Parents delivered more food to male-biased than female-biased broods. However, factors determining parental provisioning rates differed between the sexes. Female provisioning rates were related to brood sex ratio in both natural and experimental broods with manipulated sex ratios. In contrast, male provisioning rates were not affected by brood sex ratio in either natural or experimental broods. However, males in established pairs provisioned at a higher rate than males in new pairs. Data on the sex ratio of 109 broods suggest that female brown thornbills adjust their primary sex ratio in response to pair bond duration. Females in new pairs produced broods with significantly fewer sons than females in established pairs. This pattern would be beneficial to females if the costs of rearing sons were higher for females in new than established pairs. This may be the case since females in new pairs provisioned experimental all-male broods at elevated rates. The condition of nestlings also tended to decline more in these all-male broods than in other experimental broods. This will have additional fitness consequences because nestling mass influences recruitment in thornbills. Female thornbills may therefore obtain significant fitness benefits from adjusting their brood sex ratio in response to the status of their pair bond.

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Theory suggests that parents should vary their level of investment in sons and daughters in response to the fitness costs and benefits accrued through male and female offspring (Fisher 1930; Trivers & Willard 1973; Charnov 1982; Frank 1990). One way individuals may vary their total investment in each sex is to modify the sex ratio of offspring produced. In contrast to invertebrates, adaptive modification of sex ratios appears uncommon in birds and mammals. Nevertheless, recent studies demonstrate that birds and mammals may adjust sex ratios in ways that appear to be adaptive (Hardy 1997; Sheldon 1998). For example, birds produce biased sex ratios when the reproductive value of sons and/or daughters varies with laying date (Dijkstra et al. 1990), resource availability (Appleby et al. 1997), territory quality (Komdeur et al. 1997), female condition (Nager et al. 1999), or male attractiveness (Ellegren et al. 1996; Sheldon et al. 1999).

Parents can also vary their investment in sons and daughters by modifying the level of care they provide in

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relation to the sex of each young or the sex ratio of their brood. This may occur when the energetic needs of the two sexes differ or when sons and daughters have different effects on parental fitness after independence as a consequence of sex-biased dispersal (Clark 1978; Malcolm & Marten 1982; Stamps 1990). Sex biases in resource allocation have been widely documented in mammals that are dimorphic in size, where sons appear to have higher energy requirements than daughters, or where offspring of one sex are more likely to compete with or help parents in future breeding attempts (reviewed by Clutton-Brock 1991). In contrast, sex-biased provisioning has been documented in only a few species of birds (reviewed by Leonard et al. 1994), although physiological studies on dimorphic species have found that the larger sex has a higher energy intake than the smaller sex (Fiala & Congdon 1983; Teather & Weatherhead 1988; Anderson et al. 1993; Riedstra et al. 1998). In both mammals and birds where sex-biased provisioning has been reported it is often unclear whether the observed differences in provisioning are an adaptive parental strategy or a response to differences in the behaviour of sons and daughters (Clutton-Brock 1991). However, the

feeding rates of male great reed warblers, *Acrocephalus arundinaceus*, increase with the proportion of sons in the brood, but not with brood size, suggesting that fathers preferentially invest in sons rather than respond to the energetic demands of the brood (Nishiumi et al. 1996; Westerdahl et al. 2000).

Experimental evidence for adaptive allocation strategies in birds remains limited despite the proliferation of studies on avian sex allocation patterns over the last decade (Sheldon 1998). Experiments have been used to provide evidence that facultative manipulation of primary sex ratios in response to a variety of factors is possible in some birds (e.g. Komdeur et al. 1997; Kilner 1988; Sheldon et al. 1999) but have rarely been used to investigate the fitness consequences to parents and offspring of particular allocation strategies (but see Komdeur 1998; Nager et al. 1999, 2000). Using both natural data and an experiment where sex ratio was manipulated early in the nestling period, I investigated sex ratio variation and parental provisioning behaviour in the brown thornbill, *Ancanthiza pusilla*.

Brown thornbills have a number of life history traits that are expected to influence an individual's sex allocation strategy. First, they are sexually dimorphic in body size (males are 14% heavier than females, Green & Cockburn 1999). Furthermore, sex differences in body mass are apparent by the time nestlings are 7 days old (unpublished data). Second, nestling condition has a significant influence on juvenile survival and recruitment to the breeding population in both males and females (Green & Cockburn 2001). Third, variance in reproductive success is likely to be higher for males than females as a result of extrapair paternity (Green 2000). Finally, 98% of clutches contain three eggs (Green & Cockburn 1999) so females do not adjust the number of offspring they produce in response to resource availability. Where sons are more expensive to rear than daughters the reproductive costs of producing sons may be dependent on the level of resources available to parents (Gomendio et al. 1990). Under these conditions female thornbills with access to fewer resources would be expected to produce female-biased broods whereas females with access to more resources would be expected to produce male-biased broods. In addition, Burley (1981) has suggested that where parental traits associated with paternal attractiveness are heritable and sons benefit more from these traits than daughters it may be adaptive for females to adjust the sex ratio of their offspring in response to these traits. Previous work suggests that female thornbills may prefer to mate with large males (Green 2000). If body size is heritable in brown thornbills pairs with large parents would therefore be expected to produce male-biased broods, whereas pairs with small parents would be expected to produce female-biased broods.

In this study I used observations on both natural broods of known sex ratio and experimental all-male and all-female broods to determine food allocation strategies of males and females. I also examined primary and secondary sex ratio variation in the brown thornbill and manipulated brood sex ratios to investigate the effect of primary sex ratio biases on parental fitness.

