



Facultative Sex Allocation and Sex-Specific Offspring Survival in Barrow's Goldeneyes

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Abstract

Sex allocation theory predicts that females should bias their reproductive investment towards the sex generating the greatest fitness returns. The fitness of male offspring is often more dependent upon maternal investment, and therefore, high-quality mothers should invest in sons. However, the local resource competition hypothesis postulates that when offspring quality is determined by maternal quality or when nest site and maternal quality are related, high-quality females should invest in the philopatric sex. Waterfowl – showing male-biased size dimorphism but female-biased philopatry – are ideal for differentiating between these alternatives. We utilized molecular sexing methods and high-resolution maternity tests to study the occurrence and fitness consequences of facultative sex allocation in Barrow's goldeneyes (*Bucephala islandica*). We determined how female structural size, body condition, nest-site safety and timing of reproduction affected sex allocation and offspring survival. We found that the overall sex ratio was unbiased, but in line with the local resource competition hypothesis, larger females produced female-biased broods and their broods survived better than those of smaller females. This bias occurred despite male offspring being larger and tending to have lower post-hatching survival. The species shows strong female breeding territoriality, so the benefit of inheriting maternal quality by philopatric daughters may exceed the potential mating benefit for sons of high-quality females.

Introduction

As shown by Fisher (1930), the partitioning of reproductive investment into males and females is not straightforward in sexual organisms, because male and female offspring may accrue to parental fitness differentially. Trivers & Willard (1973) refined Fisher's (1930) original sex allocation theory, by showing that parental state or environmental quality may influence the optimal sex allocation strategy. Interestingly, such facultative sex allocation by parents does not necessarily lead to population level biases in sex ratios, because the differences in sex allocation between parents tend to cancel out in the population (Trivers & Willard 1973).

Parental quality affects sex allocation (Trivers & Willard 1973; Nager et al. 1999; Thuman et al. 2003). Perhaps, the most studied maternal trait affecting sex allocation is female condition (e.g. Nager et al. 1999; Thuman et al. 2003), but also female size may affect it (Kojola & Eloranta 1989; Arnbohm et al. 1994; Rehan & Richards 2010). Because of the heritable component to both structural size (Merilä & Sheldon 2001) and body condition (Merilä et al. 2001), large females should produce large offspring and good-condition females good-condition offspring, respectively. However, being large or in good condition may have a larger effect on the fitness of one sex than on that of the other (e.g. Clutton-Brock et al. 1984; Kojola & Eloranta 1989). Parents should therefore optimize

their fitness by adjusting their sex allocation according to their own state (Trivers & Willard 1973).

The environment influences sex allocation by modulating the costs and benefits of producing males and females (e.g. Fisher 1930; Korpimäki et al. 2000). Sex-specific body size plays a crucial role in steering parental sex allocation, so that the smaller sex is preferred under harsh conditions, mainly due to the lower production cost and lower resource requirements (reviewed in Benito & González-Solís 2007). The larger sex is in turn more costly to produce and to care for, but when produced under benign conditions, it may achieve high reproductive output and should then be favoured (Benito & González-Solís 2007; Clutton-Brock et al. 1984).

Sexual asymmetry in dispersal behaviour may lead to biased sex allocation (Emlen et al. 1986; Gowaty 1993). The philopatric sex may experience local resource competition between relatives (Clark 1978), which parents may counteract by adjusting their sex allocation towards the dispersing sex (Gowaty 1993). However, when breeding sites vary in quality, parents with high-quality nest sites should invest more in the philopatric sex and more in the dispersing sex at low-quality sites (Komdeur et al. 1997; Julliard 2000; Wild & West 2007). Such patterns have so far mainly been studied in cooperatively breeding birds, while little is known about their role in other animals. Paralleling the predictions regarding the effect of habitat quality on sex allocation, high-quality mothers that are above average at acquiring nest sites or food resources should invest in the philopatric sex given that offspring inheritance of maternal phenotypic quality is strong enough (Leimar 1996). By doing so, high-quality females will ensure that their offspring are successful in competing for local resources. The interplay between sexual size dimorphism (SSD) affecting sex ratios through resource limitation and sex-biased philopatry affecting sex ratios through habitat or parental quality may create the possibility for different and sometimes even opposing mechanisms of sex ratio control (Wild & West 2007).

