The intensity of sexual selection and the absence of assortative mating patterns in *Prunella modularis* (Aves: Passeriformes)

First author: Grazieli da Silva Cerqueira[1] (https://orcid.org/0009-0005-6495-7519)

Co-author: Eduardo S. A. Santos[2,3,4] (https://orcid.org/0000-0002-0434-3655)

Benedikt Holtmann[2] (https://orcid.org/0000-0002-2995-7274)

Carlos Esteban Lara[5] (https://orcid.org/0000-0001-5425-0935)

Shinichi Nakagawa[2,3] (https://orcid.org/0000-0002-7765-5182)

Last author: Renato C. Macedo-Rego[4,6*] (https://orcid.org/0000-0002-2973-9912)

[1]Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

[2]Department of Zoology, University of Otago, Dunedin, New Zealand

[3]COSSEE, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

[4]LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

[5]Dirección Académica Sede de La Paz, Universidad Nacional de Colombia, La Paz, Colombia

[6]Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

*Corresponding author: rcmacedorego@gmail.com

Abstract

When females and males prefer large mating partners, a size-assortative mating pattern can occur, and larger individuals tend to obtain more partners, thereby increasing the intensity of sexual selection. Considering this, we studied a population of dunnocks (*Prunella modularis*), a species with a variable mating system. We tested whether (A) assortativity (based on body size and/or condition) occurs, (B) sexual selection is higher in males than in females, as is typically expected, and (C) the sex ratio influences the strength of selection. Despite assessing multiple breeding seasons (individually and combined), we found no evidence of assortative mating. Because we found little evidence that large (or higher-condition) individuals produce more offspring, there should be no strong preference for body size or condition, and assortativity should not occur, as observed. We also found that males faced stronger sexual selection than females, which conforms to long-standing predictions within sexual selection theory. However, this sex difference was of little to moderate magnitude, which is reasonable for a polygynandrous species. Finally, both sexes faced stronger selection when the sex ratio was more male-biased, indicating that (a) some females are better than others in obtaining more than one mate, even when males are abundantly available, and/or (b) males are more willing to accept co-breeding males as the sex ratio becomes more biased.

Keywords: Bateman gradient; mate choice; mating success; reproductive success; opportunity for sexual selection; sex ratio; sex roles.

1. Introduction

Mating success is often associated with an individual's attractiveness to potential partners. In turn, an individual's attractiveness is ultimately linked with direct benefits — protection from predators (Balmford et al., 1992; Breuer et al., 2010), better territories (Castillo & Arce, 2021; Pribil & Searcy, 2001), more resources (Temeles & Kress, 2010), or parental care (Goldberg et al., 2020; Olsen et al., 2008) — or indirect benefits to partners, through offspring carrying advantageous genes (Jennions & Petrie, 2000; Weatherhead & Robertson, 1979). Attractiveness, therefore, evolves as a signal of an individual's quality because partners that respond to it gain these direct or indirect benefits. For instance, in many taxa, large females have more energy and internal space to produce eggs and are therefore more fecund than small females (Andersson, 1994a, 1994b; Darwin, 1871; Fairbairn, 2007; Székely et al., 2007). So female body size can signal a fecundity benefit to choosing males; analogous size- or quality-linked benefits can favour female choice of males. Mate choice can also track body condition: individuals in good condition outperform rivals in intrasexual competition (Juola & Searcy, 2011; Macedo-Rego et al., 2016; Shine et al., 2004; Blukacz et al., 2010; Correa et al., 2011; Kahrl & Cox, 2015) and territory defence (Meuche et al., 2012; Snijders et al., 2017), and thereby secure the resources, territories, or breeding opportunities that translate into greater direct or indirect benefits for their partners.

When traits signal the fitness returns of potential sexual partners, individuals are expected to prefer partners who provide greater fitness benefits. Accordingly, a meta-analysis has shown that males tend to prefer mating with high-quality females (Pollo et al., 2022). High-quality males also show stronger preferences than low-quality males, who cannot afford to be choosy when females, too, favour high-quality partners (Pollo et al., 2022). This mutual preference for quality has two measurable consequences. First, when a single trait signals quality in both sexes, assortative mating tends to evolve, as high-quality individuals pair with

one another (Jiang et al., 2013). Second, strong preference for a trait increases the variance in mating success among individuals bearing it, thereby intensifying sexual selection (Andersson, 1994a; Emlen & Oring, 1977).

In this study, we assess the intensity of sexual selection and test for assortative mating patterns in the well-studied bird species *Prunella modularis*, the dunnock. First, dunnocks display a variable mating system — monogamy, polyandry, and polygynandry co-occur in breeding populations (Davies & Lundberg, 1984; Holtmann et al., 2022) — so both sexes can vary in mating success, creating scope for sexual selection. Second, both sexes defend territories year-round and provide parental care (Santos & Nakagawa, 2013), so size or condition could signal a partner's direct benefits and favour assortment; polyandrous trios indeed achieve higher hatching success than pairs (Santos et al., 2015). Third, indirect benefits also matter, as monogamous females produce more extra-pair offspring than polyandrous females (Santos et al., 2015). Despite this rich background, neither the occurrence of assortative mating nor the intensity of sexual selection has been quantified in this species — the two questions we address here.