METHODS

Study Species and Population

The brown thornbill is a small, yet long-lived (up to 17 years), passerine that is common in the eucalypt forests and woodlands of southeastern Australia (Blakers et al. 1984; Baker et al. 1999). Males are larger and heavier than females (mean body mass: males 7.3 g, females 6.4 g; Green & Cockburn 1999). I studied a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, between 1995 and 1998. The vegetation in the 40-ha Botanic Gardens consists of both plantations of Australian native plants and natural woodland that is contiguous with a large area (ca. 9 km²) of dry sclerophyll forest in Canberra Nature Park. Brown thornbills bred both in the Garden and in the adjacent reserve. I followed the fate of 15 pairs in 1995 and ca. 30 pairs per year between 1996 and 1998. Adult survival rates were relatively high (males 63%, females 62%; Green & Cockburn 1999) and divorce was rare (7% of pairs where both partners survived to breed the following year; $N=42$ pair-years) so, on average, 42% of pair bonds persisted from one year to the next (unpublished data). Pairs defended small (ca. 2 ha) territories year round. Females laid up to three clutches but rarely fledged more than one brood during a breeding season that extended from late July (mid-winter) to December (early summer). Females started to incubate after they had laid the final egg in a clutch and eggs hatched synchronously 16–23 days later. Nestlings fledged after 15–18 days and reached independence ca. 6 weeks after fledging (Green & Cockburn 1999).

The work was conducted under permits from the A.N.U. Animal Experimentation and Ethics Committee, A.C.T. Parks and Conservation, Canberra Nature Park and the Australian Bird and Bat Banding Scheme.

Field Methods

I monitored the study population throughout the year. During the nonbreeding season (January to June) I visited the study area at least once a month to census pairs and associated young, and to determine when colour-banded juveniles gained a breeding vacancy or new birds entered the population. During the breeding season I observed pairs at least three times a week to confirm the identity of the social parents, locate nests, and monitor the progress of each nesting attempt. The majority of birds monitored during the breeding season (>95% in each year) were banded with an Australian Bird and Bat Banding Scheme aluminium band and a unique combination of three coloured bands. I located nests by watching females when they were nest building, following females back to their nests during incubation, or watching adults feed nestlings (73% of 173 nests were found before egg laying was completed). I determined hatch dates by daily visits to the nest towards the end of the incubation period and/or

the appearance and size of nestlings. I banded and weighed nestlings when they were 6–9 days old. In 1997 and 1998, I also reweighed nestlings when they were 10–12 days old. I collected blood samples from all birds when they were banded for the first time (adults 10–70 μ l; nestlings 10–60 μ l), using heparinized capillary tubes after puncturing the brachial vein with a sterilized hypodermic needle. This procedure had no apparent adverse effects on either adults or nestlings.

I conducted feeding watches on 31 complete broods (brood composition: five all male, 12 each with two of one sex and one of the other, and two all female) produced by 24 pairs to examine factors influencing the amount of food delivered to nestlings and the feeding rates of males and females. Watches were conducted between mid-August and early December in 1996, 1997 and 1998. Watches on 12 broods began when nestlings were 1–2 days old and continued, at 2-day intervals, until the broods fledged ($N=11$) or were taken by a predator ($N=1$). Watches on the remaining 19 broods began when nestlings were 9–10 days old and continued, at 2-day intervals, while nestlings remained in the nest. All watches took place between 0900 and 1200 or 1400 and 1700 hours and lasted 30 min. During focal watches I counted the number of times each parent visited the nest with food. The amount of food delivered was not estimated but there was no obvious variation among individuals in the size or quantity of prey delivered to the nest during a feeding visit. Watches were not conducted if it was raining and were abandoned if either parent became agitated by my presence. Abandoned watches were attempted again later in the day from further away if time allowed.

Pair Bond Duration, Adult Age and Size

Pairs were classified as being either new pairs if they were breeding together for the first time, or established pairs if they had bred together in a previous year of the study. Adults were classified as being either yearlings or older. Adults were known to be yearlings when breeding in the study area for the first time if they had been banded either as a nestling or as a juvenile. Juvenile brown thornbills have brown eyes whereas those of an adult are red (Rogers et al. 1986). I also assumed that adults were yearlings if they traversed more than one territory to fill a vacancy in the study area since adults in this study rarely moved more than one territory after divorce or the death of their mate (two of 61 adults that lost a partner; unpublished data).

I used scores from the first component of a principal component analysis of three linear size measurements (tarsus, head–bill and wing) as an index of body size. Separate analyses were conducted for males and females. Mean values for each trait were used when individuals were captured multiple times. PC1 explained 41% of the variation in male size and 50% of the variation in female size. The respective character loadings for tarsus, head–

bill and wing were 0.71, 0.71 and -0.06 for males, and 0.71, 0.66 and 0.20 for females.

Sexing of Adults and Offspring

It is not possible to sex brown thornbill adults or nestlings by morphology or plumage. To determine the sex of all parents and offspring I therefore used a DNA-based test that relies on PCR amplification of a section of the CHD1 genes (CHD1-W and CHD1-Z) located on the avian sex chromosomes (see Griffiths et al. 1998 for details of the method). The DNA used to sex individuals was isolated from blood samples, using either a chelex extraction or a standard phenol/chloroform extraction. Molecular sexing always confirmed the gender of adults sexed by behavioural cues ($N=58$ pairs). Nestlings that subsequently obtained vacancies in the study area were also always sexed correctly ($N=28$ males, 1 female).

