



Reproductive skew and female trait elaboration in a cooperatively breeding rail

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Intrasexual competition for reproduction is thought to be an important factor in the evolution of ornaments and weapons in males. However, the evolution of morphologically similar traits in females is often explained through other mechanisms, and the role of intrasexual competition in female trait elaboration has received little attention. Here, we explore the factors associated with female trait elaboration in the cooperatively breeding Pukeko (the New Zealand race of the Purple Swamphen *Porphyrio porphyrio melanotus*) by comparing sexual dimorphism in an ornament across two populations. Importantly, the two populations considered differ in several social factors that could affect the degree of female–female competition, and could thereby produce differential selection on elaborate female traits. Recent studies have suggested that high reproductive skew (i.e. monopolization of reproduction by dominant individuals) could influence the intensity of intrasexual competition and select for female elaboration. However, we found that sexual dimorphism was diminished and Pukeko females had more elaborate ornaments under conditions of low reproductive skew. We discuss alternative factors that could influence the degree of female–female competition, and show that reproductive skew may not always provide an accurate estimate of the scope for intrasexual competition.

Keywords: competition, joint laying, mate choice, ornament, Pukeko, sexual dimorphism, sexual selection, social selection, weapon.

INTRODUCTION

Darwin (1871) noted that males often compete intensely for mates, either directly through physical combat or indirectly through attempts to ‘excite or charm those of the opposite sex’. Such competitions usually involve secondary sexual characteristics (Hunter 1837), traits that are not involved in reproduction per se, but are important in competition for breeding opportunities (e.g. Bergeron *et al.* 2010). Such traits are typically more developed in males than in females (Clutton-Brock 2009). However, females of many species have highly developed secondary sexual traits, and the mechanisms underlying their evolution have

received less research attention than have similar traits in males. Elaborate female traits are sometimes attributed to genetic correlation between the sexes (Lande 1980), but there has been recent interest in whether intrasexual competition might be a driving force in the evolution of female secondary sexual characteristics (LeBas 2006, Clutton-Brock 2009, Rubenstein & Lovette 2009, Watson & Simmons 2010).

Cooperatively breeding birds provide an excellent model for investigating how female intrasexual competition influences trait elaboration. In these species, direct reproduction is often unequally distributed among females within each breeding attempt or season, a social factor known as high female reproductive skew (Vehrencamp 1983). Thus, in cooperative breeders, intrasexual competition can be intense in both males and females (Clutton-Brock *et al.* 2006) because it

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often pays both sexes to compete for breeding positions. Also, because females often compete for breeding positions in these species, the role of mate choice by males is reduced (Clutton-Brock 2009, Rubenstein & Lovette 2009) and therefore female trait elaboration in cooperative breeders is likely to be caused by selection on traits that enhance success in intrasexual competition (Clutton-Brock 2009, Rubenstein & Lovette 2009). Indeed, across species of African starlings cooperative breeders have reduced sexual dimorphism in comparison with non-cooperatively breeding species, resulting from differential selection on female traits that enhance access to breeding opportunities (Rubenstein & Lovette 2009). To date, no study has examined patterns of female trait elaboration and reproductive skew within a single species, but such studies are necessary to understand fully how social structure influences female trait evolution.

Here, we explore the factors influencing sexual dimorphism in the frontal shield of the cooperatively breeding Pukeko, the New Zealand race of Purple Swamphen *Porphyrio porphyrio melanotus*. The fleshy frontal shields of rails are testosterone-dependent characters (Gullion 1951, Eens *et al.* 2000) that are prominently displayed in aggressive interactions. Shield size is correlated with social status in Pukeko (Craig 1974) and social status is important in defining female reproductive success (Jamieson & Craig 1987, Craig & Jamieson 1990). Pukeko show population differences in social structure, providing a rare opportunity to explore the effect of social factors on female trait elaboration within a single species. New Zealand's North Island Pukeko are sedentary and defend territories year-round. The groups are large, comprised of related members and are characterized by high female reproductive skew (Craig & Jamieson 1988, Lambert *et al.* 1994, Jamieson 1997). Conversely, South Island Pukeko only defend territories during the breeding season, after which the group may partially or completely disband. Groups are small, consist of unrelated individuals and have low female reproductive skew (Jamieson *et al.* 1994, Jamieson 1997).

