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Sex allocation in black-capped chickadees *Poecile atricapilla*

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Optimal sex allocation for individuals can be predicted from a number of different hypotheses. Fisherian models of sex allocation predict equal investment in males and females up to the end of parental care and predict brood compositions based on the relative costs of producing males and females. The Trivers-Willard hypothesis predicts that individual females should alter the sex ratio of their broods based on their own condition if it has a differential impact on the lifetime reproductive success of their sons and daughters. The Charnov model of sex allocation predicts that females should alter sex allocation based on paternal attributes that may differentially benefit sons versus daughters. Because females are the heterogametic sex in birds, many recent studies have focussed on primary sex ratio biases. In black-capped chickadees *Poecile atricapilla*, males are larger than females suggesting they may be more costly to raise than females. Female condition affects competitive ability in contests for mates, and thus may be related to variance in fecundity. Females prefer high-ranking males as both social and extrapair partners. These observations suggest that females might vary the sex ratio of their broods based on the predictions of any of the above models. Here, we report on the results of PCR based sex determination of 1093 nestlings in 175 broods sampled from 1992 to 2001. Population-wide, we found a mean brood sex ratio of 0.525 ± 0.016, with no significant deviation from a predicted binomial distribution. We found no effect of clutch size, female condition, hatch date, parental rank or paternity. Our results reject the idea that female black-capped chickadees systematically vary sex allocation in their broods.

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Over the last fifty years, there has been continuous interest in sex ratio theory. A number of theoretical perspectives have been taken such as natural selection for equal investment in both sexes (Fisher 1958), population level variation of sex ratio (Hamilton 1967), and optimal sex allocation for individuals when conditions provide some advantage for offspring of one sex over the other (Trivers and Willard 1973, Charnov 1982). In birds, adaptive manipulation of sex ratio has attracted considerable interest because females are the heterogametic sex and there is the potential for manipulation of the primary sex ratio (reviewed in Ellegren and Sheldon 1997). In addition, molecular techniques now provide the necessary tools to address sex allocation in non-invasive ways (Ellegren and Sheldon 1997, Griffiths et al. 1998, Fridolfsson and Ellegren 1999).

Numerous studies have found evidence of optimal sex allocation, with females biasing their broods based on a number of different factors. For example, maternal condition and environmental factors that influence the relative success of males and females at maturity have been shown to influence sex allocation (e.g. Bortolotti 1986, Dijkstra et al. 1990, Lessells et al. 1996, Komdeur et al. 1997, Whittingham et al. 2002). Paternal quality has also been implicated in some studies (e.g. Burley 1986, Ellegren et al. 1996, Svensson and Nilsson 1996, Kempenaers et al. 1997, Albrecht and Johnson 2002). Still other studies have found no pattern of variation (e.g. Koenig and Dickinson 1996, Hartley et al. 1999). In this study we investigate whether black-capped chickadees *Poecile atricapilla* use adaptive sex allocation as a reproductive tactic.

Black-capped chickadees are small (~ 11 g), socially monogamous passerines that live in dominance structured flocks outside the breeding season (Smith 1976). Social rank is based on sex (males dominant to females) and age (older birds dominant to younger birds), where high-ranking birds have priority access to food and roost sites in winter (Smith 1976). Partnerships form within winter flocks and are assortative by social rank (Smith 1976, Otter et al. 1999). Evidence from removal studies suggests that there is strong female choice for high-ranking males (Otter and Ratcliffe 1996, Ramsay and Ratcliffe unpubl. data), and natural patterns of divorce confirm female choice for high-ranking males (Ramsay et al. 2000). Social rank has important consequences for reproductive success. For females, clutch size, hatching success, and fledging success are all related to the rank of both partners (Otter et al. 1999). The mechanisms underlying female variance are unknown, but female condition may be a factor; high-ranking females lay more eggs and spend longer periods incubating than low-ranking females in spite of the fact that high-ranking males do not provision their partners more than low-ranking males (Otter et al. 1999). High-ranking females also make more feeding trips to the nest during the nestling stage than low-ranking females (Otter et al. 1999). Variation in hatching success, which is related to rank (Otter et al. 1999), could be due to maternal effects such as condition or genetic factors, paternal effects, or it may be a combination of effects from both parents. For males, variation in reproductive success is not only related to female fecundity but is also affected by social rank through its influence on extrapair matings. High-ranking males gain the fitness benefits of their partner's enhanced fecundity plus the benefits of additional young sired in the nests of neighbouring, lower ranking pairs (Otter et al. 1998).