Like most waterfowl, goldeneyes (*Bucephala* spp.) exhibit female-biased philopatry (Greenwood 1980; Anderson et al. 1992). Nest-site safety is an important aspect of nest-site quality, and female common goldeneyes (*B. clangula*) are demonstrably able to assess the relative safety of nest sites (Pöysä 2006). Because of local resource competition expected among philopatric females (Pöysä et al. 1997), mothers may benefit from investing differentially into the production of males and females depending on the safety of their nest. A female returning to breed close to her safe

natal site may obtain higher fitness returns than a female returning to an unsafe area, whereas the fitness returns of male offspring are presumably less dependent of natal nest-site safety due to dispersal (hereafter, habitat quality hypothesis; Ruusila et al. 2001). Because competitive interactions can often result in a positive relationship between phenotypic quality and the probability of settling in high-quality habitat (reviewed in Stamps 2006), large body size or good body condition may provide females with a competitive advantage in gaining access to the safest nest sites. In waterfowl, we may therefore hypothesize that although one would expect good-quality parents to produce male-biased broods, because males should be more costly to produce because of their larger size at hatching (hereafter, production cost hypothesis), this relationship may be negated, or even reversed, under strong female nest-site competition (hereafter, local resource competition hypothesis; cf. Leimar 1996; Wild & West 2007). However, this possibility has never been directly tested in a species characterized by male-biased SSD and female-biased philopatry.

The generality and the evolutionary importance of facultative sex allocation is still debated (e.g. Saino et al. 2008), especially in vertebrates (Wild & West 2007). Furthermore, the effects and fitness consequences of state-dependent and environmental effects on sex ratios have only rarely been examined simultaneously (but see Lindström et al. 2002). With this in mind, our aim was to elucidate the occurrence of facultative sex allocation in Barrow's goldeneyes (*B. islandica*) and whether the allocation patterns follow the production cost, the habitat quality or the local resource competition hypotheses, respectively. To this end, we used molecular sexing tools to determine the female-specific offspring sex ratios. The Barrow's goldeneye is an excellent study species for investigating the potentially complex outcome of offspring SSD and sex-biased dispersal on sex allocation in relation to parental state. This is because of the combination of male-biased SSD (Eadie et al. 2000), which may suggest that males are more expensive to produce, but female-biased philopatry (Savard & Eadie 1989), which, due to local resource competition, may in turn render the production of females less beneficial. Here, we investigated the effects of female structural size and body condition (maternal resources) and nest-site quality, on offspring sex allocation, while controlling for the timing of reproduction. Second, we evaluated how female and nest-site characteristics were related to the survival of individually marked offspring of both sexes.

Material and Methods

Study Area and Population

The study was conducted at Riske Creek, close to the town of Williams Lake (51°52'N, 122°21'W), British Columbia, Canada, during 2004–2007. The study area consists of a prairie plateau approx. 200 km² in size, interspersed with a large number of ponds and lakes with trembling aspen (*Populus tremuloides*) stands along the shores. The plateau is surrounded by mixed coniferous forest consisting mainly of lodge pole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*). Nest boxes were erected in the aspen and coniferous stands in 2004, as close to the shorelines of the wetlands as possible, resulting in a total of 127 nest boxes being placed around 36 ponds and lakes. The density of nests was significantly higher in the open prairie habitat (mean number of active nests \pm SD within a 1 km radius from a focal nest = 6.57 ± 4.14) than in the coniferous forest (2.45 ± 1.18 ; Wilcoxon rank-sum test: $W = 537.5$, $p < 0.0001$). The coordinates of all nest boxes were recorded using a GPS unit.