In societies where dominant females monopolize reproduction, competition for social status is expected to be intense, as there are substantial reproductive consequences associated with social status (Keller & Reeve 1994, Reeve 2000). Societies with high reproductive skew typically have

high inter-individual variation in lifetime reproductive success (Hauber & Lacey 2005), which increases the scope for selection on traits that enhance success in intrasexual competition (Andersson 1994, Rubenstein & Lovette 2009). As a result, selection on female secondary sexual characteristics is expected to be more intense when reproductive skew is high. However, Pukeko differ from most avian species in that females, as well as males, can be highly philopatric (Craig & Jamieson 1988). As patterns of philopatry affect the spatial and temporal distribution of related individuals (Clutton-Brock & Parker 1992, Lambin 1994), they may alter the degree of intrasexual competition by influencing the local abundance of kin and non-kin competitors. As a result of female philopatry, the patterns of female intrasexual competition and trait elaboration observed in cooperative breeding African starlings (Rubenstein & Lovette 2009) may not hold for Pukeko. Thus, our comparison of sexual dimorphism between two populations of Pukeko with differing social structure provides an indication of whether reproductive skew or other social factors are more important in driving female trait elaboration in the Pukeko.

METHODS

Field methods

Pukeko were studied at the Otokia Wildlife Refuge (South Island, 45°56'S, 170°10'E) from 1990 to 1995 and at the Tawharanui Open Sanctuary (North Island, 36°22'S, 174°49'E) from 2008 to 2010. The methods used to capture, sex and measure birds have been published elsewhere (Craig *et al.* 1980, Jamieson & Craig 1987, Jamieson *et al.* 1994). Briefly, birds were caught using funnel or remote-controlled box traps baited with grain. Both adults and juvenile birds were caught in this manner, but only adults were considered in this study. Upon capture, standardized measurements were taken from each individual, including maximum shield width. Measurements were taken by different researchers at each study site (I.G.J. at Otokia, J.S.Q. and C.J.D. at Tawharanui). However, this is a very straightforward measurement that is well illustrated in Craig *et al.* (1980). There is very little subjectivity in this measurement (width of a red structure on a black background) and thus inter- and intra-individual measurement error should be low. Birds were marked with col-

oured leg rings prior to release and if individuals were caught more than once, only data from the first capture were used. Group size and dynamics, as well as territory location, were determined by daily observations during the breeding season at both dawn and dusk. The number of breeders in each group was determined by clutch characteristics (see below) and observation of copulations. Because we did not always capture all individuals in each focal group at Tawharanui, we could not always discriminate the sex of non-breeding helpers. When mating behaviour was observed, suitable nesting habitat within the territory of interest was searched until a nest was located. Philopatry and group composition was tracked by monitoring group membership (via marked individuals) and territory occupancy among years.

Female reproductive skew was estimated by the number of eggs laid by each female in a communal clutch (Jamieson 1997). Nests were checked daily during the laying period, and eggs were separated into clutches laid by individual females based on size, shape, colour and spot patterns. This method of clutch separation has been previously shown reliably to distinguish among eggs laid by different females (Craig 1980, Jamieson & Craig 1987, Jamieson *et al.* 1994, Haselmayer 2000). Reproductive skew was then calculated by the formula:

$$S = (N_T - Q_E) / (N_T - 1)$$

where N_T is the total number of potential breeders and Q_E is the effective number of breeders (defined as $Q_E = 1 / \sum p_i^2$, where p_i is the reproductive contribution of the i th breeder; Pamillo & Crozier 1996). As we could not always determine the number of non-reproductive females in a group (because we did not capture all individuals in each focal group at Tawharanui), we excluded non-reproductive females from our skew calculations. Also, one might expect differences in female reproductive skew based solely on the fact that non-breeding helpers are common at North Island sites and very rare or absent at South Island sites (Jamieson 1997). Thus, by excluding non-breeding helpers we could explore patterns of reproductive partitioning that are not merely driven by the presence of helpers in one population and not the other. By excluding helpers, the measure of reproductive skew used in this study should underestimate the actual difference in reproductive skew between the populations.

