Original Article

Identifying the selective pressures underlying offspring sex-ratio adjustments: a case study in a wild seabird

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Sex allocation theory predicts that parents should bias offspring sex according to the costs and benefits associated with producing either sex in a given context. Accurately interpreting sex-ratio biases, therefore, requires a precise identification of these selective pressures. However, such information is generally lacking. This may partly explain the inconsistency in reported sex allocation patterns, especially in vertebrates. We present data from a long-term feeding experiment in black-legged kittiwakes (*Rissa tridactyla*) that allowed us to increase investment capacity for some breeding pairs. Previous findings showed that these pairs then overproduced sons compared with control parents. Here, our aim was to test the underlying assumptions of the 2 appropriate sex allocation models for our context: the "cost of reproduction hypothesis" and the "Trivers–Willard hypothesis." The former assumes a sex difference in rearing costs, whereas the latter assumes a difference in fitness returns. 1) Independent of feeding treatment, rearing sons was energetically more demanding for parents (as revealed by higher energy expenditure and higher baseline corticosterone levels) than rearing daughters, thereby corroborating the underlying assumption of the "cost of reproduction hypothesis." 2) Evidence supporting the assumptions of the "Trivers–Willard hypothesis" was less convincing. Overall, our results suggest that drivers of parental sex allocation decisions are probably more related to offspring sex-specific energetic costs than to their future reproductive success in our study species. Assessing the adaptive value of sex-ratio biases requires precise investigation of the assumptions underlying theoretical models, particularly as long as the mechanisms involved in sex-ratio manipulation remain largely unknown.

Key words: **corticosterone, cost of reproduction hypothesis, daily energy expenditure, investment capacity, Trivers–Willard hypothesis.**

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INTRODUCTION

Sex allocation theory predicts that parents should overproduce offspring of the sex with the 'lowest cost–benefit ratio in a given context (Charnov 1982; Frank 1990; West 2009). The causal pathways leading to a given sex-specific cost–benefit ratio can be diverse and form the underlying assumptions of the numerous sex allocation models (reviewed in Hardy 2002; West 2009). The identification and quantification of these pathways is thus crucial for making appropriate predictions and for assessing the adaptive nature of sex allocation biases (West 2009; Komdeur 2012). For instance, in cooperatively breeding vertebrates, offspring of one sex are often more likely to stay on the parental territory to help raise future offspring. If having more helpers provides more benefits than costs, it is predicted that parents with no current helpers should overproduce the helping sex, whereas they should overproduce the opposite sex if costs are higher than benefits (Griffin et al. 2005). The best illustration for this sex allocation model is that of the Seychelles warbler (*Acrocephalus sechellensis*) where Komdeur and colleagues (reviewed in Komdeur 2012) measure the fitness costs and benefits of having sons or daughters in relation to the number of helpers and territory quality (Richardson et al. 2002) and found that offspring sex-ratio maximized benefits (Komdeur et al. 1997).

However, information on the fitness costs and benefits of producing sons or daughters is generally lacking, even in well-studied systems (West 2009; Komdeur 2012). A number of studies have found that, as predicted, females mated to attractive males overproduced sons (reviewed in West 2009; Komdeur 2012), but the underlying assumptions of this model have rarely been tested (but see Ellegren et al. 1996). For example, there are at least 4 studies showing an offspring sex-ratio bias in the predicted direction in blue tits (*Cyanistes caeruleus*) (reviewed in West 2009), but no study yet demonstrated that the father's attractiveness influences the reproductive value of sons more than that of daughters (West 2009). The adaptive value of the sex-ratio bias observed in blue tits thus remains unclear.

The need for identifying the fitness benefits and costs of producing sons or daughters is all the more important given that different sex allocation models may generate identical predictions, despite being mediated by different fitness return pathways. Hence, without prior knowledge on the validity of the underlying assumptions, it can be impossible to attribute a given sex-ratio bias to a particular model and to interpret its adaptive nature. This is particularly true among birds and mammals for which many models have been proposed (Cockburn et al. 2002). For example, one frequently tested prediction is that parents with higher investment capacity should produce more sons than parents with lower investment capacity. However, this pattern could be obtained through at least 2 pathways linked to the sex-specific costs and benefits of producing either sex. The "cost of reproduction hypothesis" (hereafter called "CRH"; Myers 1978) states that parents with low investment capacity (either because they are in poor condition or breeding during poor environmental conditions) should overproduce the cheaper sex to reduce the risks of failure and/or reduce the impact on their residual reproductive value (Myers 1978; Cockburn et al. 2002). The Trivers–Willard hypothesis (Trivers and Willard 1973) in its generalized formulation (hereafter called "gTWH"; Hewison and Gaillard 1999) states that parents with higher investment capacity (e.g., in better than average condition; Blanchard et al. 2005) should invest more in the sex that will gain more benefits from the additional investment (Hewison and Gaillard 1999).