Brood Sex Ratio Manipulation

I manipulated the sex ratio of broods provisioned by six new pairs and four established pairs in 1998 by transferring chicks between broods when they were 6–7 days old. Chicks had been sexed on the day prior to being transferred, with DNA extracted from the blood sample collected at banding. I created five all-male and five all-female broods. Each brood contained three chicks, and the chicks in each brood had all hatched within 24 h of one another. The brood size of experimental pairs was held constant. All experimental broods contained both foster chicks and chicks that had not been transferred. Nests used in this experiment had, wherever possible, been covered by wire-mesh cages prior to hatching to reduce the likelihood of predation. These cages did not appear to have any effect on adult behaviour and resulted in the fledging success of manipulated nests being greater than that of unmanipulated nests (90 versus 50%). I weighed nestlings to 0.1 g using a Pesola balance both at the start of the experiment and 4 days later when nestlings were 11 days old. Nestlings were always weighed between 0800 and 0900 hours. I used changes in the residuals from known sex-specific growth curves (Green & Cockburn 2001) to determine how nestling condition changed during the experiment. Nestling condition on day 11 varied slightly between treatments (see Results) but always fell within the range observed in natural broods. I conducted feeding watches at experimental nests when nestlings were 10, 12 and 14 days old. All watches took place between either 0900 and 1200 or 1400 and 1700 hours and lasted 60 min. During focal watches I counted the number of times each parent visited the nest with food. To catch adults provisioning experimental broods I used a single mist net situated near the nest when nestlings were 13 days old. Mist nets were in place for a maximum of 60 min. I used the residuals from sex-specific regressions between body mass and body size (PC1 score) to estimate the condition of any adult captured.

Statistical Analysis

I carried out analyses with a statistical modelling approach using Genstat 5.4.1 for Windows (Genstat 5 Committee 1997). The data collected during this study were rarely independent as pairs provisioned one to two broods and were watched between three and 16 times, females produced between one and six clutches, and broods contained three nestlings. I therefore used mixed models, which incorporate random effects to account for dependence associated with multiple sampling, to examine parental provisioning behaviour, brood sex ratios and changes in nestling condition during the brood manipulation experiment.

I examined the behaviour of pairs provisioning unmanipulated broods by fitting separate linear mixed models to two dependent variables: the total number of feeding visits/h and the proportion of feeding visits made by the female. Explanatory variables considered were brood sex ratio (male biased, female biased), nestling age, hatch date (1 January=1), year, time (am/pm) and territory type (natural woodland or watered plantation). Provisioning rates of male and female thornbills were also examined separately. These models included either 'male age/pair bond duration' (yearling male, older male in a new pair, older male in an established pair), or 'female age/pair bond duration' (yearling female, older female in a new pair, older female in an established pair) as an additional explanatory variable. A composite variable was used to examine how age and pair bond duration affected male and female provisioning rates as the two variables are not independent (a yearling has to be in a new pair). All models were fitted using the restricted maximum likelihood (REML) procedure in Genstat, with 'pair' specified as a random term. Models initially contained all explanatory variables and all two-way interaction terms. A final model was selected by progressively eliminating nonsignificant interaction terms ($P>0.05$), and then nonsignificant main effects until only significant terms remained. To avoid any confounding order effects I re-evaluated any term eliminated by adding and dropping it from the final reported model. The statistics presented refer to the change in deviance (which approximates to a χ^2 distribution) associated with dropping each term from the final model.

I examined variation in brood sex ratios by fitting a generalized linear mixed model with binomial errors and a logit link using the GLMM procedure in Genstat. In this model 'adult female identity' was specified as a random term, the number of males in a brood was used as the response variable and brood size was used as the binomial denominator. I first examined how 'data quality' (entire clutch sexed/part clutch sexed) and the explanatory variables hatch date, year and territory type influenced brood sex ratio since these data were available for all 109 broods. I subsequently examined the effect of body size, male age, female age and pair bond duration on brood sex ratio in the subset of broods where these data were available. A composite variable ('age/pair bond duration') was used to examine the effect of age and pair bond duration since these variables are interrelated. This variable classified

pairs into five types: yearling male/yearling female, older male/yearling female, yearling male/older female, older male/older female in a new pair, and older male/older female in an established pair. In both the first and second series of models I initially included all relevant explanatory variables and all two-way interaction terms and selected a final model by progressively eliminating nonsignificant interaction terms ($P>0.05$) and then nonsignificant main effects. The significance of terms was evaluated with the Wald statistic (which have a similar distribution to χ^2 calculated when the term of interest was fitted last in the model).

Preliminary analyses indicated that the sex ratio of broods where the sex of every egg was known did not differ from the sex ratio of broods where one or more eggs were not sampled ($\bar{X} \pm \text{SE}$; entire clutch sexed: 0.54 ± 0.03 , $N=70$; part clutch sexed: 0.48 ± 0.06 , $N=39$; $\chi^2_1=0.6$, NS). I therefore did not exclude partially sampled clutches from analyses. However, restricting analyses to broods where the entire clutch was sexed does not alter any of the results presented.

I also used mixed models to examine male and female feeding rates, and changes in nestling condition between 7 and 11 days of age, at experimental broods. These models were fitted with the REML procedure described previously. The identity of the pair was specified as a random term to control for the dependence associated with having three feeding observations or three nestlings per pair. Explanatory variables considered were pair bond duration (new or established pair), experimental treatment (male or female broods), nestling age (10, 12 and 14 days), type of chick (foster or biological), hatch date, time of day and territory type. I again initially fitted a full model that contained all the explanatory variables of interest and two-way interactions, and selected a final model by progressively eliminating nonsignificant interaction terms ($P>0.1$) and then nonsignificant main effects.