Estimates of lifetime reproductive success

Lifetime inclusive fitness estimates of Pukeko breeding on the North and South Island were estimated in terms of offspring equivalents (Koenig & Mumme 1987). Long-term reproductive data were not available for the Tawharanui population and thus we compared data collected at Otokia (South Island, see above) with data collected at Shakespear Regional Park (North Island, 36°36'S, 174°49'E, 25.8 km from Tawharanui, data collected from 1979 to 1985). As inter-island differences in Pukeko social structure are thought to be based on climatic differences (colder, harsher weather in the South Island), and associated mortality rates and ecological constraints on dispersal (Jamieson 1997, I.G. Jamieson unpubl. data), we would expect the general characteristics of North Island Pukeko populations to be consistent between Tawharanui and Shakespear, as well as over time. Furthermore, the two North Island sites are alike in habitat and have similar Pukeko population densities, group sizes and reproductive skew (Jamieson 1997, this study). Thus, our reproductive success data from Shakespear should be a reasonable proxy for patterns of fitness variation at Tawharanui.

The direct component of fitness for an individual bird was estimated by dividing the annual number of offspring produced by the number of same-sex breeders in the group and totalling across years in which the individual bred. The indirect component was estimated by subtracting an individual's annual number of direct offspring equivalents from the total number of offspring produced in the group, multiplying this number (i.e. the remaining offspring) by an estimated coefficient of relatedness between co-breeders of the same sex and totalling across years of group membership as a breeder. Both males and females at Shakespear are highly philopatric (Craig & Jamieson 1988); thus, for this population, the coefficient of relatedness between group members was estimated at either 0.50 for groups that had no known immigrants (i.e. full siblings) or 0.37 for groups in which one or more birds had joined during the time the individual was breeding. To this total (direct plus indirect component) we added an estimate of the average number of offspring equivalents an individual would have raised as a non-breeding helper, which was based on group reproductive success and estimated relatedness

values during seasons in which the individuals did not breed. It was estimated that male helpers gained 0.58 offspring equivalents per year and helped for 2 years on average, while females gained 0.32 offspring equivalents per year and helped for an average of 4 years (I.G. Jamieson unpubl. data) before becoming a breeder. At Otokia, co-breeders were unrelated and non-breeding helpers were extremely rare (Jamieson *et al.* 1994), and thus only direct components of fitness were calculated.

Statistical analyses

Statistical analyses were performed with JMP (8.0.2) and R (2.12.1) with a level of significance (α) of 0.05. In all analyses, model residuals were visually examined for normality using a quantile–quantile plot, and transformed when necessary. Population differences in social structure were analysed with *t*-tests. We used a linear mixed model (LMM) fit with restricted maximum likelihood variance components to investigate population differences in frontal shield dimorphism. In this analysis, maximum shield width was square-root-transformed and used as a response variable. This measure is highly correlated with total shield area (C.J. Dey unpubl. data). Performing this analysis with body mass-corrected shield size as the response variable did not qualitatively change the results, and thus body mass was not considered in our reported analysis of shield size. Population (North Island or South Island), sex and the interaction of population and sex were included in this model as fixed effects. In these models we used sum-to-zero contrasts, as described in Schielzeth (2010), to allow for the interpretation of main effects in the presence of interactions (Engqvist 2005). Year was included as a random effect to account for the potential variance between field seasons. Following a significant interaction effect in this model, a Holm–Bonferroni multiple comparison test was conducted (Holm 1979) to assess if population differences in males or females were driving population differences in sexual dimorphism. Additionally, we assessed patterns of phenotypic variation in shield size. Because variance in a trait tends to increase with mean value of that trait, we instead calculated the coefficient of variation (sample standard deviation divided by sample mean) for each sex within each population, and used the correction for bias suggested by Sokal and Braumann (1980). Then we used two separate