Black bears (*Ursus americanus*) are the most frequent predators of nests: they pull down nest boxes and devour the eggs within (KJ, personal observation). While goldeneye females have not been observed to be killed by bears in this population, mustelids, such as the fisher (*Martes pennanti*), take both eggs and females (KJ, personal observation). In addition, unknown predators, suspected to be ravens, pierced the eggs in several nests in 2007 (KJ, personal observation). We assessed the relative safety of the two habitats by scoring all nests (2006: $n = 58$, 2007: $n = 67$) with known fate as predated or not predated. Years did not significantly differ in the probability of nest predation (logistic regression: $b = 0.43$, $df = 122$, $p = 0.30$), while the prairie habitat was found to be significantly more prone to nest predation than the coniferous habitat (logistic regression: $b = 1.24$, $df = 122$, $p = 0.009$).

Field Methods

The main body of data for this study was collected in 2006–2007 when 457 newly hatched ducklings from 51 nests were sampled for DNA. Furthermore, 74 females were caught, either by hand or with hand net from the nest aperture, during the breeding seasons 2004–2007 for banding, taking structural measurements (body weight and length of tarsus) and DNA sampling. Thirty-eight of these 74 birds (51%) successfully hatched broods during 2006–2007, and 11

(14.9%) did so in both years. Of all 49 successful nests, 28 (57%; 2006: $n = 16$, 2007: $n = 12$) were situated in the prairie habitat and 21 (43%; 2006: $n = 14$, 2007: $n = 7$) in the forested habitat. The ducklings from one nest were not included in the analysis because data on the female inhabiting the nest were lacking.

To estimate the date of incubation onset, we used the egg flotation method of Kilpi & Lindström (1997), modified to Barrow's goldeneyes with an incubation period of approx. 32 d. The method provides a reliable estimate of the number of days the eggs have been incubated and hence allows the estimation of brood hatch date and the capture of ducklings in the nest box prior to nest exodus. It is important to note that the hatchability of eggs in successful nests is very high (91%; Jaatinen et al. 2009a) and it is therefore highly unlikely that sex-biased embryonic mortality would be the cause for any sex ratio biases observed after the eggs are hatched. Furthermore, the hatchability of eggs is not associated with clutch size (Jaatinen et al. 2009a), further diminishing the potential for bias arising from unhatched eggs. Nests were visited 2 d prior to the estimated hatch date to avoid missing the hatching dates and to get a more accurate estimate of hatch date, enabled by observing cracks of holes in the eggs. On the day of hatching, the brood was captured and the ducklings were sampled for DNA, weighed, the length of their tarsi was measured and they were marked with a uniquely coloured plastic nape tag for individual identification (Traylor & Alisauskas 2006; Arnold et al. 2011). The tags were manufactured from shorebird leg-band blanks (A. C. Hughes, Middlesex TW12 1NA, England) and attached to the nape of the ducklings with small, sterilized brass safety pins, as described by Arnold et al. (2011). The nape tags are eventually rejected from the skin of the ducks, and the use of such markers has been shown not to raise any concern related to animal care (Arnold et al. 2011). Furthermore, the use of nape tags has not been found to affect the survival of ducklings, as long as they are applied correctly, and the behaviour of marked ducklings is also natural and unaffected by the nape tags (KJ personal observation; Arnold et al. 2011). All the duckling markings were applied by one experienced person (KJ) to diminish variation in marker retention and to ensure the well-being of animals (Arnold et al. 2011). Female DNA was sampled using a syringe to extract approx. 400 μ l of blood from the carpal vein. Ducklings were sampled upon hatching by collecting ca. 100 μ l of blood from the medial metatarsal vein

using small-gauge lancets and capillary tubes. All blood samples were stored in tubes containing 70% ethanol and frozen at -20°C until the DNA was extracted.