I used a two-way analysis of variance to examine, separately, the condition of male and female thornbills from new and established pairs after they had provisioned either all-male or all-female broods for 6 days. In these analyses pair bond duration and experimental treatment were treated as factors, and their interaction term was included in the model.

In all analyses residual plots and normal probability plots were used to examine for unequal variance and deviations from normality among residuals. Feeding rates to natural broods were log transformed so that they conformed to the assumptions of the mixed models. Means are presented \pm SEs unless stated otherwise. Brood sex ratios throughout the paper refer to the proportion of a brood that are male.

RESULTS

Parental Provisioning Behaviour

The total number of feeding visits parents made to the nest/h increased with nestling age ($\chi^2_7=133.1$, $P<0.0001$; Fig. 1). Parents fed male-biased broods significantly more

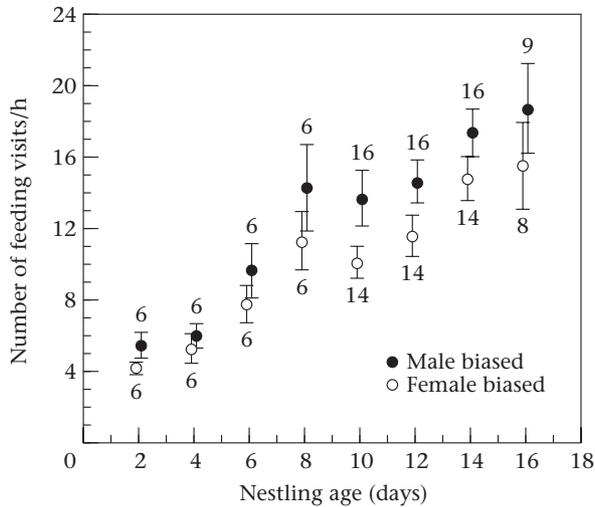


Figure 1. Relation between nestling age and the total number of feeding visits made by parents to unmanipulated nests with female-biased or male-biased broods. Broods all contained three nestlings. Means are presented \pm SEs. For clarity nontransformed delivery rates are presented. Numbers above or below the points refer to the number of male- or female-biased broods observed at each nestling age.

than female-biased broods ($\chi^2_1=12.7$, $P=0.0004$; Fig. 1). The total number of visits varied from year to year and across the day, being higher in 1996 than in 1997 or 1998 ($\chi^2_2=24.1$, $P<0.0001$) and in the morning than the afternoon ($\chi^2_1=3.9$, $P=0.05$). The total number of visits/h was not affected by the hatch date of a brood ($\chi^2_1=0.4$, $P=0.53$) or the location of the territory ($\chi^2_1=0.9$, $P=0.34$).

Females did not make significantly more feeding visits to the nest than males, being responsible for $52 \pm 2\%$ of the feeding visits during the nestling period ($t_{23}=1.42$, $P=0.17$). The proportion of feeding visits made by females was not influenced by nestling age ($\chi^2_7=5.19$, $P=0.64$) or the sex ratio of the brood ($\chi^2_1=0.1$, $P=0.92$). The proportion of feeding visits made by females also did not vary from year to year ($\chi^2_2=2.7$, $P=0.26$) or across the season ($\chi^2_1=1.3$, $P=0.25$), and was not dependent on the time of day ($\chi^2_1=0.04$, $P=0.84$) or the location of the territory ($\chi^2_1=1.1$, $P=0.30$).

Female and male provisioning rates both increased with nestling age (females: $\chi^2_7=88.5$, $P<0.0001$; males: $\chi^2_7=121.2$, $P<0.0001$) and were higher in 1996 than in 1997 or 1998 (females: $\chi^2_2=23.6$, $P<0.0001$; males: $\chi^2_2=19.6$, $P<0.0001$). Female provisioning rates were higher to male-biased broods ($\chi^2_1=10.1$, $P=0.001$; Fig. 2), but unrelated to female age and pair bond duration ($\chi^2_2=0.7$, $P=0.70$). In contrast, male provisioning rates were influenced by male age and pair bond duration ($\chi^2_2=10.6$, $P=0.005$; Fig. 3), but unrelated to brood sex ratio ($\chi^2_1=0.0$, $P=1.0$). The former relationship was driven more by pair bond duration than male age since older males in established pairs had higher delivery rates than both yearling and older males in new pairs (Fig. 3). Neither female nor male provisioning rates were related to the hatch date of the brood (female: $\chi^2_1=0.1$, $P=0.75$; male: $\chi^2_1=0.2$, $P=0.65$), the time of the focal watch

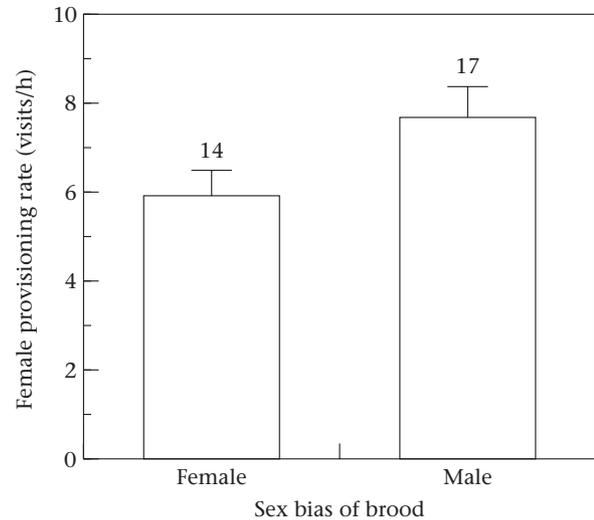


Figure 2. Relation between the sex ratio bias of unmanipulated three-chick broods and the provisioning rate \pm SE of female brown thornbills when nestlings were 10–15 days of age. Numbers above the bars are the number of broods observed. The provisioning rate at each brood was calculated from three focal watches.

