Birds bias offspring sex ratio in response to livestock grazing

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Livestock grazing, which has a large influence on habitat structure, is associated with the widespread decline of various bird species across the world, yet there are few experimental studies that investigate how grazing pressure influences avian reproduction. We manipulated grazing pressure using a replicated field experiment, and found that the offspring sex ratio of a common upland passerine, the meadow pipit Anthus pratensis, varied significantly between grazing treatments. The proportion of sons was lowest in the ungrazed and intensively grazed treatments and highest in treatments grazed at low intensity (by sheep, or a mixture of sheep and cattle). This response was not related to maternal body condition. These results demonstrate the sensitivity of avian reproductive biology to variation in local conditions, and support growing evidence that too much grazing, or the complete removal of livestock from upland areas, is detrimental for common breeding birds.

Keywords: meadow pipit; uplands; cattle; sheep; molecular sexing

1. INTRODUCTION

Livestock grazing is a major driver of environmental change [1] and is associated with the widespread decline of grassland bird populations [2,3]. Grazing intensity and the species of grazing animals influence the structural complexity of vegetation, significantly affecting the availability of arthropod prey [4] and ultimately determining habitat quality for a range of foraging and breeding birds [5]. Experimental studies indicate that livestock grazing can influence the breeding abundance of birds [6,7], but the effects on their reproductive performance are unclear [8].

Offspring sex ratio is an important aspect of population demography for sexually reproducing organisms and, for dimorphic species, has been shown to vary with maternal condition [9] and in response to the quality of the current breeding environment [10]. In these species, production of the larger, more costly, sex is typically reduced under poor conditions [9,11]. However, the advent of molecular-genetic sexing techniques has revealed that some species that are monomorphic in size (or show little sexual size dimorphism) can also show biases in sex ratio [12]. Given that the costs of rearing the young of such species are not expected to differ [13], these findings suggest that factors other than offspring size may have important effects on the fitness consequences of different sex ratios, for example sex-dependent environmental sensitivity [14] or sex-biased dispersal [15], although these mechanisms are poorly understood.

Here, we use an experimental manipulation of grazing pressure, and hence of habitat quality [4], to investigate for the first time, to our knowledge, whether grazing management influences the primary sex ratio of a common upland passerine, the meadow pipit Anthus pratensis.

2. MATERIAL AND METHODS

(a) Study site

Data were collected between May and July in 2007 and 2008 at Glen Finglas, Scotland (200–500 m a.s.l., 56°16' N, 4°24' W). A grazing experiment was established in 2003 in three discrete areas. Each study area contained two replicates and within each replicate four grazing treatments were randomly allocated to 3.3 ha plots: high sheep—nine ewes per plot (2.72 ewes ha−1), low sheep—three ewes per plot (0.91 ewes ha−1), low mixed—two ewes (0.61 ewes ha−1) and two cattle with their unweaned calves at an equivalent grazing pressure as the low sheep treatment, and ungrazed. Sheep were only removed from plots in the winter months (December–March) and cattle were added for four weeks in the autumn (for more details, see Dennis et al. [4]).

(b) Nest monitoring and sampling

Nests were located by flushing incubating females from the nest or observing the foraging behaviour of parent birds. Females incubating eggs were caught using a modified mist-net set at the entrance of the nest and measurements of tarsus length (±0.1 mm) and mass (±0.1 g) were taken from all birds. Blood samples were taken from nestlings, at least 6 days old, by brachial venipuncture and stored in an equal volume of TES buffer (50 mM EDTA, 1% SDS, 50 mM Tris (pH 8)). Unhatched eggs and dead nestlings were collected and tissue samples were used for DNA analysis. Thus, for all nests, the sex ratio at the time of conception was known. All samples were kept cool in an ice box and then stored in a –20 °C freezer. A DNA test [16] was used to sex individuals using P2 and P8 forward and reverse primers.

(c) Data analysis

Because not all females nesting in the grazing treatments were caught and measured, only a subset of data (M1, n = 37) was used in a generalized linear mixed model (GLMM) to determine the influence of maternal condition on offspring sex ratio. Maternal condition (standardized residuals from a regression of body mass adjusted for tarsus length) was specified as a continuous covariate. Year (2007/2008) was included to determine whether sex ratio differed between years. To assess whether sex ratio varied across the breeding season, nests were classified as 'early' or 'late' attempts using the median incubation date (Julian day = 148) (following Evans et al. [17]). This method maximized the use of data because incubation date was unknown for a number of nests. An interaction between maternal condition and incubation date (early/late) was also included. A second GLMM (M2) was used to examine the relationship between offspring sex ratio and grazing treatment. Two nests were excluded due to missing data (n = 76). Categorical factors were grazing treatment (four levels), year (2007/2008) and incubation date (early/late). Continuous covariates were clutch size and the breeding density of meadow pipits in a plot (derived from an annual census; for methods, see Evans et al. [6]). An interaction between grazing treatment and incubation date (early/late) was also included. Differences in sex ratios between the grazing treatments were assessed using post hoc Tukey HSD pairwise comparison tests with alpha adjusted to 0.0083 using a false discovery rate (FDR) correction.
The ‘low mixed’ and ‘low sheep’ treatments were also combined to produce a 3-level factor but the statistical relationships remained similar. Results are therefore reported from the models described above.