In this study we examine the sex ratios of chickadee broods under three hypotheses. Under the Fisherian model, sex ratio varies with the cost of producing each sex, although sex ratios at equilibrium should achieve equality (Fisher 1958). In our study population, males are larger than females by 10 days post-hatch (Boon 2002) and adult males are 5% larger in mass, wing length, and tail length (Desrochers 1990, Ramsay et al. unpubl. data). Fisher (1958) stated that individuals should invest equally in the sexes. Since males are larger and thus more expensive to produce, a female using a flexible allocation strategy could partition her investment into a few expensive offspring, or a greater number of less-expensive offspring. Thus, we predict a negative relationship between clutch size and sex ratio. Because of limits on parental investment imposed by timing of egg laying, we might predict a negative relationship between hatch date and sex ratio; more males will be produced in earlier broods. Evidence from great tits, however, suggests the opposite pattern (Lessells et al. 1996). Consequently, under this model we have reasons to predict a sex ratio bias in either direction with hatch date. Under Trivers and Willard's (1973) model, sex ratio varies with maternal condition. Since males are larger than females, sons may benefit more from good maternal condition than their sisters. Therefore, we predict that females in good condition will produce male-biased broods, and females in poor condition will produce female-biased broods. Charnov's (1982) model, which was an expansion of the Trivers-Willard hypothesis, predicts that sex ratio could also vary with paternal quality. Since there is greater variation in reproductive success among males than females, sons that inherit characteristics from their fathers which influence their own quality will benefit more than their sisters. Since female chickadees preferentially choose males with high social rank, we predict that the offspring of high-ranking males, within-pair or extrapair, will be male biased, while the offspring of low-ranking males will be female biased. We tested these hypotheses using 10 years of data from our long-term study of black-capped chickadees.

Methods

Study area and dominance assessment

This study was conducted from 1992 to 2001 at Queen's University Biological Station, Chaffey's Lock, Ontario, Canada (44°34′N, 76°19′W). The study site encompasses approximately 150 ha of mixed deciduous-coniferous forest where approximately 20 small flocks (4 to 10 individuals each) of black-capped chickadees are permanent residents. Throughout the study site we used 5 to 14 winter feeding stations to attract birds for ringing and dominance observations. Each feeder attracted from 3 to 5 flocks of birds. In each year, approximately 95% of the individuals in the population were captured using Potter's traps and marked with unique combinations of Canadian Wildlife Service number rings and two or three plastic colour rings. At the time of ringing, we measured mass, wing chord, tail length, and tarsus length.

We determined the social rank of individuals through observation of dyadic interactions at winter feeders. We inferred dominance between opponents when an individual (i) supplanted or chased an opponent, (ii) resisted a supplanting attack by an opponent, (iii) elicited a submissive posture in an opponent or (iv) fed while an opponent waited to approach a feeder (Ficken et al. 1990, Otter et al. 1998). Dominance hierarchies were determined for each flock by tallying the outcomes of pairwise interactions between individuals. For any pair of individuals, the winner of the majority of interactions was considered to be dominant. We observed approximately 27 000 interactions at feeders between 1992 and 2001. In addition, while tracking each year flocks to determine home range, approximately 15 dominance interactions between flock mates were noted and included with the feeder tallies. These additional interactions always agreed with feeder observations. Dominance relationships are known to be consistent across feeding sites in this species (Smith 1991).