Though leading to similar predictions, these models are not based on the same causal pathways: CRH focuses on the impact of the sex-specific difference in costs of reproduction on parental residual reproductive value, whereas gTWH focuses on how parents can maximize their inclusive fitness through manipulating the reproductive value of their offspring. The underlying assumptions of these models are thus not identical and need to be evaluated for each specific system in order to predict and correctly interpret observed sex-ratio biases. Firstly, the CRH assumes that one sex is more costly than the other. Although the degree of sexual dimorphism has been used as a proxy of the between-sex difference in the energetic cost of producing sons or daughters (e.g., Magrath et al. 2007), the reality is more complex (Stamps 1990). There is evidence that even marked sexual dimorphism does not necessarily translate into differential energetic cost (e.g., Torres and Drummond 1999; McDonald et al. 2005; Townsend et al. 2007) or that this difference is lower than expected based on the degree of sexual dimorphism (Anderson et al. 1993; Krijgsveld et al. 1998; Magrath et al. 2007). Hence, accurately assessing the sex-specific energetic costs of producing offspring requires a more direct measurement of parental energy expenditure (Magrath et al. 2007). In contrast, the gTWH assumes that parental investment capacity (e.g., condition) will influence the fitness of sons and daughters differentially. To validate this hypothesis as a potential explanation for sex-ratio biases requires data on the reproductive success of offspring of both sexes born to parents of known investment capacity.

We addressed these issues in the black-legged kittiwake (*Rissa tridactyla*), a long-lived seabird in which we have previously demonstrated sex-ratio variation in relation to food availability. Experimentally fed parents ("Fed") produced relatively more sons than control parents ("Unfed") during 3 seasons of relatively poor food availability (Merkling et al. 2012). As experimental feeding has been shown to increase chick condition and fledging success (Gill and Hatch 2002; Gill et al. 2002), we inferred that Fed parents had a greater investment capacity than Unfed parents. However, we were unable to satisfactorily interpret this sex-ratio pattern as our results were compatible with both the CRH and the gTWH and, at that time, we had no information on the relative costs and benefits of producing male or female chicks. Our aim here is to elucidate these costs and benefits with respect to the underlying assumptions of the CRH and gTWH using data from a long-term feeding experiment. 1) To test the assumption of the CRH, we examined whether one sex is energetically more costly than the other by measuring parental energy expenditure and baseline corticosterone levels (the main glucocorticoid in birds indicative of a physiological response to increased parental workload). As sons grow faster and reach a larger size and mass at fledging than daughters (Merkling et al. 2012), we predicted that parents rearing more sons would face a higher workload (increased energy expenditure facilitated by higher baseline corticosterone levels; Ouyang et al. 2013; Love et al. 2014) than parents rearing more daughters, especially among Unfed parents. 2) To test the assumption of the gTWH, we examined whether parental supplemental feeding before and during chick rearing increased the reproductive success of offspring subsequently recruiting to our experimental site in a sex-specific manner. Male kittiwakes typically arrive earlier than females on the breeding colonies and compete intensively for access to the most attractive nest sites (Cullen 1957; Wooller and Coulson 1977), as nest site characteristics affect reproductive success (Regehr et al. 1998; Massaro et al. 2001). The heavier and better competitors can obtain the best sites and start to breed earlier than others (Wooller

and Coulson 1977; Coulson and Thomas 1985). Earlier onset of reproduction increases chick postfledging survival and future reproductive performance (Cam et al. 2003). Given that breeding performance is higher in Fed than in Unfed nests (Gill and Hatch 2002; Vincenzi et al. 2013), and that kittiwakes are known to use information about conspecific breeding performance to choose breeding sites (Danchin et al. 1998; Boulinier et al. 2008), it is very likely that Fed nests are more attractive than Unfed nests so that only heavier and better competitors gain access to Fed sites. Therefore, we predicted that supplementary feeding should increase the reproductive success of sons more than daughters, whereas the difference in reproductive success between sons and daughters should be smaller among offspring born to Unfed parents.

MATERIALS AND METHODS

Study species and site

The black-legged kittiwake (*R. tridactyla*) is a medium-sized, colonial seabird living throughout the northern part of the Northern Hemisphere (Coulson 2011). It nests on vertical cliffs and parents share all parental duties such as nest building, incubation, and chick rearing almost equally (Hatch et al. 2009). Females lay 1–3 eggs, with a usual clutch size of 2 (Coulson 2011). Alaskan adults have low mortality (often <10%; Hatch et al. 2009), survive about 13 years, on average, in our study population (Hatch et al. 1993) and show high nest site fidelity (Coulson 2011).

The study was conducted on a group of individually marked birds nesting on an abandoned U.S. Air Force radar tower on Middleton Island (59°26′N, 146°20′W), Gulf of Alaska. The tower is a 12-walled polygonal building where artificial nest sites have been added on the upper walls. Nest sites are fitted with 1-way mirror glass window panes and hence can be conveniently accessed and monitored from within the building (for more details, see Gill and Hatch 2002). This setup facilitated observations, rapid capture, and handling of both adult birds and their offspring. Nests were checked regularly (usually once or twice daily) throughout each breeding season to document events such as laying, hatching, and chick mortality. Adult sex was determined either from copulation behavior or morphologically at capture (Jodice et al. 2000).