tests of heterogeneity of relative variance based on *t*-distributions (described in Sokal & Braumann 1980) to compare variation between males and females in each population. This test is sensitive to departure from normality and we therefore used square-root-transformed shield size as the dependent variable. We were also interested in population and sexual differences in the variation in lifetime reproductive success. However, due to our coarse method of estimating lifetime inclusive fitness, we thought it inappropriate to make inter-population comparisons in this analysis. Instead, we performed intra-population analyses using two separate Levene's tests to compare the variance in estimated reproductive success between males and females. Also, we estimated the opportunity for selection *I* for each sex within each population. This value is calculated as the variance in reproductive success divided by the mean reproductive success squared and is an empirical estimate of the maximum change in phenotypic distribution per generation (Crow 1958, Arnold & Wade 1984, Shuster 2009). Unfortunately, we know of no statistical test to compare two *I* values and therefore these data are presented without statistical analysis.

RESULTS

Population demographics

Consistent with previous comparative studies of North and South Island Pukeko populations (Jamieson 1997), our North Island population had a larger group size (*t*-test: $t_{80} = 7.56$, $P < 0.0001$, Table 1) and a higher female reproductive skew ($t_{33} = 3.00$, $P = 0.005$, Table 1) than our South Island population. On the North Island, both adult and juvenile birds tended to remain on the same territory, with the same group mates across years. However, on South Island, group membership and territory ownership typically changed between years.

Dimorphism in frontal shields

Across populations, males had larger shields than females ($F_{1,329} = 140.26$, $P < 0.0001$, Fig. 1). There was no significant difference in shield size between the two populations ($F_{1,6} = 5.50$, $P = 0.057$), although there was a trend for larger shields overall on South Island. The degree of

Table 1. Comparison of social structure between two populations (Otokia, South Island; Tawharanui, North Island) of Pukeko. Sample size is shown in parentheses. Quantitative data on the number of non-breeding helpers and the degree of philopatry were not available and thus qualitative comparisons are shown. See text for details of statistical analysis.

	South Island	North Island
Average group size	2.9 ± 0.14 (46)	6.7 ± 0.54 (36)
Female reproductive skew	0.04 ± 0.01 (14)	0.19 ± 0.04 (21)
Non-breeding helpers	Rare	Common
Natal philopatry	Rare	Common
Percentage of breeding units:		
Pairs	41	0
Polygynous groups	13	4
Polyandrous groups	33	30
Polygynandrous groups	13	67

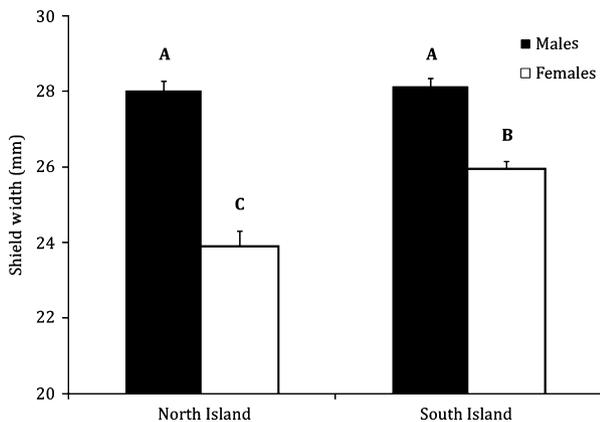


Figure 1. Sexual dimorphism in frontal shield size in two populations of Pukeko. Data are untransformed group means (+ se) for North Island (high reproductive skew; males $n = 67$, females $n = 79$) and South Island (low reproductive skew; males $n = 105$, females $n = 88$) birds. There is a significant difference in sexual dimorphism between the two populations (see text for details of statistical analysis). Letters indicate significantly different groups as determined by Holm-corrected multiple comparison tests (Holm 1979).