In both GLMMs, binomial errors and logit links were used with broods as the unit of analysis. The proportion of males in each brood was used as the dependent variable, with brood size as the binomial denominator. Random effects followed the structure of the experimental design (study area/replicate/plot). Model simplification was conducted with a reverse stepwise procedure, using Akaike’s information criterion to determine the minimum adequate model. All statistical tests were carried out using R v. 2.11 [18].

3. RESULTS

Data were available for 78 meadow pipit broods (2007/2008: high sheep = 11/13, low sheep = 7/13, low mixed = 10/11, ungrazed = 6/7). Maternal condition (M1, \( p = 0.69 \)), incubation date (\( p = 0.25 \)) and their interaction (\( p > 0.10 \)) had no effect on offspring sex ratio. Offspring sex ratio was not statistically different between years (\( p = 0.18 \)).

Because maternal condition was not significant, the larger dataset (M2, \( n = 76 \)), which included birds whose body condition was not known, was used to assess the relationship between grazing and offspring sex ratio. The proportion of sons was lowest in the ‘ungrazed’ (32%) and ‘high sheep’ (41%) treatments and highest in the low sheep (55%) and low mixed (54%) treatments. Grazing treatment was the only significant explanatory factor of offspring sex ratio; birds nesting in treatments grazed at low intensity produced significantly more sons than those in the ungrazed treatment (GLMM: low sheep: \( 0.97 \pm 0.38, z = 2.52, \ p = 0.012 \); low mixed: \( 0.93 \pm 0.38, z = 2.42, n = 21, \ p = 0.015 \). Although fewer sons were produced in the high sheep treatment compared with both the low-intensity treatments, this difference was not significant (Tukey HSD: both \( p = 0.08 \), figure 1). The proportion of sons also did not differ significantly between the low sheep and low mixed treatments (Tukey HSD: \( p = 0.8 \), figure 1), or between the high sheep and the ungrazed treatments (\( p = 0.4 \), figure 1). Offspring sex ratio was not influenced by any other factor or the interaction term (\( p > 0.05 \)).

4. DISCUSSION

We demonstrate for the first time, to our knowledge, that livestock grazing pressure can influence the offspring sex ratio of a free-living common upland passerine. The proportion of sons was lowest in the ungrazed and intensively grazed treatments and highest in treatments grazed at low intensity (by sheep or a mixture of sheep and cattle). This research supports growing evidence that birds manipulate offspring sex ratio in response to local habitat conditions [10] and that too much grazing, or the complete removal of livestock from upland areas, is detrimental to common breeding birds. While additional research is necessary to understand the observed variation in sex ratio, the most likely explanation relates to the effect of grazing manipulation on the quality of the breeding environment.

In this system, areas that are ungrazed or grazed at high intensity by sheep represent low-quality habitats for breeding birds [6,8]. If sex differences affect the costs and benefits of rearing nestlings [12,14], then parents occupying these grazing treatments may have overproduced the sex that requires fewer resources, presumably in this case females, to mitigate the impacts of suboptimal conditions within these areas. An alternative explanation, but one also based on the quality of the environment, is that in many passerine species females are the dispersing sex and a strategy of overproducing daughters may reduce competition for resources at the natal site [15]. Additional research is warranted as it is not known whether there are sex differences in growth rates or dispersal in this species.

Although maternal condition was not a significant predictor of offspring sex ratio, it is possible that the measurement we used did not fully capture the physiological condition of female meadow pipits. This supports recent research which demonstrates that meadow pipits breeding in ungrazed areas or areas grazed at high intensity by sheep had significantly higher corticosteroid (CORT) levels, the primary avian stress hormone, than birds breeding in areas grazed at low intensity by sheep and cattle [19]. Given the findings of Bonier et al. [20] that high levels of CORT are correlated with female-biased broods in female white-crowned sparrows (Zonotrichia leucophrys), further research on the link between CORT and sex ratios is clearly merited.

That grazing influences an individual’s reproductive strategy has broader implications for the management of bird species, particularly those of conservation concern. Sex ratio is an important aspect of population demography and deviations from parity can have catastrophic consequences for the viability of small populations [21]. If a species alters the sex ratio of its progeny in response to the quality of the environment then developing management strategies based on demographic models that assume an equal sex ratio...
could have important repercussions for species nesting in degraded habitats [22].

We thank The Woodland Trust and Fiona Leckie, Richard Griffiths and Kate Griffiths for help in the field and laboratory. This research was part of The Glen Finglas project (formerly Grazing and Upland birds, GRUB) funded by the Scottish Government (RERAD) and was conducted under project and personal licence authority under the UK Animal (Scientific Procedures) Act as implemented by the MLURI local ethical committee.