Feeding treatment

The data presented here are part of a long-term experiment begun in 1996 (for more details, see Gill and Hatch 2002) where half of the pairs were assigned to a Fed group and the other half to an Unfed group. Three panels (a panel being 1 wall of the tower) of Fed sites alternated with 3 panels of Unfed sites. Treatments were assigned to the same panels over years and individuals only very rarely changed between feeding treatments once they recruited to a nest site. Supplemental food consisted of thawed Atlantic capelin (*Mallotus villosus*), which is similar to their naturally preferred prey at this site (Hatch 2013). It was provided ad libitum to both parents and chicks of Fed nests 3 times a day (at 09:00, 14:00, and 18:00 local time) from a few weeks before laying until chick fledging or death. Food was delivered through a plastic tube at the nest site and was inaccessible to neighboring birds (see more details in Gill and Hatch 2002). Fed birds also foraged at sea and the amount of supplemental food consumed varied in relation to natural food availability, as judged by the breeding performance of unfed birds (Gill and Hatch 2002; Hatch 2013).

Are sons energetically more costly than daughters?

Experimental design

To investigate the energetic cost of rearing sons versus daughters, we used a subset of data from a brood size manipulation experiment conducted in 2011 (for more details, see Supplementary Material and Welcker et al. 2015). At the time of hatching, pairs were either left to rear their 2 chicks ("Control" group) or were given an extra chick to rear ("Enlarged" group). In kittiwakes, fostering is facilitated by the absence of parent–young recognition when chicks are young (Storey et al. 1992; Mulard and Danchin 2008). Moreover, natural chick adoption is common in this species (Helfenstein et al. 2004) and population (Roberts and Hatch 1994). In each group, half of the nests were provided with supplemental food (see above). Some chicks died before parents were sampled for physiological measures (see below). To be consistent, we thus considered only nests with at least 2 chicks at the time of sampling. In total, we considered 28 nests, 16 Fed, and 12 Unfed (i.e., 56 individual parents).

Sampling and physiological measures

We sampled blood for molecular sexing (~50 μL from the tarsal vein) from all chicks whose parents were included in the brood size manipulation experiment ($N = 71$) (see Merkling et al. 2012 for a detailed protocol).

In all adult birds, daily energy expenditure (hereafter called "energy expenditure") was estimated by the doubly labeled water method (Lifson and McClintock 1966; Butler et al. 2004) and baseline plasma concentrations of corticosterone were measured (hereafter called "CORT"). CORT levels are known to increase with increased parental workload (Ouyang et al. 2013; Love et al. 2014), and in the kittiwake, they have been shown experimentally to decrease survival (Kitaysky et al. 2001, 2010; Goutte et al. 2010; Satterthwaite et al. 2010; Schultner et al. 2014). Each adult was captured twice. At first capture, birds were injected with oxygen and deuterium isotopes and a blood sample was taken from the alar vein to estimate the initial enrichment of isotopes (see Supplementary Material). We recaptured all individuals 3 days after injection (mean ± standard deviation: 70.0 ± 4.7 h), as extended measurement periods reduce the error due to day-to-day variation in energy expenditure (Speakman et al. 1994; Berteaux et al. 1996). Each bird was also weighed to control for the effect of body mass on energy expenditure. On recapture, a second blood sample was taken (<3 min after capture, as recommended for baseline CORT levels; Romero and Reed 2005) to estimate final enrichment of isotopes and to determine CORT. Blood for hormone analysis was centrifuged immediately after sampling, and the plasma frozen at −20 °C.

Sampling started when the A-chick (the first hatched in a nest) had reached the age of 8 days. We sampled both parents of all nests, usually within a day of each other. Sampling was completed when chicks were approximately 12 days old. Chick age at capture did not differ significantly between mothers and fathers (Wilcoxon test: $W = 396$; $P = 0.95$) or between treatments (Kruskal–Wallis test: $\chi_3^2 = 3.3$; $P = 0.34$).

Energy expenditure was assayed using isotope ratio mass spectrometry as described in Speakman and Król (2005; more details in Welcker et al. 2015). The CORT assay is described in detail in Kitaysky et al. (2007).

Does supplemental feeding have a stronger effect on the reproductive success of sons than daughters?

Since 1996, all chicks born in the tower have been banded with a uniquely numbered metal band and 1 color band per cohort. This enabled us to monitor all chicks that were born on, and subsequently recruited as breeders to, the tower between 2001 and 2013 (N = 226). For all these birds, we had information on the feeding treatment of their parents, their year of birth, sex, age at recruitment, the number of years during which they were recorded as breeders, and the feeding treatment of the nest to which each individual recruited (hereafter "recruitment feeding treatment"). We considered recruitment successful when at least 1 egg was laid.

As each nest was monitored at least once daily from before laying until chick fledging, we were able to estimate the reproductive success of all adults on the tower. Reproductive success was calculated as the sum of the number of fledglings produced by an individual over its different breeding attempts. Chicks that already fledged and chicks that were still alive when monitoring ceased (i.e., about to fledge when the field crew left the island) were considered fledglings. We excluded 1) data from 2011 for those parents that were part of the brood size manipulation experiment (see above and Supplementary Material), 2) chicks that were born on the tower but that recruited to panels that were not part of the long-term experiment because they may have been involved in other experiments that could have influenced their fledging success (e.g., Merkling et al. 2014), and 3) chicks that recruited after 2010 because estimates of their reproductive success were unreliable due to the low number of breeding events. Our final sample size was N = 128.