sexual shield dimorphism was significantly different between the two populations (interaction effect $F_{1,329} = 7.53$, $P = 0.006$, Fig. 1). Sexual dimorphism in shield size was lower in the South Island population than on North Island (Fig. 1), a pattern driven by population differences in female, but not male, shield size (Holm test, North Female vs. South Female adjusted P -value = 0.0006, North Male vs. South Male adjusted P -value = 0.45). Furthermore, we observed patterns in phenotypic

variation in shield size. In the South Island population, males and females did not differ in shield width variance (Sokal–Braumann test, $t_{191} = 0.14$, $P = 0.89$). However, in the North Island population, females had significantly greater variance in shield width than did males ($t_{144} = 5.68$, $P < 0.0001$).

Variation in lifetime reproductive success

On South Island, females had greater estimated variance in lifetime reproductive success than did males (Levene's test, $F_{1,42} = 51.96$, $P < 0.0001$, Fig. 2), whereas on North Island, males and females did not differ in estimated variance in lifetime reproductive success ($F_{1,26} = 0.48$, $P = 0.49$, Fig. 2). The calculated values of the 'opportunity for selection' were more than three times higher for males than for females in the North Island population (Table 2), but were only slightly higher for females than males in the South Island population (Table 2).

DISCUSSION

The results of this study show that female trait elaboration is greater in the South Island population than in the North Island population. South Island Pukeko showed decreased sexual dimorphism in

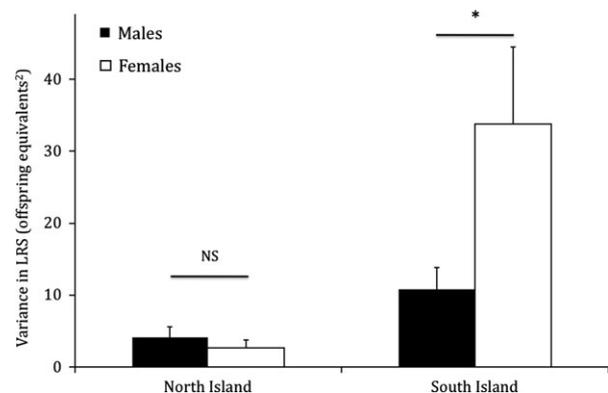


Figure 2. Variation in lifetime reproductive success (LRS) in two Pukeko populations. Data shown are group variances (+ standard error of the variance; Wilks 1963) for Pukeko sampled in the North Island (high reproductive skew; males $n = 16$, females $n = 12$) and South Island (low reproductive skew; males $n = 24$, females $n = 20$). Asterisks indicate significantly different variances between sexes within a population (see text for details of statistical analysis).

Table 2. The opportunity for selection (I) in North Island (Shakespeare) and South Island (Otokia) Pukeko. Sample sizes used to calculate I values are in parentheses. See text for details of reproductive success estimates.

	Males	Females
North Island	0.17 (16)	0.05 (12)
South Island	0.67 (24)	1.08 (20)

shield size when compared with the North Island population. Our data also suggest that selection on female shields may be more intense on South Island. Whereas South Island males and females show similar variation in shield size, North Island females had significantly higher variation in shield size than North Island males. Although there are opposing predictions about the magnitude of variation of traits under selection (e.g. traits under selection can have either low variance (Van Homrigh *et al.* 2007) or high variance (Kotiaho *et al.* 2001)), under both predictions the variation in males and females should be similar if they are experiencing similar selective pressure (Rubenstein & Lovette 2009). Thus, our data suggest that South Island females experience similar selection on shield size as males in that population, whereas North Island males and females experience differential selection on shield size. If shield size positively influences reproductive success, as is typical for avian ornaments that signal quality (Dale 2006), then our data suggest that South Island females are also subject to strong selection on shield size, whereas North Island females are not. Certainly, our reproductive success estimates suggest that North Island males have much greater opportunity for selection than do North Island females whereas in the South Island the scope for selection is more equitable between the sexes.