Female Barrow's goldeneyes are extremely philopatric to their particular breeding habitat (Jaatinen et al. 2011) and rarely change their breeding habitat type (prairie and coniferous forest, respectively) during their breeding career. Thus, none of the eleven females breeding successfully during both years of this study switched habitat type. This means that prospecting for safe nest sites almost exclusively occurs within a particular habitat type, and thus, relative safety within a particular habitat type, rather than absolute safety pooled over the entire landscape, is likely to be more important in breeding habitat selection. The usefulness of absolute nest-site safety measures pooled over the entire study area is further compromised by the significant difference in nest density between habitats. To make the nest-site safety measures in the two habitats comparable, the habitat-specific annual relative safety of each nest site in the years 2006 and 2007 was calculated as the distance to the closest predated nest in each year, after standardizing these distances within habitats. The standardized distances have a mean of zero (0) and a standard deviation of one (1). Distance to the closest predated nest is likely to be an informative proxy for nest-site safety, considering that nest predation in goldeneye species is often spatially concentrated, so that the fate of neighbouring nest boxes is correlated (e.g. Pöysä 1999).

Female body condition was calculated as the standardized residuals from a regression of body weight on structural size as reflected by the length of the tarsus (Regression: $\text{weight} = -454.60 + 24.96 \times \text{tarsus}$; $F_{1,43} = 26.7$, $R^2 = 0.38$, $p < 0.0001$). Female body condition did not depend on the number of days between capture and hatching of her clutch [Linear mixed model (LMM): $b = 0.074$, $t = 1.63$, $n = 45$, $p = 0.14$], suggesting that our body condition index is unbiased with respect to variation in female incubation stage upon capture.

Offspring survival was estimated during two consecutive breeding seasons (2006–2007) as the number of days individually marked ducklings survived. Broods (2006: $n = 29$; 2007: $n = 20$) were visited every 3–4 d until they reached the age of 21 d. Little mortality occurs after Barrow's goldeneye ducklings have reached the age of 21 d (Savard et al. 1991), and thus, the number of offspring surviving at this time is a good estimate of fledging success (Eadie & Lyon 1998). Brood-tending females at territories close to

the boundaries of the study area that were seen only once with their broods were excluded from the analysis (2006: $n = 4$, 2007: $n = 2$), because it is likely that they had moved off the study area and thus were still alive. Females in more central territories seen only once but without broods were included in the analyses because it is highly probable that their ducklings had died. The survival surveys were generally discontinued after the ducklings had reached the age of 21 d, and therefore, the data from the broods with observations spanning past the age of 21 d ($n = 17$ of 43 broods included in the analysis) were truncated to 21 d for the data to be comparable across broods. To ascertain that our survival estimates are not affected by undetected adoption of young occurring after nest exodus, we based our survival estimates on marked ducklings only. Because mortality and marker loss will both decrease the number of marked individuals in the brood, we explored the extent to which marker loss may bias survival estimates based on marked individuals only (i.e. excluding ducklings who had lost their tags but were still present in the brood). This was done by utilizing a LMM with restricted maximum likelihood estimation (REML), where the total number of ducklings in a brood at a specific observation date was explained by the number of individually marked ducklings present in that brood. Female identity was used as a random factor. This analysis clearly showed that the number of individually marked ducklings very accurately reflects actual (total) brood size, because a reduction of one marked duckling corresponded to a reduction of 0.94 ducklings from the total brood (LMM: $b = 0.94$, $t_{152} = 46.31$, $p < 0.0001$). The implication of this result is that loss of marked ducklings from broods almost invariably (at least 9 times of 10) represented fatalities rather than loss of markings. Hence, our survival estimates based on marked ducklings only portray actual survival accurately.