Data analyses

Following recent recommendations to produce model estimates that are comparable between and within studies (Gelman 2008; Schielzeth 2010; Grueber et al. 2011), we standardized every input variable by centering and dividing it by 2 standard deviations using the arm package (Gelman and Su 2014). We always started with a full model and tested the explanatory power of the component terms by successively removing each one, beginning with the highest order interactions, and comparing the change in deviance after removal of that term with a likelihood-ratio test. All analyses were conducted with R 3.0.2 (R Core Team 2014). Predicted values (mean ± standard errors) were calculated using the AICcmodavg package (Mazerolle 2013). Where possible, we also provide the R^2 of the final model as a measure of its goodness of fit, calculated using the MuMIn package (Bartoń 2013) and based on equations from Nakagawa and Schielzeth (2013).

For the analyses of energy expenditure and CORT, we ran separate models for Control and Enlarged broods to avoid collinearity issues between experimental brood size and sex-ratio (Wilcoxon test: W = 528; P = 0.015). Moreover, the distribution of brood sex-ratios within brood size treatments was somewhat unbalanced: that is, there were very few all-female broods in the Control broods and very few all-male broods in the Enlarged broods. Therefore, we pooled some sex combinations to ensure that extreme sex-ratio values did not exert a disproportionately large influence on the observed relationship with the physiological parameters. In Control broods, we compared all-male broods with other broods, whereas for Enlarged broods, we compared those with at most 1 male with those which contained at least 2 males. To meet model assumptions of normality, CORT was log-transformed. As there was no effect of handling time on levels of CORT (P = 0.14), and as including handling time as a covariate in the models did not change parameter estimates, we present results of models without this covariate. As we were more interested in fixed effects (Bolker et al. 2009), we used linear mixed models with maximum likelihood rather than restricted maximum likelihood estimates in the package lme4 (Bates et al. 2011). Pair identity was included as a random effect to account for the nonindependence of mates. The full models contained all 2-way interactions between brood sex-ratio, parental sex, and feeding treatment. Individual mass (only for models concerning energy expenditure), pair-bond duration (i.e., "0" for first breeding attempt together, "1" for ≤2 previous breeding attempts together, and "2" for ≥3 previous breeding attempts together), and parental age were included as additional covariates. Parental age was determined either precisely for marked birds born on the tower or approximately by assuming that they recruited at 7 years old (i.e., the mean recruitment age in our population; Vincenzi et al. 2013). Finally, we tested for the correlation between energy expenditure and CORT levels using a Spearman's correlation test. We calculated the correlations for the whole data set and also separately by brood size.

For analyses of reproductive success (i.e., total number of fledglings over the study period), we ran generalized linear mixed models (GLMMs) with maximum likelihood and a negative binomial error distribution, using the package glmmADMB (Fournier et al. 2012; Skaug et al. 2013). Using a negative binomial instead of a Poisson distribution allowed us to take overdispersion into account. However, there is no accurate method to calculate model predictions from a negative binomial GLMM, so we used a Poisson GLMM for the figures. To test the underlying assumption of the gTWH, we needed to test for an interaction between the sex of the individual and its parental feeding treatment. The full model contained the 2-way interaction between the sex of the individual and its parental feeding treatment, as well as recruitment feeding treatment, age at recruitment, and number of breeding events (to account for differences in the number of times a given individual appeared in the data set) as covariates. We also included recruitment year as a random effect to account for nonindependence among birds recruiting in the same year.

RESULTS

Are sons energetically more costly than daughters?

Prior to manipulation, there was no sex-ratio bias according to feeding treatment (sample sizes, Fed: 17 males and 12 females; Unfed: 16 males and 10 females; chi-square test: $\chi_i^2 = 0$; P = 1).

Energy expenditure was positively related to CORT levels in the whole data set (r = 0.28; P = 0.035). However, this relationship only held true in Control broods (r = 0.37; P = 0.04), but not in Enlarged broods (r = 0.11; P = 0.60).

In Control broods (in which parents reared their 2 chicks), energy expenditure was significantly higher in parents with male-biased broods (Table 1 and Figure 1). In addition, energy expenditure decreased with increasing parental age and increased with increasing body mass (Table 1). In Enlarged broods (in which parents were given an extra chick), energy expenditure was independent of brood sex-ratio and did not vary in relation to any of the additional variables included in the model (Table 1 and Figure 1).