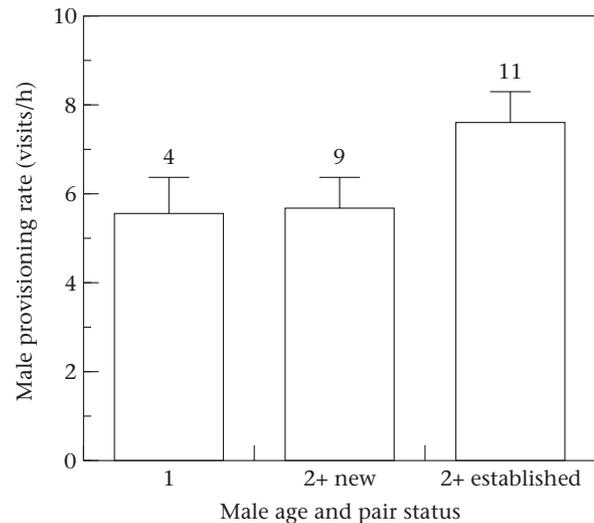


Figure 3. Relation between male age (1 or 2+ years) and pair bond duration (new or established) and the provisioning rate \pm SE of male brown thornbills when nestlings were 10–15 days of age. Numbers above the bars are the number of broods observed. The provisioning rate at each brood was calculated from three focal watches.

(female: $\chi^2_1=0.2$, $P=0.65$; male: $\chi^2_1=0.9$, $P=0.34$) or the territory type (female: $\chi^2_1=1.7$, $P=0.19$; male: $\chi^2_1=0.3$, $P=0.58$).

Sex Ratio Variation

The overall sex ratio of the 280 nestlings sampled (109 clutches, 49 females) was 53.2% male. The sex ratio of the 215 nestlings from clutches where the sex of every egg was known (72 clutches, 41 females) was 54.4% male. Neither of these sex ratios differs from parity (binomial tests: both $P>0.5$).

Table 1. Summary of analysis examining sex ratio variation in brown thornbill broods, modelled using the GLMM procedure

Explanatory variable	N	df	Single variable		With pair bond duration	
			χ^2	P	χ^2	P
Data quality*	109	1	0.6	NS	0.3	NS
Year	109	3	2.5	NS	0.9	NS
Hatch date	109	1	0.2	NS	0.1	NS
Territory type	109	1	0.4	NS	2.2	NS
Female body size	105	1	0.0	NS	0.1	NS
Male body size	104	1	0.5	NS	1.0	NS
Age/pair bond duration	69	4	12.1	<0.05	—	—
Pair bond duration	83	1	7.5	<0.001	—	—

Female was specified as a random term in the mixed model, and the Wald statistics are reported for each term when entered in the model either alone or after controlling for the effect of pair bond duration.

*Indicates whether either the entire clutch or part of the clutch was sexed.

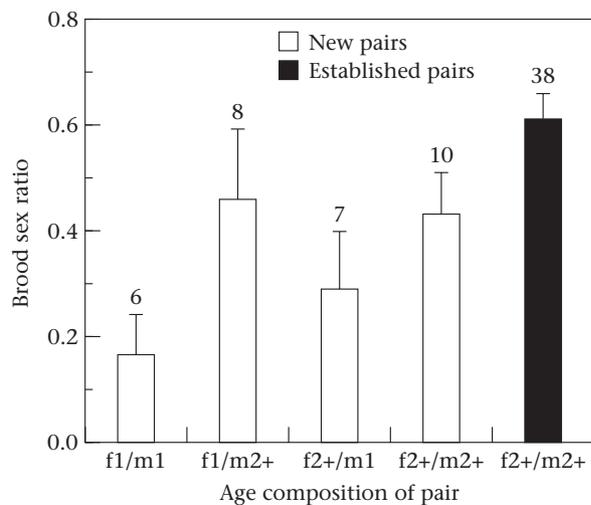


Figure 4. Relation between the age composition (1 or 2+ years) and shared breeding experience of a pair (m=male, f=female) and the sex ratio (proportion of males) of broods produced by female brown thornbills. Numbers above the bars represent the number of broods sampled. These broods were produced by 5, 8, 5, 9 and 22 females, respectively.

Brood sex ratios did not vary significantly between years (1995: 0.58 ± 0.07 , $N=17$ broods; 1996: 0.56 ± 0.07 , $N=29$; 1997: 0.47 ± 0.06 , $N=31$; 1998: 0.51 ± 0.05 , $N=32$; Table 1), across the breeding season (Table 1), or between territory types (natural woodland: 0.56 ± 0.04 , $N=52$ broods; watered plantation: 0.48 ± 0.05 , $N=57$ broods; Table 1). Brood sex ratios were also unrelated to the body size of either females or males (Table 1).