Laboratory Methods

Genomic DNA was extracted using the Chelex method of Walsch et al. (1991), and the molecular sexing method of Fridolfsson & Ellegren (1999) was used for sex identification of ducklings. Polymerase chain reactions (PCR) were performed in 10 μl volumes using 2 pmol of each primer (2550F and 2718R, Fridolfsson & Ellegren 1999), 0.05 U of Biotaq DNA polymerase (BIO-21060, Boline), 200 μM of dNTP (F-560 XL), $1 \times \text{NH}_4$ -buffer (BIO-37025, Boline), 3 mM of MgCl_2 (Bio-37026, Boline) and ca. 20 ng of DNA. We used a cycling

profile of 95°C for 3 min, followed by a touchdown scheme, where the annealing temperature was lowered by 1°C per cycle, starting from 60°C, until reaching 50°C. An additional 40 cycles were run at a constant annealing temperature of 50°C. Denaturation was performed at 95°C for 30 s, annealing for 30 s and extension at 72°C for 40 s. A final extension step of 72°C for 5 min was added after the last cycle. After amplification, 3 µl of PCR product was run on a 2% agarose gel (BIO-41025 Bionline) with 1× loading dye. The results were scored visually. Of the 457 sampled ducklings, 417 (91.2%) were successfully sexed (2006: $n = 275$ and 2007: $n = 142$).

Individuals were genotyped at 19 microsatellite loci described in Jaari et al. (2009), using exactly the same genotyping protocol as in Jaatinen et al. (2009b). Loci were tested for deviations from Hardy–Weinberg equilibrium and linkage disequilibria using Fstat 2.9.3.2 (Goudet 1995). Maternities were assigned to the sampled ducklings using the likelihood approach implemented in Cervus 3.0 (Kalinowski et al. 2007). Cervus estimates the likelihood ratios for each mother–offspring pair over all loci, given the genotypic data provided. Using the difference in likelihoods between the most likely and second likeliest pair, Cervus can assign parentage and estimate confidence levels for the assignment through simulation. We used the default confidence levels of 80% and 95%, but only considered mother–offspring pairs assigned with the stricter confidence criterion (95%) in the further analyses. Our estimation was based on a 1% genotyping error rate and 60% of all breeding females in the population sampled and was run for 10 000 iterations. According to our previous studies from the same population, results are robust with respect to the sampling proportion; using a 40% or a 90% sampling rate leads to the same conclusions as the chosen 60% sampling rate (Jaatinen et al. 2009b). We used all the sampled females from 2004 to 2007 as potential parents for the ducklings sampled in 2006 and 2007. Offspring not assigned to the owner of the nest were deemed parasitically laid. Our maternity analysis revealed that 193 of 457 (42%) sampled ducklings were not assigned to the female in the nest and are most likely of parasitic origin. The non-natal offspring were excluded from the sex ratio analyses, because they do not relate to the sex allocation strategy of the focal nesting female. All ducklings irrespective of genetic origin were, however, included in the survival analyses. This is justified because females show no discrimination against parasitic offspring resulting from pre-hatch brood amalgamation – hence being an integral part of the brood – and because we were

interested in the effect of the traits of the caring female on offspring survival. No loci were found to deviate significantly from the Hardy–Weinberg equilibrium, and no linkage disequilibria were detected.

Statistical Methods

Because 11 females were present in both years, we tested the need for including female identity as a random effect to account for potential pseudoreplication. For this, we constructed a generalized linear mixed model (GLMM) with a binomial error distribution. We discovered, however, that the random effect (female identity) did not explain any of the variation in the data. This is likely due to the low number of repeated observations of the same females. We therefore removed the random effect and constructed a generalized linear model (GLM) with a binomial error distribution to assess the influences of maternal and environmental factors on sex allocation. In this GLM, the brood-specific sex ratio (excluding parasitic offspring; see above) was explained by female size (length of the tarsus), female body condition, relative safety of the nest site, hatch date and year. We tested for potential significant interactions, but none were found, leading us to include only main effects (Engqvist 2005). After removing broods that were missing data for some explanatory variables, the analysis was run with a total of 45 broods.