Table 1

Summary of the mixed model describing variation in daily energy expenditure levels in Control broods and Enlarged broods
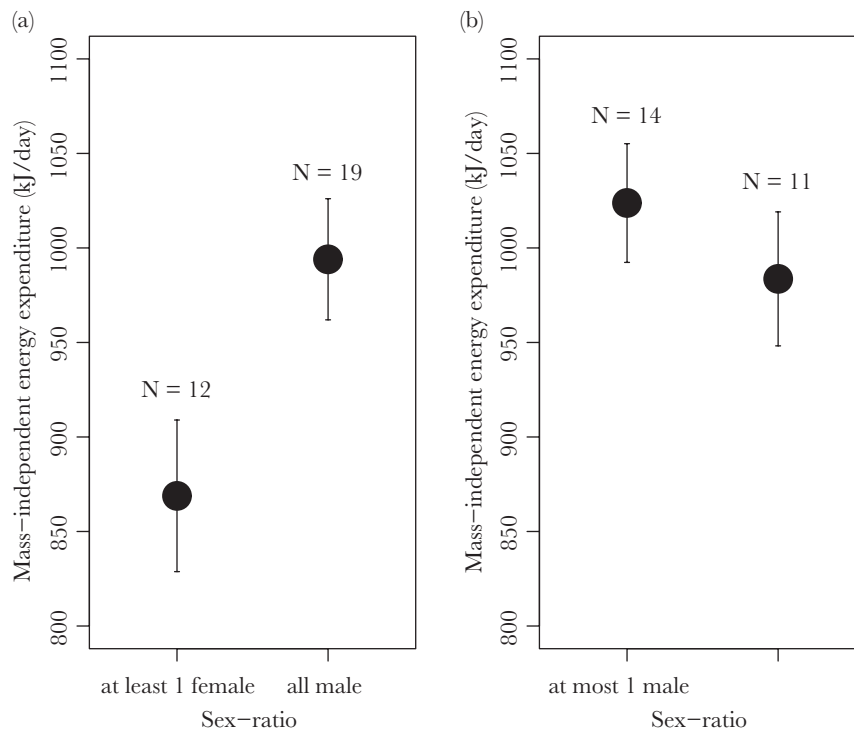
	Control broods ($R^2 = 0.47$)			Enlarged broods ($R^2 = 0$)		
	$\beta \pm SE$	χ^2_1	P	$\beta \pm SE$	χ^2_1	P
Intercept	946.0 ± 24.9			961.2 ± 21.9		
Breeding experience	-7.4 ± 53.9	0.018	0.90	-50.6 ± 56.7	0.78	0.38
Unfed treatment[a]	101.7 ± 59.6	2.52	0.11	-31.1 ± 51.6	0.36	0.55
Mass	**158.0 ± 42.7**	**4.40**	**0.036**	115.5 ± 70.1	2.57	0.11
Parental age	**-99.8 ± 43.1**	**4.57**	**0.032**	18.2 ± 53.7	0.11	0.73
Sex-ratio[b]	**126.4 ± 52.1**	**4.25**	**0.039**	-39.1 ± 52.1	0.56	0.45
Male parent[c]	-21.9 ± 78.1	0.07	0.79	-76.4 ± 65.1	1.34	0.25
Unfed treatment[a] × male parent[c]	-100.2 ± 76.8	1.62	0.20	-111.2 ± 104.1	1.11	0.29
Unfed treatment[a] × sex-ratio[b]	73.9 ± 97.2	0.57	0.45	-114.9 ± 99.2	1.31	0.25
Sex-ratio[b] × male parent[c]	-62.7 ± 84.3	0.54	0.46	-45.7 ± 95.5	0.23	0.63

Significant terms (i.e., retained in the final model) are in bold type. β values are the standardized parameter estimates (with their standard error) taken prior to removal for terms not retained in the final model. χ^2 and P are values from the corresponding likelihood-ratio tests (with a difference in degrees of freedom of 1 for each term). R^2 values refer to the final model.
[a]Relative to Fed treatment.
[b]Relative to broods with >1 female in Control broods and to broods with <1 male in Enlarged broods.
[c]Relative to female parent.

Figure 1

Effect of the proportion of males in a brood on mass-independent daily energy expenditure in (a) Control broods (broods with at least 1 female vs. all-male broods) and in (b) Enlarged broods (broods with at most 1 male vs. broods with at least 2 males). Predicted values ± standard errors are presented (see Materials and Methods).

In Control broods, baseline corticosterone (CORT) levels varied significantly in relation to the 2 two-way interactions involving feeding treatment (Table 2). First, CORT levels did not vary with sex-ratio among Fed parents, but were significantly increased in broods with a male-biased sex-ratio among Unfed parents, which had higher CORT levels overall (Figure 2). Similarly, parental sex did not influence CORT levels among Unfed parents, but it did among Fed parents, such that Fed fathers had significantly higher CORT levels than Fed mothers (Table 2). In Enlarged broods, however, CORT levels were significantly higher in male-biased broods

regardless of parental sex and feeding treatment, and Unfed birds had generally higher CORT levels than Fed birds, although not significantly so (Table 2 and Figure 2).

Does supplemental feeding have a stronger effect on the reproductive success of sons than daughters?