We tested five hypotheses: the first two concerned assortative mating, and the remaining three concerned the intensity of sexual selection. First, because large individuals in animal species usually have an advantage when fighting for territories (Araya-Salas et al., 2018; Desrosiers et al., 2021; Ippi et al., 2018), we expected both females and males to prefer larger partners; when such mutual preferences combine with competitive exclusion of smaller individuals from the most-preferred partners, the resulting pattern is size-assortative pairing (large with large, small with small; Hypothesis 1). Second, because individuals with higher body condition should have more resources to invest in parental care (Angelier & Chastel, 2009; Jaatinen et al., 2011; Nishida & Takagi, 2018) and because body condition can be an indicator of genetic quality (Kempenaers et al., 1992), both sexes should prefer high-

condition partners; by the same competitive-sorting logic, we expected an assortative mating pattern based on body condition in dunnocks (Hypothesis 2). Third, because males usually face higher levels of sexual selection than females across animal taxa (Janicke et al., 2016), a pattern hypothesized to emerge from anisogamy (Lehtonen, 2022), we tested whether female dunnocks face lower sexual selection intensity than males (Hypothesis 3). Fourth, because Bateman's principle predicts that male fitness rises more steeply with mating success than female fitness (Bateman, 1948; Lehtonen, 2022), we tested whether the marginal fitness return per additional mating is higher for male than for female dunnocks (Hypothesis 4). Fifth, sex ratios have been shown to correlate with the intensity of sexual selection in males but not in females across animal species (Janicke & Morrow, 2018; Moura & Peixoto, 2013). We therefore tested whether the intensity of sexual selection in dunnocks increases among males, but not among females, as the sex ratio becomes more male-biased (Hypothesis 5).

2. Materials and methods

2.1 Data collection

To test whether assortative mating patterns occur and to quantify metrics of sexual selection, we used data from an extensively studied population of dunnocks inhabiting Dunedin, New Zealand (45.87° S, 170.50° E; Dunedin Botanic Garden population). Data collection spanned three breeding seasons: 2012-2013, 2013-2014, and 2014-2015 (which we refer to as seasons A, B, and C, respectively). For more details on fieldwork, see Santos & Nakagawa (2013), Santos et al. (2015), Holtmann et al. (2017), Lara et al. (2020) and Holtmann et al. (2022).

From September to January of each breeding season, nests were located by inspecting vegetation and/or following adult individuals. Each nest found was checked every two days until oviposition. During egg laying, nests were checked daily, allowing us to quantify the laying order and, later, the order of egg hatch. Until hatching, we visited nests every other

day. At > 9 days of age, chicks were banded with a unique combination of color-coded rings. To capture adults, mist nets were placed along territory borders and near nests. Each captured individual was banded with a unique combination of color-coded rings, and its body weight (g) and tarsus length (mm) were measured. From these measurements, we calculated a proxy for body condition by obtaining the residuals of a least-squares regression of body weight on tarsus length (Hutton et al., 2018; Labocha & Hayes, 2012; Snijders et al., 2017). Finally, for each breeding season, we calculated the operational sex ratio (Moura & Peixoto, 2013). For each breeding group, the numbers of adult females and adult males were also recorded.

To obtain DNA samples and run paternity analyses, blood samples were collected from each captured offspring and adult individual. When unhatched eggs contained embryos, tissue samples were extracted. Paternity analyses were done with the premise that the social mother of a given egg was the respective genetic mother. The fact that the DNA samples from all chicks matched those of their social mothers strongly supports the premise (Santos et al. 2015). Finally, all sampled males were considered as potential fathers when determining the father of each offspring. For a detailed description of the protocol for extracting DNA samples and running paternity analyses, see Santos et al. (2015), Lara et al. (2020), and Holtmann et al. (2022).

2.2 Assortativity

To test whether dunnocks mate assortatively, we assessed three traits: tarsus length and body weight (our proxies for body size) and body condition. For these analyses, each individual was paired with its social partner. If a female had two social partners, she was paired with the larger male or the male with higher body condition, depending on the trait being analyzed. For each trait, we calculated the slopes of least-squares regressions of the male estimate on the respective female estimate. Positive slopes would indicate an assortative mating pattern,

136 negative values would indicate a disassortative mating pattern, and slopes that do not differ
137 from zero would indicate that no assortativity occurs.
138 Finally, to better understand our results and test whether the assessed traits relate to
139 fitness, we conducted additional analyses. For each sex, we ran least-squares regressions of
140 reproductive success on tarsus length, body weight, and body condition. These analyses were
141 run per season and combined across all seasons. Reproductive success was measured in two
142 ways: (i) early measure (i.e., number of embryos, number of fertilized eggs, and/or number of
143 hatchlings), and (ii) late measure (i.e., number of fledged offspring). While the latter is more
144 influenced by natural selection (Anthes et al., 2016; Bergeron et al., 2012) – there are more
145 events in which natural selection can operate until offspring fledge than until embryos are
146 formed – the number of fledged offspring also provides a further proxy of an individual's
147 success because its genes will not effectively spread in case its offspring do not reach
148 adulthood and reproduce.