Because our sex ratio analysis revealed that female size but not body condition was linked to sex ratio variation (see Results), body condition was dropped from further analysis. We conducted two analyses to assess the potential adaptive value of sex allocation. First, we studied whether the potential production costs of sons and daughters differ by examining the presence of a sex difference in offspring body size, as proxied by the length of offspring tarsus. Prior to this, we examined the need for including female identity as a random effect, to account for potential pseudoreplication arising from some females being present in both years, and concluded that the random effect was needed in this analysis. We then constructed a LMM where the length of offspring tarsi (parasitic offspring removed) was explained by offspring sex. Second, focusing on the potential effects of female size on the survival of ducklings after nest exodus, we analysed offspring survival using a proportional hazards model (Cox 1972). In this model, survival is modelled as a function of an unspecified baseline hazard at time t , which is modified by the explanatory variables (size of the female caring for the brood, nest-site safety index, duckling sex, year and brood

size at the start of the observation period), included in the model:

$$h(t, x_1, x_2, x_3, \dots) = h_0(t) * \exp(b_1 * x_1(t) + b_2 * x_2 + b_3 * x_3 + \dots)$$

with h_0 being the baseline hazard; x_1 a time-dependent explanatory variable; x_2, x_3 explanatory variables; and b_1, b_2, b_3 the corresponding coefficients.

The main advantage of this model here is that it can handle censored data, that is, it is possible to include individuals that were still alive at the end of the follow-up time (21 d of age). To account for the fact that survival of ducklings from the same brood is unlikely to be independent as it may depend on traits of the female caring for the brood, which we tested here, female identity was included as a random effect in a mixed-effects Cox model (Therneau et al. 2003). All other explanatory effects were included as fixed factors or covariates, respectively. Statistical significance of explanatory variables was tested by comparing model fit of full vs. reduced model with log-likelihood ratio tests with 1 df. Statistical significance of explanatory variables that were included in significant interactions was not tested.

Results

In 2006, the production of ducklings was male biased at the population level, and 118 of the 275 successfully sexed ducklings were females (binomial test: probability of female \pm 95% CI = 0.43 ± 0.06 , $p = 0.02$). In 2007, the duckling production in the population was not sex biased, and 80 of the 142 successfully sexed ducklings were females (binomial test: probability of female \pm 95% CI = 0.56 ± 0.09 , $p = 0.15$).

The probability of producing a female duckling increased with female size (GLM: $b = 0.33$, $z_{43} = 2.38$,

$p < 0.02$; Fig. 1a), it was higher in 2007 than in 2006 (GLM: $b = 0.98$, $z_{43} = 3.24$, $p = 0.001$; Fig. 1b), but was unaffected by nest-site safety (GLM: $b = 0.24$, $z_{43} = 1.49$, $p = 0.14$), female condition (GLM: $b = 0.05$, $z_{43} = 0.38$, $p = 0.70$) and hatch date (GLM: $b = -0.02$, $z_{43} = -1.32$, $p = 0.19$). No collinearity between explanatory variables was detected (all VIFs < 1.13). There was no difference between years in female size (LMM: $b = 0.039$, $t = 0.18$, $n = 45$, $p = 0.86$), so the increasingly female-biased brood sex ratio with maternal size cannot be attributed to a year effect.

Male offspring were larger than female offspring at hatching (LMM: $b = 0.21$, $t_{262} = 2.13$, $p < 0.03$). The post-hatching mortality hazard depended on brood size ($b = -7.11 \pm 3.38$), female body size ($b = -1.73 \pm 0.74$), year ($b = -1.63 \pm 0.35$, $\chi^2 = 22.0$, $p < 0.001$) and the interaction between brood size and female body size ($b = 0.16 \pm 0.07$, $\chi^2 = 4.65$, $p = 0.03$). The sex of the individual duckling had a marginally non-significant effect (0.26 ± 0.14 , $\chi^2 = 3.63$, $p = 0.06$). Consequently, ducklings in larger broods and in broods that were cared for by larger females had a lower hazard, that is, higher survival, but the effect of female size was smaller in larger broods as indicated by the interaction. Furthermore, there was a strong year effect and a tendency for female ducklings to survive better than their male brood mates.