Neither the interaction between parental feeding treatment and sex nor the individual main terms had a significant effect on the mean number of fledglings (Table 3 and Figure 3). However, birds

Table 2

Summary of the mixed model describing variation in baseline corticosterone (CORT) levels (log-transformed) in Control broods and Enlarged broods
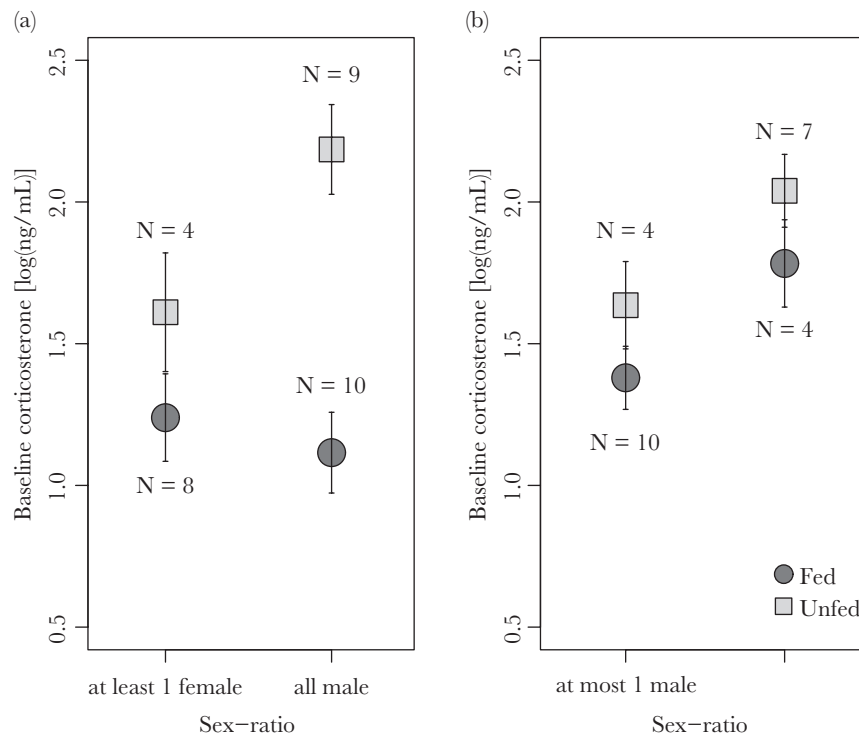
	Control broods ($R^2 = 0.69$)			Enlarged broods ($R^2 = 0.28$)		
	$\beta \pm SE$	χ^2_1	P	$\beta \pm SE$	χ^2_1	P
Intercept	1.48 ± 0.07			1.67 ± 0.07		
Breeding experience	-0.02 ± 0.15	0.026	0.87	0.22 ± 0.18	1.46	0.23
Unfed treatment[a]	0.84 ± 0.14	—	—	0.25 ± 0.16	3.50	0.06
Parental age	-0.01 ± 0.13	0.001	0.97	-0.07 ± 0.17	0.17	0.68
Sex-ratio[b]	0.17 ± 0.14	—	—	**0.40 ± 0.16**	**6.68**	**0.01**
Male parent[c]	0.26 ± 0.13	—	—	0.23 ± 0.14	2.39	0.12
Unfed treatment[a] × male parent[c]	**-0.75 ± 0.26**	**6.95**	**0.008**	-0.34 ± 0.31	1.17	0.28
Unfed treatment[a] × sex-ratio[b]	**0.71 ± 0.28**	**5.01**	**0.025**	0.15 ± 0.30	0.25	0.61
Sex-ratio[b] × male parent[c]	0.04 ± 0.28	0.027	0.87	-0.25 ± 0.30	0.71	0.40

Significant terms (i.e., retained in the final model) are in bold type. β values are the standardized parameter estimates (with their standard error) taken prior to removal for terms not retained in the final model. χ^2 and P are values from the corresponding likelihood-ratio tests (with a difference in degrees of freedom of 1 for each term). R^2 values refer to the final model. — indicates that we did not test for the significance of terms included in retained interactions.
[a]Relative to Fed treatment.
[b]Relative to broods with >1 female in Control broods and to broods with <1 male in Enlarged broods.
[c]Relative to female parent.

Figure 2

Effect of the proportion of males in a brood on baseline corticosterone (CORT) levels (log-transformed) in relation to parental feeding treatment in (a) Control broods (broods with at least 1 female vs. all-male broods) and (b) Enlarged broods (broods with at most 1 male vs. broods with at least 2 males). Dark gray circles and light gray squares indicate Fed and Unfed birds, respectively. Predicted values ± standard errors are presented (see Materials and Methods).

recruiting to Unfed nests produced significantly less fledglings than those recruiting to Fed nests (Table 3). Moreover, the mean number of fledglings increased as the age at recruitment increased and, logically, as the number of breeding events increased (Table 3).

DISCUSSION

Our findings indicate that, in kittiwakes, sons are energetically more costly to rear than daughters. This argument is supported by the observations that in Control broods (in which parents reared their 2 chicks), parents rearing sons spent more energy than parents rearing daughters and, in Enlarged broods (in which parents were given an extra chick), the former had higher CORT levels (likely due to the increased parental workload) than the latter. These results support the underlying assumption of the CRH (Myers 1978; Cockburn et al. 2002), which states that one sex of offspring is more costly to produce than the other. In contrast, we found no support for the gTWH (Trivers and Willard 1973; Hewison and Gaillard 1999) in kittiwakes, as sons of Fed parents did not achieve higher reproductive success than daughters (Figure 3), although this

Table 3

Summary of the negative binomial GLMM model describing variation in reproductive success for birds born in Fed nests and in Unfed nests and later recruited as breeders on the tower