Taken together, these data do not support the hypothesis that high female reproductive skew should enhance selection on traits involved in intrasexual competition and instead suggest that in some situations, selection on female ornaments can be more intense in conditions of low reproductive skew (i.e. our South Island population). We suggest two possible, non-mutually exclusive, explanations for why the observed patterns of shield dimorphism differ from the predicted relationships between reproductive skew and trait elaboration. First, in typical avian societies females disperse from their natal territory and establish territories

with unrelated individuals (Greenwood 1980). However, in our North Island Pukeko population, both females and males are highly philopatric (see also Craig & Jamieson 1988). When females are philopatric, they will have long-standing associations with related females in their group, and social status may be more strongly defined by past residence than by direct competition between females (i.e. gerontocratic inheritance of dominance; Bridge & Field 2007). As the strength of selection on secondary sexual characteristics is directly dependent on the effect that the trait has on reproductive success (Andersson 1994), we would expect there to be relatively weak selection on female secondary sexual characteristics in populations with female natal philopatry if elaborate traits have a reduced role in determining social hierarchies. In South Island groups, females frequently disperse from their natal group and must compete for group membership and dominance status each year (Jamieson *et al.* 1994). Therefore, female ornaments are likely to be of increased importance in determining social status and reproductive success in this population.

Second, the hypothesis that high reproductive skew should lead to increased selection on traits involved in access to breeding opportunities is based on the premise that high reproductive skew leads to high intrasexual variation in lifetime reproductive success (Hauber & Lacey 2005, Rubenstein & Lovette 2009). While this pattern may be generally true, it is important to note that reproductive skew measures are not always accurate predictors of the variance in lifetime reproductive success. Reproductive skew values describe the degree to which direct reproduction is monopolized in a single breeding attempt or season. But if subordinate individuals inherit a dominant breeding position in subsequent breeding seasons (Lucas *et al.* 1997), they may end up having equivalent fitness to the current dominant individuals over their entire lifetime, even if reproductive skew is high within each breeding season. Furthermore, measures of reproductive skew may not capture the variation in inclusive fitness since they do not include indirect fitness benefits. Many cooperatively breeding groups are composed of kin and there may be intersexual or population differences in relatedness that complicate the relationship between reproductive skew and variation in lifetime inclusive fitness (Creel 1990). As such, reproductive skew may not reflect the variation in

inclusive fitness on which sexual and social selection can act (Hauber & Lacey 2005). Interestingly, our analysis of lifetime reproductive success provides evidence of such a disconnect between reproductive skew and variance in inclusive fitness in the Pukeko. Despite high reproductive skew, our data show that North Island female Pukeko have low variation in lifetime inclusive fitness (and low opportunity for selection), perhaps due to the kin-based structure and method of dominance inheritance that occurs in North Island groups. In such a situation, high reproductive skew may not necessarily lead to increased intrasexual competition, as all individuals expect relatively equal lifetime fitness and thus there is little incentive to compete for social status. Pukeko may represent a rare situation in this regard, as many cooperative breeding mammals are known to have female-biased philopatry and high levels of kinship among group females (Armitage 1987), yet these societies also show high variation in female reproductive success (Hauber & Lacey 2005).