Discussion

The overall sex ratio in the study population did not show any consistent bias. This result is not unexpected, because population sex ratio can be biased in either direction when local resource competition between females and maternal quality simultaneously influence sex allocation strategies (Wild & West

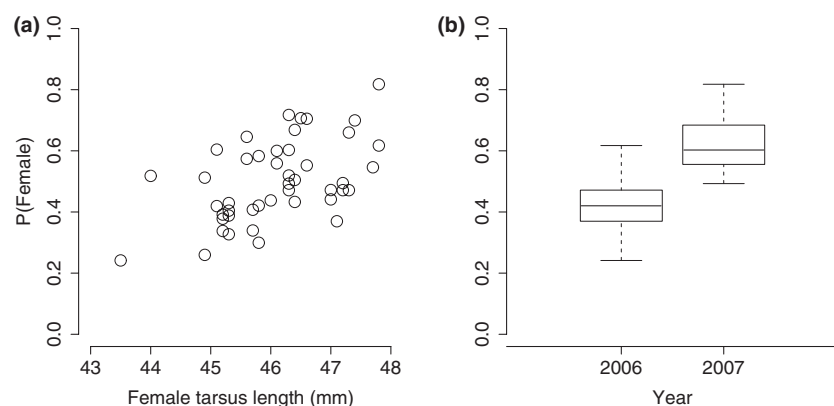


Fig. 1: The probability of producing a female. The probability of producing a female duckling increases with maternal size (panel a) and year (panel b).

2007). However, our results showed that brood sex ratios often deviate from unity. Our results indicate that male offspring may potentially be more dependent on maternal investment in eggs and parental care and they may also be more sensitive to shortage of these resources, as portrayed by their tendency towards lower survival. The SSD is relatively large in this species (adult males average >50% heavier than females; Eadie et al. 2000), and this size difference was already evident at hatching (this study). In accordance with the production cost hypothesis, one would then expect parents with plentiful resources at their disposal to invest in males, the sex with the greater energy requirements (Charnov 1982). In fact, the opposite was observed: larger females produced female-biased broods. This is a notable finding as it is consistent with the local resource competition hypothesis under which local resource competition between females may drive facultative sex allocation in this species. This conclusion is consistent with theory, which suggests that the sex ratio of high-quality individuals is expected to show a female bias if philopatry is female biased and maternal quality is inherited by daughters (Leimar 1996) and/or linked to nest-site quality (Wild & West 2007).

With respect to the fitness consequences of sex allocation decisions, offspring survival increased with the size of the caring female and female ducklings tended to survive better than male ones. Brood size affected offspring survival, but the effect was modulated by the size of the brood-tending female, so that the positive effect of female size on offspring survival was larger for small broods than for large ones. This may possibly indicate that the dilution of predation risk in large broods may be effective enough to allow high *per capita* survival irrespective of the level of post-hatch maternal investment in offspring, whereas female size-mediated maternal investment may play a larger role for offspring survival in small broods.