Locating nests and blood sampling

In each year, from mid-March onward, pairs spent increasing amounts of each day on their territories. We identified pairs using the following criteria: individuals foraging together in the absence of other birds, nest cavity excavation by the pair, nuptial feeding, copulation, male defence of a female against other males, and cooperation in territory defence (Otter and Ratcliffe 1996). We found nests by regularly tracking pairs from mid-March through late May. We monitored parent's nesting activities through behavioural observations (Smith 1991) and direct observations into cavities using mirrors.

We collected blood samples from nestlings between 4 and 11 days following hatching. Using brachial or tarsal venipuncture, we collected between 10 and 50 μl of blood in microcapillary tubes, from each nestling. We stored blood in either 1 ml 1 × TNE, or 1 ml Queen's Lysis Buffer (Seutin et al. 1991). All samples were frozen until DNA was extracted.

Sexing nestlings

We amplified extracted DNA under standard polymerase chain reaction (PCR) conditions using the P8/P2 primer set (Griffiths et al. 1998). In black-capped chickadees, this reaction yields a 350 bp product from the Z-chromosome (present in both males and females) and a 450 bp product from the W-chromosome (present only in females). We ran 10 μl of each PCR sample mixed with 5 μl of loading dye on 3% agarose gel at 120–135 V for 1:20 to 2:00 h. A 12 μl aliquot of Gene Ruler 100 bp DNA ladder (Fermentas) was run alongside each row of samples. Gels were stained in ethidium bromide prior to electrophoresis. We photographed gels under UV light and assigned sex by counting the number of visible bands in each lane.

Parentage analysis

We used parentage data collected in the course of other studies (Otter et al. 1998, Mennill et al. 2002, Ramsay and Mennill unpubl. data) to examine sex ratios in relation to extra-pair paternity. We assessed paternity of nestlings from 1992–1994 using multilocus DNA fingerprinting, and paternity of nestlings from 1995 using PCR amplification of two microsatellite loci (PAT MP2-14 and PAT MP2-43) as well as a single-locus minisatellite probe (cPdoMS14; see Otter et al. 1998 for complete details). Paternity of nestlings from 1996–2001 was assessed using three microsatellite loci (PAT MP2-14 and PAT MP2-43, Otter et al. 1998; PCA4 AJ279810, Dawson et al. 2000), which provided high power to discriminate extra-pair young (EPY) from within-pair young (WPY; average exclusion probability > 0.99). We assigned paternity to EPY using an exclusionary approach. In no case did we have more than one possible extrapair sire.

Statistical analyses

We report sex ratios as the proportion of sons in each brood. We used a goodness of fit test to compare the distribution of brood sex ratios across the population with expected values based on the binomial probability of having a given number of sons in a brood of a particular size. To examine the sexes of individual offspring from mixed paternity broods, we used a binomial test to determine whether males were more likely to occur than females. To compare brood sex ratio by parental rank, female condition, hatch date, and brood size, we used the GENMOD procedure of SAS (1990) with a logit link function and binomial error distribution, where the number of sons was the dependent variable and the number of nestlings in each brood was the binomial denominator. The difference between the model and the data is reported by the deviance, which is distributed as χ^2 (Crawley 1993). All other analyses were conducted using JMP 4.0 (SAS Institute). All tests are two-tailed and all values are reported as mean ± standard error.

Results

We determined the sex of 1093 nestlings representing 175 complete broods across all years. We confirmed the accuracy of the molecular sexing technique using 12 individuals that had been sexed by laparotomy by an independent observer, and an additional 73 adults for whom sex was known based on breeding activities. Our molecular results matched the independent data in all cases.

The sex ratio (proportion male) across all broods was 0.525 ± 0.016. Brood size ranged from 2 to 11 (average = 6.25 ± 0.12) and the maximum number of males in a brood was 6. The distribution of brood sex ratios was not different from binomial prediction ($\chi^2 = 42.4$, df = 74, P = 1.0; Fig. 1). Brood sex ratio did not differ between years (Bartlett ANOVA $F = 1.30$, df = 8, P = 0.24), thus we pooled all years for the remaining analyses. Chickadees in our population show very low levels of nestling mortality unless an entire clutch is depredated; consequently sex-biased post-hatch mortality was unlikely to influence our measurement of sex ratios.