Brood sex ratios varied with 'age and pair bond duration' (Table 1). This relationship was driven principally by differences associated with pair bond duration and not male or female age since established pairs produced male-biased broods whereas new pairs, regardless of the age composition of the pair, produced female-biased broods (Fig. 4). Pair bond duration, alone, had a highly significant effect on brood sex ratio (new pairs: 0.42 ± 0.05 , $N=45$ broods; established pairs: 0.61 ± 0.05 , $N=38$; Table

1). Furthermore, pair bond duration had an almost significant effect on brood sex ratio when both male and female age were controlled ($\chi^2_1=3.0$, $P=0.08$), whereas neither male nor female age had a significant effect on brood sex ratio when the remaining two variables were controlled (male age: $\chi^2_1=0.5$, $P=0.48$; female age: $\chi^2_1=0.1$, $P=0.75$).

Few within-female contrasts shed light on the relative influence of age and pair bond duration on brood sex ratios as both age and pair bond duration usually increase from one breeding attempt to the next. However, all four females (aged 2+ years) in established pair bonds whose mate died produced fewer sons with their new mate in the following year (mean change in brood sex ratio: -0.46 ± 0.22). In contrast, only four of seven yearling females whose mate died and were therefore in new pair bonds in both their first and second year produced more male-biased broods in their second breeding season (mean change in brood sex ratio: -0.03 ± 0.17). These data are consistent with the hypothesis that pair bond duration and not female age influences brood sex ratios in brown thornbills.

Experimental Manipulation of Brood Sex Ratio

All males increased their delivery rates as nestlings increased in age ($\chi^2_2=17.8$, $P=0.0001$; Fig. 5a). Males in new pairs tended to have lower delivery rates, although not significantly so, than males in established pairs ($\chi^2_1=3.3$, $P=0.07$; Fig. 5a), but delivery rates of males in new and established pairs were not affected by the sex of the brood (treatment effect: $\chi^2_1=1.4$, $P=0.24$; pair status \times treatment interaction: $\chi^2_1=0.3$, $P=0.58$; Fig. 5a). Male delivery rates were also unrelated to the hatch date of the brood ($\chi^2_1=0.6$, $P=0.44$), the time of the focal watch ($\chi^2_1=0.9$, $P=0.34$), or the territory type ($\chi^2_1=0.9$, $P=0.34$).

All females increased their delivery rates as nestlings increased in age ($\chi^2_2=28.8$, $P<0.0001$; Fig. 5b). Females, in both new and established pairs, made more deliveries to male broods than female broods, although females in new pairs were more affected by the sex of the brood than

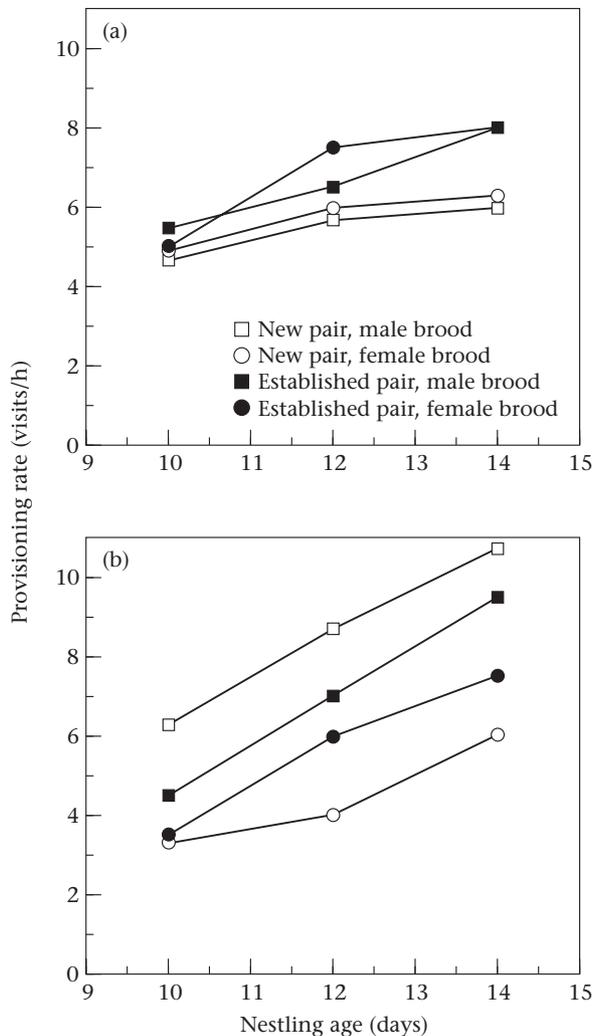


Figure 5. Relation between the age and sex of the experimental brood fed by new and established pairs and the provisioning rates of (a) male thornbills and (b) female thornbills. Points represent means for the two all-male and two all-female broods provisioned by established pairs and three all-male and three all-female broods provisioned by new pairs.

females in established pairs (pair status \times treatment interaction: $\chi^2_1=11.9$, $P=0.0005$; Fig. 5b). Female delivery rates were unrelated to the hatch date of the brood, ($\chi^2_1=0.5$, $P=0.48$), the time of the focal watch ($\chi^2_1=0.03$, $P=0.86$), or the territory type ($\chi^2_1=0.9$, $P=0.34$).

The condition of nestlings in all-male broods provisioned by new pairs declined more than the condition of nestlings in other experimental broods provisioned by either new or established pairs, although this result was not statistically significant (pair status \times treatment interaction: $\chi^2_1=2.7$, $P=0.1$; Table 2). Changes in nestling condition were not affected by hatch date ($\chi^2_1=0.2$, $P=0.65$) or territory type ($\chi^2_1=2.3$, $P=0.23$). The change in condition of foster chicks was also no different to the change in condition of biological chicks ($\chi^2_1=0.10$, $P=0.75$).