Parental size has rarely been found to affect sex allocation in birds (Olsen & Cockburn 1991; Kölliker et al. 1999), but sometimes in mammals and arthropods (e.g. Arnombom et al. 1994; Rehan & Richards 2010). Common for these studies is that large parents, producing large offspring, bias their sex allocation towards the sex benefitting more from being big (Olsen & Cockburn 1991; Kölliker et al. 1999). Resource competition between female Barrow's goldeneyes may be a more important determinant of sex allocation than the (presumably) increased mating success of high-quality sons, especially because the breeding ecology of the species suggests that large females may indeed have an advantage in local

resource competition. Barrow's goldeneyes are highly territorial, and females are solely responsible for defending a brood-rearing territory (Savard 1988), and in doing so, a large body size may be advantageous. Furthermore, larger females may be more likely to win aggressive encounters (Savard 1987), resulting in brood amalgamation, where the winner monopolizes the combined brood and may thereby gain more efficient dilution of predation risk (e.g. Treherne & Foster 1982), as indicated by the higher offspring *per capita* survival in larger broods of this species (Smith et al. 2005). Taken together, this evidence supports the local resource competition hypothesis and suggests that Barrow's goldeneye females should bias their primary sex ratio towards females if they can give them a competitive advantage, such as large body size, despite the fact that waterfowl in general are expected to bias sex allocation towards males, the dispersing sex suffering less from local resource competition (Gowaty 1993).

It is likely that habitat quality and individual quality act in concert to determine the inheritance of maternal quality by daughters. Inheritance of natal habitat quality is common in nature, and such 'silver spoon' effects on habitat selection are partly due to individual quality attributes affecting competitive ability (e.g. Stamps 2006). In analogy to our findings, high-quality females overproduce daughters in Cape mountain zebra (*Equus zebra zebra*), a species in which there is strong maternal transmission of social rank (Lloyd & Rasa 1989). We also found that offspring survival increased with female size. This effect may be due either to female quality *per se*, for example, large females may show better brood-protection abilities or it may be a corollary of larger females monopolizing better territories. A third possibility for how habitat and individual quality could be linked relates to the potential connection between nest-site availability and individual quality. Primary sex ratios should be biased towards the philopatric sex in areas with many vacant breeding territories, resulting in relaxed local resource competition (Kruuk et al. 1999; Hjernquist et al. 2009). However, we find this possibility unlikely, because there are no indications that larger females would inhabit less densely populated parts of our study area. In fact, the opposite may be true, as there is a slight preponderance of large females nesting in the prairie habitat characterized by higher nest densities.

We failed to find support for the habitat quality hypothesis because no effect of nest-site safety on sex allocation was detected. Because the general breeding ecology of goldeneye species would seem to be favourable for the evolution of sex allocation based on nest-site safety (this study; Pöysä 1999, 2006), the

observed lack of effect may simply be due to sample size limitations. Of course, the mere presence of the prerequisites for sex allocation based on habitat quality does by no means dictate that such effects need to be strong or even present, especially if any such effects are overshadowed by the stronger effects of local resource competition on sex allocation. We therefore encourage further work on the role of habitat quality on sex allocation in this group of birds, preferably using large sample sizes.

Female body condition had no effect on sex allocation in this species. First, whereas size may be an advantage when fighting to defend a brood-rearing territory, carrying larger fat reserves may in fact decrease manoeuvrability and thereby fighting ability (cf. Kemp & Alcock 2003). Second, goldeneye ducks are income breeders, that is, they increase energy intake to compensate for increased energy required for breeding, and thereby, body condition may have a lesser importance in their life histories than in capital breeding species. Our study also uncovered significant year effects on brood sex ratios, indicating the presence of uncontrolled factors (also see Thuman et al. 2003). For example, temperature during egg laying may demonstrably affect sex ratios (e.g. Saino et al. 2008), and thus, it may prove informative to study the effect of climatic factors on sex allocation in this species, especially in the light of tendency towards differential survival of sexes.

The results from this study suggest that an interplay of female state-dependent and extrinsic factors steers facultative sex allocation in Barrow's goldeneyes. Sex allocation was female biased when mothers presumably can provide their philopatric female offspring with a competitive advantage. We therefore stress the importance of future work focusing on the question whether female offspring born from large mothers and surviving until breeding age really achieve higher fitness than female offspring born from smaller mothers.

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