Brood sex ratio did not vary between the offspring of high-ranking males (0.507 ± 0.024, n = 76) versus low-ranking males (0.536 ± 0.024, n = 74; $\chi^2 = 0.64$, P = 0.59). Mother's winter condition (measured as residual mass over tarsus length) in 143 broods had no effect on sex ratio ($\chi^2 = 2.76$, P = 0.10). Hatch date varied across years so we used standardised values to express hatch date as days before or after the annual mean. There was no pattern of sex ratio variation for 137 broods with known hatch dates ($\chi^2 = 0.59$, P = 0.44). Brood size had no effect on sex ratio ($\chi^2 = 0.87$, P = 0.35).

Female reproductive strategy did not influence offspring sex ratio. There was no difference in sex ratio between broods that contained no EPY (0.533 ± 0.018, n = 117) versus broods that contained one or more EPY (0.513 ± 0.028, n = 57; $\chi^2 = 0.64$, P = 0.59). We also examined the sexes of individual EPY; of 118 EPY detected in 57 broods from 1992 to 2001, 62 were males and 56 were females (Binomial test, P = 0.54). We were able to assign the paternity of 81 EPY to individual males for whom we had rank information. The sex ratio of the extra-pair offspring of high-ranking males (0.543, n = 57 EPY) was similar to the overall sex ratio of the extra-pair offspring of low-ranking males (0.500, n = 24 EPY; $\chi^2 = 0.13$, P = 0.72).

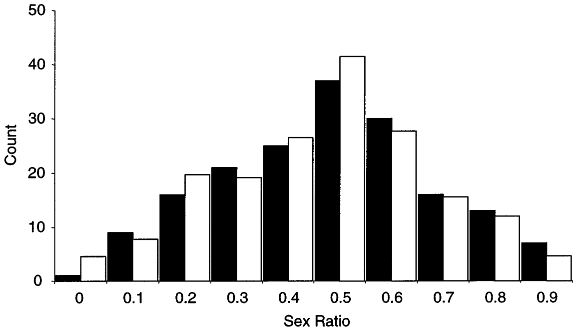

Fig. 1. The distribution of observed (black bars) and expected (open bars) sex ratios in black-capped chickadee broods from 1992 to 2001 at Queen's University Biological Station. Predicted values were derived from binomial probabilities for all observed brood compositions (size and sex ratio). The observed distribution did not differ from the predicted ($\chi^2 = 42.4$, df = 74 P = 1.0).

Discussion

This study, drawn from a ten-year investigation, shows no evidence for adaptive sex allocation by female black-capped chickadees. We examined five different factors that predict patterns of sex ratio variation including clutch size, maternal condition, parental rank, hatch date and paternity. We found no patterns of variation related to any of these factors.

Based on previous observations of clutch size variation (Otter et al. 1999), and size variation in offspring (Boon 2002) in our population, we predicted that females might alter sex allocation based on clutch size. Since male nestlings are larger than females in a number of morphological characters by 10 days post-hatch, a female with a limited amount to invest in offspring could choose to produce a smaller male-biased clutch, or a larger female-biased clutch. As long as the average investment in male and female offspring across the population was equal, then Fisher's hypothesis would be satisfied. Rather than this level of fine control over sex allocation, we saw no pattern based on clutch size.

Under the Trivers and Willard (1973) hypothesis, we predicted that offspring sex ratio would vary with maternal condition, but we found no such effect. Examining two of the assumptions of this hypothesis may help to explain our results. The Trivers-Willard hypothesis assumes a correlation between maternal condition during parental investment and the condition of young at the end of parental investment. Trivers and Willard (1973) suggested that this assumption is probably true for species with small brood sizes but may not hold for species with large, highly variable brood sizes. Average clutch size in chickadees is high by passerine standards, and is highly variable (range 2 to 11 in our population), and therefore the first assumption of the Trivers-Willard hypothesis may not hold. The second assumption of the Trivers-Willard hypothesis is that differences in condition at the end of parental investment endure into adulthood. We have no data to examine this assumption in chickadees, and thus we cannot confirm its validity in our population. Finally, we measured maternal condition at the time of ringing during the winter, and it may be that this measure does not accurately reflect condition during nesting. In a separate study, we found that winter condition was an accurate predictor of competitive ability among females in the weeks leading up to egg-laying (Ramsay and Ratcliffe unpubl. data). Therefore, although a measure of maternal condition taken during nesting would have been ideal, we are confident that our winter measure is an index of nesting condition.