	$\beta \pm SE$	χ_i^2	P
Intercept	1.24 ± 0.06		
Male[a]	-0.15 ± 0.13	1.39	0.24
Unfed parental feeding treatment[b]	-0.12 ± 0.11	1.34	0.25
Unfed recruitment feeding treatment[c]	**-0.37 ± 0.11**	**8.66**	**0.003**
Number of breeding events	**1.08 ± 0.12**	**74.22**	**<0.0001**
Age at recruitment	**0.36 ± 0.12**	**8.06**	**0.004**
Male[a] × Unfed parental feeding treatment[b]	0.01 ± 0.25	0.002	0.96

Significant terms (i.e., retained in the final model) are in bold type. β values are the standardized parameter estimates (with their standard error) taken prior to removal for terms not retained in the final model. χ^2 and P are values from the corresponding likelihood-ratio tests (with a difference in degrees of freedom of 1 for each term).
[a]Relative to female.
[b]Relative to Fed parental treatment.
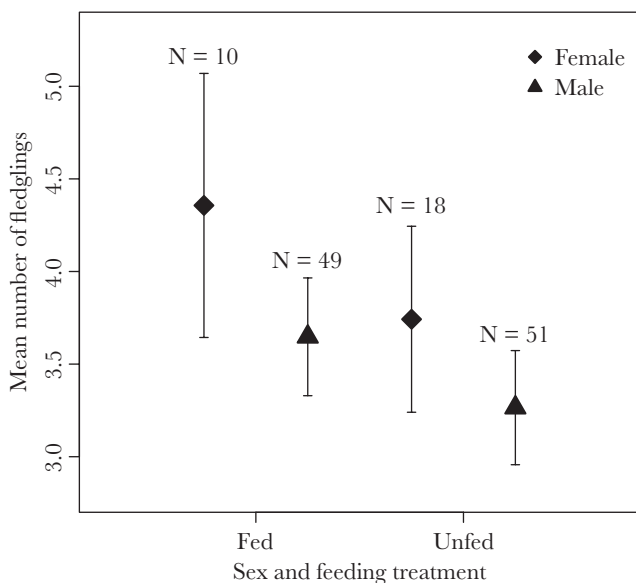[c]Relative to Fed recruitment treatment (i.e., birds that recruited to a Fed nest).

Figure 3

Reproductive success in relation to parental feeding treatment (Fed vs. Unfed) and sex of the individual. Diamonds and triangles indicate females and males, respectively. Predicted values ± standard errors from a Poisson GLMM are presented (see Materials and Methods).

might have been expected given the behavioral differences between the sexes in this species (see Introduction). These results suggest that Unfed parents, which were shown to produce relatively more daughters than Fed parents during 3 seasons of relatively poor food availability (Merkling et al. 2012), do so most likely because they avoided producing the more costly sex during poor conditions. Our study thus illustrates the importance of data focusing on the underlying assumptions of the different sex allocation models to correctly interpret and/or predict sex-ratio biases (e.g., Robert et al. 2010; Bowers et al. 2015). Indeed, the overuse of a posteriori interpretations is one of the main causes of confusion on the adaptive nature of sex-ratio variation in birds and mammals (Festa-Bianchet 1996; West 2009; Komdeur 2012).

Are sons energetically more costly than daughters?

We found clear evidence that sons (the larger sex) were energetically more demanding to rear than daughters, as parental energy expenditure was higher for male-biased broods in the Control treatment (Figure 1). Hence, even though chick sexual dimorphism is relatively slight in kittiwakes (Merkling et al. 2012), we still found a difference in rearing costs, contrary to other more sexually dimorphic species (e.g., Torres and Drummond 1999; McDonald et al. 2005; but see Magrath et al. 2007). This contrast highlights the difficulty of predicting whether one sex is more costly to rear than the other based on sexual dimorphism and confirms the need to measure energy expenditure rather than sexual dimorphism to infer sex-specific rearing costs. Feeding treatment affected the relationship between sex-ratio and CORT in Control broods, so that CORT levels were higher in male-biased broods only for Unfed parents (Figure 2). CORT levels are known to be positively related to nutritional stress in kittiwakes (e.g., Kitaysky et al. 2007, 2010), and there is substantial evidence that increased parental workload is facilitated by increased CORT levels (Ouyang et al. 2013; Love et al. 2014), as suggested here by the positive correlation between energy expenditure and CORT levels in Control broods. Therefore, it seems that rearing more sons increased parental effort of Unfed parents more than that of Fed parents, most likely because sons required more food than daughters and because Unfed parents, unlike Fed parents, could not rely on supplementary food. Contrary to our prediction, this did not translate into a sharper increase in energy expenditure with sex-ratio among Unfed parents compared with Fed parents. A possible explanation is that parents of both treatments already reached an energetic ceiling when rearing all-male broods (Welcker et al. 2010, 2015). We cannot, however, exclude the possibility that we lacked statistical power to detect sex-dependent effects of feeding treatment on energy expenditure. Alternatively, this result could be explained by high food availability during the study year (Hatch 2013), which might have buffered the effect of feeding treatment on energy expenditure. The same argument may explain why we observed no effect of feeding treatment on sex-ratio in this data subsample, contrasting with the results previously reported in the same population (Merkling et al. 2012). Hence, in years of low food availability (Merkling et al. 2012), Unfed parents may avoid the production of costly sons in the way predicted by the CRH (e.g., Wiebe and Bortolotti 1992). By doing so, they avoid incurring reproductive costs of a potentially higher magnitude than those that we report in this study, as these were measured in parents producing sons, that is, individuals that are expected to be able to cope with the rearing of a son in a CRH context. Alternatively, rearing a son may impose similar energetic costs for both Fed and Unfed parents, but with an impact on fitness mainly for Unfed birds. These fitness costs might be expressed in terms of reduced parental survival, known to be negatively affected by higher CORT levels (Goutte et al. 2010; Kitaysky et al. 2010; Satterthwaite et al. 2010), and/or future reproductive success (Gomendio et al. 1990; Bérubé et al. 1996; Weimerskirch et al. 2000). Hence, the next step toward a clearer picture of the adaptive value of sex-ratio bias in this offspring sex-dependent reproductive costs context would require manipulation of the offspring sex-ratio raised by the parents (e.g., Rutkowska et al. 2011). This was not feasible in our study as sexual dimorphism near hatching is not a good predictor of chick sex in kittiwakes (Vincenzi S, unpublished data), and our field site is in a remote location with no access to laboratory facilities to determine chick sex molecularly.