The degree of sexual dimorphism in secondary sexual characteristics is affected by selection on both males and females. In this study, there were no significant population differences in male shield size and thus it seems that shield dimorphism in Pukeko is largely determined by differences in female shield size (Fig. 1). Shield size is correlated with social dominance in male Pukeko (Craig 1974, C.J. Dey, unpubl. data) and thus we might also have expected to see population differences in male shield size, as there are population differences in male (as well as female) philopatry and territoriality (Jamieson 1997). There are several possible reasons why we did not observe such differences. First, previous studies have suggested that social dominance may not predict reproductive success in male Pukeko (Jamieson *et al.* 1994, Lambert *et al.* 1994). If socially dominant males do not have greater reproductive success than socially subordinate males, there may be no basis for strong selection on male shields. Secondly, it is uncertain how variation in male reproductive success differs between the populations. Jamieson (1997) found no significant difference in male reproductive skew between a North Island and South Island population; however, this comparison was conducted on a small number of groups. If North Island and South Island males have similar variation in lifetime reproductive success then the scope for selection

on male shield size may be similar between the populations. Although we were able to calculate *I* values for males from each population, we did not compare these values because of our coarse methods for estimating reproductive success. Clearly, further research into the functional and adaptive role of male shields is required fully to understand sexual dimorphism in this trait.

To our knowledge, the current study is the first to assess how patterns of female reproductive skew influence trait elaboration and sexual dimorphism within a single species. Because our study is based on only two populations, we present this paper as an exploratory analysis of the social factors associated with female trait elaboration in the Pukeko rather than an explicit and powerful test of the predictions derived from Rubenstein and Lovette (2009). An intraspecific comparison of many populations that differ in terms of reproductive skew but not other factors that could influence trait expression (opportunity for dispersal, breeding season length, group size and composition, etc.) would be a stronger test of the relationship between reproductive skew and female traits. However, such a situation may be challenging to find, as reproductive skew tends to co-vary with many environmental and social parameters (e.g. Hatchwell & Komdeur 2000) and intraspecific variation in reproductive skew is rarely studied and therefore poorly characterized. Also, in comparing patterns of variation in fitness, the current study estimates lifetime reproductive success from group reproduction success and observations of copulations. In our analysis, we estimated equivalent direct reproductive success for same-sex breeders in each group for each year. While this may be appropriate for South Island Pukeko (in which reproductive skew is low; Jamieson *et al.* 1994), it is known that North Island groups have a highly unequal distribution of reproduction amongst breeders (Jamieson 1997). Thus, our estimation method could dampen true variation in lifetime reproductive success in the North Island by underestimating variation in fitness between same-sex breeders. However, it is important to note that non-breeding helpers were not estimated to have gained direct reproduction and thus there is still within-group variation in fitness considered with our methods. Indeed, variation in direct fitness as a result of non-breeding helpers is probably a large component of total variation in inclusive fitness in many cooperative breeders (Hauber & Lacey

2005) and thus our methods are likely to retain most of the true variation in lifetime reproductive success. Nonetheless, because North Island within-group variation in reproductive success may be underestimated by our methods, we did not make inter-population comparisons of variation in lifetime reproductive success or the opportunity for selection. Future studies with the ability to determine true variation in lifetime reproductive success (e.g. using parentage analysis) will be valuable in understanding how reproductive skew and variation in lifetime reproductive success influence female trait elaboration.

Both social and mating systems have long been considered important components in defining the dynamics of sexual and social selection in animals (Andersson 1994). But, to our knowledge, no previous study has examined how female traits vary between populations of a single species that differ in social structure. Whereas reproductive skew may be important in defining the intensity of female intrasexual competition in some avian societies, it is not always an accurate predictor of the variation in lifetime reproductive success and thus researchers should be cautious about using reproductive skew comparisons to infer patterns of variation in lifetime fitness. Instead, our data suggest that life-history characteristics other than reproductive skew (i.e. philopatry, group structure and patterns of dominance inheritance) can also influence the intensity of female intrasexual competition and this may be particularly true when females are philopatric. Further research examining the role of these factors on the intensity of female–female competition is necessary for a more complete understanding of female ornamentation. In particular, we suggest that intraspecific studies may be particularly valuable in teasing apart the relative importance of reproductive skew and variation in reproductive success on the evolution of female traits.

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