Charnov's (1982) model of sex allocation predicts that sex ratio should vary with paternal characteristics that might differentially influence the reproductive success of sons versus daughters. Under this hypothesis, we predicted that parental rank might have an effect on sex ratio, with high-ranking pairs raising male-biased broods and low-ranking pairs raising female-biased broods, however, our results do not show such an effect. This contrasts with a previous study in blue tits which showed an effect of paternal quality on sex ratio (Svensson and Nilsson 1996). The measure of male quality used by Svensson and Nilsson (1996) was survivorship; we used male social rank because of its value as a target of female choice. It may be that paternal rank does not differentially influence male and female reproductive success in chickadees. Under the Charnov hypothesis, we also predicted that extrapair offspring would be more likely to be male and would occur in male-biased broods. In contrast with the results of a previous study in blue tits which found an effect of paternity (Kempenaers et al. 1997), we found no such pattern in chickadees; indeed the sex ratio among extrapair young matches our population sex ratio exactly. It may be that the benefits that female chickadees seek from their extrapair partners, as in the case of the quality of social partners, do not differentially benefit sons over daughters. Alternatively, female chickadees may not have sufficiently fine control over sex allocation and sperm usage to manipulate the sex of an individual offspring based on its paternity. If this were true we might expect to find mixed paternity broods to be male-biased compared to broods with single paternity, even though individual extrapair young may not be predominantly male. Again, this was not the case, further supporting the idea that paternal quality may not differentially affect sons and daughters.

At the outset we predicted that females might bias sex allocation as a complement to the fitness benefits they achieve through high-ranking partnership, such as improved overwinter survivorship and enhanced fecundity. However, we found no pattern of systematic variation of sex allocation by the females in our population. Fisher's hypothesis of equal investment in males and females can be interpreted as occurring across a population as a whole, with random variation among broods. Alternatively, we might see Fisher's hypothesis as applying to individual broods with females exercising fine control over their investment in male and female offspring. Our results support the former idea over the latter. Koenig and Dickinson (1996) suggested a number of precautions when interpreting data that appear to support biased sex allocation, including sex ratio being affected by a number of factors, small sample size, and limited time span of studies. Following these precautions we can conclude that female black-capped chickadees in our population do not use sex allocation as an adaptation.

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Satellite tracking of male rockhopper penguins *Eudyptes chrysocome* during the incubation period at the Falkland Islands

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Pütz, K., Smith, J. G., Ingham, R. J. and Lüthi, B. H. 2003. Satellite tracking of male rockhopper penguins *Eudyptes chrysocome* during the incubation period at the Falkland Islands. – J. Avian Biol. 34: 139–144.

The foraging patterns of ten male rockhopper penguins *Eudyptes chrysocome* from the Falkland Islands were recorded during the incubation period by using satellite telemetry. Irrespective of study site and year, two different foraging areas could be identified. Three foraging trips were directed towards the slope of the Patagonian Shelf c. 140 km to the northeast of the breeding colony and these trips had a duration of 11–15 days. The seven other rockhopper penguins travelled c. 400 km towards the edge of the Falkland Islands' waters; all these foraging trips followed an anti-clockwise direction and lasted 16–27 days. The calculated mean daily travelling speed, based on the time spent underwater and the distance covered between two positions, was significantly higher in birds travelling to the edge of the Falkland Islands' waters compared with those foraging at the shelf slope (4.4 ± 1.6 km/h vs. 3.4 ± 2.0 km/h, respectively). The consistent foraging patterns exhibited during the long trips may be linked to the Falklands current, allowing the penguins to reach remote areas while reducing their energy expenditure. Potential interactions between commercial fisheries and hydrocarbon exploration are discussed.

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