The sex of the experimental brood did not have a significant effect on the condition of the parents in either

new or established pairs (males: sex effect: $F_{1,4}=0.7$, $P=0.45$; pair status \times sex interaction: $F_{1,4}=1.2$, $P=0.33$; females: sex effect: $F_{1,4}=0.64$, $P=0.47$; pair status \times sex interaction: $F_{1,4}=2.2$, $P=0.22$). However, the small sample size makes the probability of detecting a difference low and there was a suggestion that females in new pairs that had provisioned all-male broods were in worse condition than all other experimental females (Table 2).

DISCUSSION

Female brown thornbills adjusted the sex ratio of their brood in response to the duration of their pair bond. Females in new pairs produced female-biased broods while females in established pairs produced male-biased broods. This pattern would be beneficial to females if the costs of rearing sons, the larger sex, are higher for females in new than established pairs. The cost of rearing sons is likely to differ for females in new and established pairs because males in new pairs provisioned at a lower rate than males in established pairs, males did not adjust their provisioning rates in direct response to brood sex ratio, and females in new pairs compensated for the low provisioning rate of their partners when feeding experimental all-male broods.

Provisioning Behaviour

Male-biased broods received more food from their parents than female-biased broods throughout the nestling period. This pattern may arise because male nestlings grow at a faster rate and reach a higher asymptotic mass than female nestlings (Green & Cockburn 2001) and consequently have a higher energy requirement. Studies on other sexually dimorphic birds have found that energy intake rates, measured using the doubly labelled water technique, are higher in the larger sex (e.g. red-winged blackbirds, *Agelaius phoeniceus*: Fiala & Congdon 1983; great-tailed grackles, *Quiscalus mexicanus*: Teather & Weatherhead 1988; peregrine falcons, *Falco peregrinus*: Boulet et al. 2001). Furthermore, Richner (1991) found little evidence to suggest that differences in the plumage development of male and female nestlings can counter the costs expected to arise as a result of differences in the body size of sexually dimorphic species. Data for brown thornbills support this conclusion: for both sexes primary feathers start to emerge when nestlings are 8 days old, but males have longer primary feathers than females by the time they are 11 days old (unpublished data). The evidence currently available is therefore consistent with the assumption that sons are more energetically expensive to rear than daughters in the brown thornbill.

The sex ratio bias of thornbill broods had a significant effect on the total number of feeding visits parents made to the nest but did not affect the proportion of feeding visits made by females. Both parents therefore provisioned male-biased broods more than female-biased broods. Sex-biased provisioning by both parents is expected if the functions relating offspring fitness to the amount of care provided differ as a result of sexual size

Table 2. Influence of the sex of the experimental brood provisioned by new and established pairs on the change in condition of nestlings between 7 and 11 days of age and the condition of parents when nestlings were 15 days old

	Sex of brood					
	Female			Male		
	N	Mean	Range	N	Mean	Range
New pairs						
Change in nestling condition	3	-0.10	(-0.4+0.1)	3	-0.39	(-0.7--0.1)
Female condition (g)	2	-0.20	(-0.3--0.1)	2	-0.50	(-0.8--0.2)
Male condition (g)	3	-0.10	(-0.3+0.1)	2	-0.25	(-0.3--0.2)
Established pairs						
Change in nestling condition	2	-0.10	(-0.2+0.0)	2	+0.05	(-0.1+0.2)
Female condition (g)	2	-0.20	(-0.3--0.1)	2	-0.05	(-0.1-0.0)
Male condition (g)	2	-0.25	(-0.3--0.2)	1	-0.20	

dimorphism or differential dispersal (Stamps 1990; Gowaty & Droge 1991; Lessells 1998), but has been documented in relatively few sexually dimorphic birds. Red-winged blackbirds are one of the few other species for which such sex-biased provisioning has been reported (Yasukawa et al. 1990; Teather 1992; Westneat et al. 1995). Studies on species with little or no sexual size dimorphism that have experimentally manipulated brood sex ratios have found no evidence for sex-biased provisioning by either males or females (western bluebirds, *Sialia mexicana*: Leonard et al. 1994; great tits, *Parus major*: Lessells et al. 1998).

Although both parents provisioned male-biased broods more than female-biased broods, male and female brown thornbills appeared to use different cues to determine their provisioning behaviour. Female provisioning rates increased with nestling age and were dependent on brood sex ratio in both natural and experimental broods. Female thornbills therefore appear to adjust provisioning rates in response to the actual demands of the brood. Male provisioning rates increased with nestling age but did not vary with brood sex ratio in natural broods when male age and pair bond duration were controlled. Males also did not alter their provisioning behaviour when feeding experimental all-male or all-female broods. Sex-biased provisioning by male thornbills therefore appears to arise because male provisioning rates are influenced by pair bond duration and female thornbills adjust brood sex ratios in response to the status of their pair bond.

It is unclear why male thornbills do not adjust their provisioning rate in direct response to the sex ratio of their brood. Other studies show that male birds are able to distinguish between male and female chicks and bias provisioning in response to brood sex ratio (e.g. budgerigars, *Melopsittacus undulatus*: Stamps et al. 1987; eastern bluebirds, *Sialia sialis*: Gowaty & Droge 1991; great reed warblers: Nishiumi et al. 1996). One plausible explanation is that male thornbills trade-off the time required to adjust their provisioning behaviour to small differences in demand associated with biased sex ratios for time spent detecting predators or in territory defence. I had the impression, although it was not measured quantitatively,

that male thornbills were more likely to give alarm calls near the nest than females. Male thornbills may therefore decide on their provisioning rate based on the age of their brood and the time constraints imposed by the status of their pair bond, while female thornbills are more sensitive to the actual demands of the broods.