Interestingly, energy expenditure was not higher in Enlarged broods compared with male-biased Control broods (Figure 1) and did not differ in relation to sex-ratio in Enlarged broods. Previous studies have shown that, during chick rearing, kittiwakes are operating close to an energetic ceiling (Welcker et al. 2010, 2015), as observed in other species (e.g., Green et al. 2009). Thus, it is perhaps not surprising that parents were unable to increase energetic investment when rearing more sons in Enlarged broods because their energy expenditure was already maximal in both feeding treatments (Welcker et al. 2015). However, the finding that CORT levels were higher in male-biased Enlarged broods, irrespective of feeding treatment, suggests that sons were still energetically more demanding than daughters but that parents could not respond to these needs. In Enlarged broods, there was thus a mismatch between chick demand and parental capacity to invest, as also illustrated by the lack of correlation between energy expenditure and CORT levels in these broods.

Finally, some studies have reported that parental feeding behavior differed according to parental sex and offspring sex-ratio, with mothers feeding sons more than daughters and fathers showing no such sex-bias (e.g., Green 2002; Mainwaring et al. 2011). However, energy expenditure was not measured in these studies and we did not record parental behavior in our study. The equal energy expenditure levels between parents we report could be due to the absence of any difference in provisioning rates between parents, as found in other species (e.g., Cameron-MacMillan et al. 2007; Michler et al. 2010).

Does supplemental feeding have a stronger effect on the reproductive success of sons than daughters?

There was no evidence that sons of Fed parents had higher reproductive success than daughters. Reproductive success did not differ between male and female offspring, regardless of parental feeding treatment (Figure 3). Therefore, it seems that Fed parents were not able to attain higher fitness returns by producing more sons. Hence, we found no clear support for the gTWH, despite the fact that we had an a priori expectation that this model could apply in the kittiwake (Merkling et al. 2012). There is intense male–male competition at the start of the breeding season for access to the best breeding sites (Cullen 1957; Wooller and Coulson 1977). This suggests that sons from parents with higher investment capacities might benefit more than daughters in terms of their future reproductive success because breeding site characteristics can greatly influence reproductive success (Regehr et al. 1998; Massaro et al. 2001).

However, although data on offspring reproductive success are valuable to test the assumption of the gTWH, we should ideally have recorded lifetime reproductive success of offspring of both sexes born to parents of each feeding treatment (Komdeur 2012). In our population, on average, individuals recruit at 6–7 years old (Vincenzi et al. 2013) and survive 13 years (Hatch et al. 1993), thereby potentially having 7 breeding attempts. In our data set, the mean number of breeding events was 4.8. Moreover, some individuals survive at least 20 years in our population (Hatch SA, unpublished data) and we monitored some individuals that had at least 11 breeding attempts. Our estimates of reproductive success were thus relatively imprecise and we can thus not completely rule out that the gTWH might play a role in sex allocation decisions of kittiwakes. For instance, it is possible that sons of Fed parents have a sharper increase in reproductive success with reproductive

experience than daughters. However, it seems unlikely that there is a marked sex difference in reproductive success given in Figure 3; hence, the gTWH likely plays at most only a minor role in sex allocation tactics in this species.

Our results suggest that, in the kittiwake, drivers of parental investment are probably more related to the sex-specific energetic cost of offspring than to their future reproductive success. More generally, given the selective publication of significant results (Festa-Bianchet 1996; Palmer 2000), and possible a posteriori interpretations of any such biases in relation to the numerous theoretical models that have been proposed (Hewison and Gaillard 1999), assessing the adaptive value of sex-ratio biases requires precise investigation of the underlying assumptions (e.g., Bowers et al. 2015), particularly as long as the mechanisms involved in sex-ratio manipulation remain largely unknown (Krackow 1995).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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