Sex Ratio Variation

Females in new pairs consistently produced broods containing more daughters, whereas females in established pairs produced broods containing more sons. Females in new pairs also had mates that provided less paternal care. Biased brood sex ratios may occur because females adjust their primary sex ratio (the sex ratio at fertilization) or result from the selective mortality of one or other sex between laying and fledging. In this study, excluding broods where the sex of one or more eggs in a clutch was unknown does not alter the conclusion that pair bond duration influences brood sex ratio. Furthermore, partial brood loss is extremely rare in brown thornbills (five cases in 109 broods that survived to banding) and nestlings have never been observed to die as a result of starvation. My data therefore suggest that female brown thornbills produce broods with biased sex ratios by manipulating their primary, rather than secondary, sex ratio. Other studies also suggest that female birds may adjust their primary sex ratio in response to paternal provisioning behaviour or resource availability at the time of breeding in order to maximize their fitness (Wiebe & Bortolotti 1992; Appleby et al. 1997; Komdeur et al. 1997; Nishiumi 1998; Westerdahl et al. 2000). Nishiumi (1998) found that in the polygynous great reed warbler females adjusted their primary sex ratios in response to their status as a primary or secondary female. Primary females that were aided by their mate produced male-biased broods whereas secondary females that cared for young alone produced female-biased broods. Female great reed warblers were argued to benefit from adjusting their primary sex ratio in response to their mating status because food supply was predicted to have a stronger influence on the subsequent reproductive value of sons

than daughters in this species. In contrast, Appleby et al. (1997) found that tawny owl, *Strix aluco*, broods contained more females (the larger sex) when vole densities were high. This pattern is likely to be adaptive because the subsequent reproductive success of females, but not males, was dependent on the density of voles in the territory on which they were reared as chicks.

There is a growing body of experimental evidence that suggests sex ratio biases observed in wild bird populations can be associated with significant fitness benefits for parents and young (e.g. Komdeur et al 1997; Komdeur 1998; Nager et al. 1999, 2000). Two results suggest that female brown thornbills in new pairs may benefit from producing female-biased broods. First, females in new pairs provisioned at a higher rate when feeding all-male broods than when feeding all-female broods. Elevated workloads may increase the risk of predation or lead to a loss of condition that reduces overwinter survival. Unfortunately, my sample sizes are too small to demonstrate such effects. However, elevated workloads have been found to reduce body mass and overwinter survival in other experimental studies (e.g. Gustafsson & Pärt 1990). Second, although females in new pairs were sensitive to the increased demand associated with provisioning sons they did not fully compensate for the lower feeding rates of their mates. The condition of nestlings in all-male broods provisioned by new pairs tended to decline more than the condition of nestlings in other experimental broods, although this result was not statistically significant. Loss of condition will reduce the reproductive value of a brood as postfledging survival and recruitment are positively related to nestling mass in brown thornbills (Green & Cockburn 2001). These results suggest that females in new pairs may both reduce their risk of death and be more likely to produce offspring that are capable of competing for a breeding vacancy if they produce female-biased broods. The extent to which females in established pairs benefit from producing male-biased broods is less clear since precise information on the relative fitness of well-fed sons and well-fed daughters is not available. However, the costs associated with producing broods containing a higher proportion of sons, the relatively expensive sex, are likely to be lower for females in established pairs in part at least because their mates provision at a higher rate than males in new pairs. Female thornbills, in both new and established pairs, are therefore likely to obtain some fitness benefit from adjusting the sex ratio of their brood in response to the status of their pair bond and the level of parental care provided by their partner.

Female birds may also adjust the sex ratio of their brood in response to parental traits associated with paternal attractiveness (Ellegren et al. 1996; Sheldon et al. 1999). For example, female collared flycatchers, *Ficedula albicollis*, adjust the sex ratio of their brood in response to the size of their mate's white forehead patch, a heritable trait associated with female choice, producing male-biased broods when paired to attractive males with large forehead patches (Ellegren et al. 1996). However, I found no evidence that female brown thornbills adjusted the sex ratio of their brood in response to either their own body

size or the body size of their mate as was predicted given that body size may influence the attractiveness of sons in this species (Green 2000). This may be because extrapair paternity is rare (ca. 6% of offspring are extrapair, Green 2000) and body size therefore does not have a large effect on the relative reproductive value of sons and daughters.

This study adds to the growing body of evidence that chromosomal sex determination does not completely prevent adaptive manipulation of the primary sex ratio in birds (Cockburn et al. 2002). Extreme sex ratio biases have been observed in the Seychelles warbler, *Acrocephalus sechellensis*, where females without helpers on high- and low-quality territories produced 13 and 77% sons, respectively (Komdeur et al. 1997). The magnitude of the sex ratio bias observed in the brown thornbill (new pairs: 42% sons; established pairs: 61% sons) is more typical of observed sex ratio biases in other wild bird populations (e.g. Nishiumi 1998; Westerdahl et al. 2000). However, there are also studies, based on large sample sizes, where no adaptive skews in sex ratio can be detected (e.g. Radford & Blakey 2000). Further studies are required to determine the extent to which diverse selection pressures have led to the evolution of mechanisms that allow control over sex ratio in birds.

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