149 **2.3 Metrics of sexual selection**

150 For each sampled individual, we quantified the mating success (number of mating partners),
151 fertilisation success (number of mating partners that fertilised or were fertilized by the
152 sampled individual), and reproductive success (for metrics of sexual selection, reproductive
153 success was only based on the total number of offspring produced; early measure, as
154 explained above). To estimate the intensity of sexual selection, we used five indices:

155 1. The opportunity for sexual selection (I_s) is a standardized measure of the variation
156 in mating success within a given sex (Henshaw et al., 2016). It was calculated as
157 the variance in mating success divided by the squared mean mating success,
158 following Crow (1958) and Wade & Arnold (1980).

2. The opportunity for pre-fertilisation sexual selection (I_{fss}) is a standardized measure of the variation in fertilization success divided by the squared mean fertilization success (Macedo-Rego et al., 2024).
3. The opportunity for selection (I) is a standardized measure of the variation in reproductive success within a given sex (Henshaw et al., 2016). It was calculated as the variance in reproductive success divided by the squared mean reproductive success, following Wade (1979).
4. The Bateman gradient is the slope of the least squares regression of reproductive success on mating success (Arnold & Duvall, 1994; Bateman, 1948). To estimate sexual selection intensity and test Hypothesis 3, we first calculated the Bateman gradient for all sampled individuals (Arnold & Duvall, 1994; Bateman, 1948; Henshaw et al., 2016). In addition, to test Hypothesis 4 and assess whether additional mates translate into higher reproductive success, we also calculated the Bateman gradient after excluding individuals with a mating success of zero.
5. The Jones index appears to be the best predictor of the strength of sexual selection (Henshaw et al., 2016). It was calculated as the slope of the Bateman gradient multiplied by the square root of I_s (Jones, 2009).

2.4 Statistical analyses

We ran linear models to calculate Bateman gradients, body condition estimates, and selection gradients (tarsus length x reproductive success; body weight x reproductive success; body condition x reproductive success), and to test whether assortativity occurs in the studied population. When analysing reproductive seasons separately, we used the *lm* function. When combining data from different reproductive seasons (i.e., individuals sampled in more than one season provide multiple measures), we used the *lmer* function (*lme4* package; Bates et

al., 2015), with the identity of each sampled individual as the random variable. All analyses were performed in the software R (R Core Team, 2026) using RStudio (Posit Team, 2026).

Given the small sample size, with only three breeding seasons, estimates of the intensity of sexual selection were contrasted without formal statistical analyses. For the Bateman gradient, comparisons between females and males were based on the confidence intervals of each estimate. This protocol was not used to estimate other metrics of sexual selection because they are calculated as absolute values.

3. Results

3.1 Assortativity and fitness (Hypotheses 1 and 2)

3.1.1 Assortativity

Analyses on assortativity encompassed 99 mating pairs (combining 48 females and 50 males; Season A: 15 pairs; Season B: 31 pairs; Season C: 53 pairs). Some individuals recur across seasons so that pair counts exceed unique-individual counts.

The length of females' tarsi did not predict their partners' tarsus length throughout the three breeding seasons (slope: -0.02 ± 0.12 SE, -0.26 to 0.21 95% CI, t = -0.21, p = 0.84; Figure 1A). The result is the same when separately analysing Seasons A (slope: -0.07 ± 0.25 SE, -0.61 to 0.47 95% CI, t = -0.28, p = 0.78), B (slope: -0.15 ± 0.15 SE, -0.46 to 0.17 95% CI, t = -1.01, p = 0.32), and C (slope: -0.04 ± 0.13 SE, -0.31 to 0.22 95% CI, t = -0.32, p = 0.75).

Similarly, regarding the second proxy for body size, females' body weight did not predict their partners' weight throughout the three breeding seasons (slope: 0.10 ± 0.09 SE, -0.07 to 0.27 95% CI, t = 1.14, p = 0.26; Figure 1B). Again, the result is the same when separately analysing Seasons A (slope: 0.25 ± 0.22 SE, -0.23 to 0.73 95% CI, t = 1.12, p = 0.28), B (slope: 0.02 ± 0.12 SE, -0.22 to 0.27 95% CI, t = 0.21, p = 0.84), and C (slope: 0.13 ± 0.12 SE, -0.10 to 0.37 95% CI, t = 1.16, p = 0.25).

Finally, female condition did not predict their partners' condition across the three breeding seasons (slope: 0.02 ± 0.09 SE, -0.15 to 0.19 95% CI, $t = 0.28$, $p = 0.78$; Figure 1C). The result is the same when separately analysing Seasons A (slope: 0.28 ± 0.22 SE, -0.21 to 0.76 95% CI, $t = 1.24$, $p = 0.24$), B (slope: -0.05 ± 0.13 SE, -0.32 to 0.21 95% CI, $t = -0.40$, $p = 0.69$), and C (slope: 0.07 ± 0.11 SE, -0.15 to 0.30 95% CI, $t = 0.64$, $p = 0.53$).

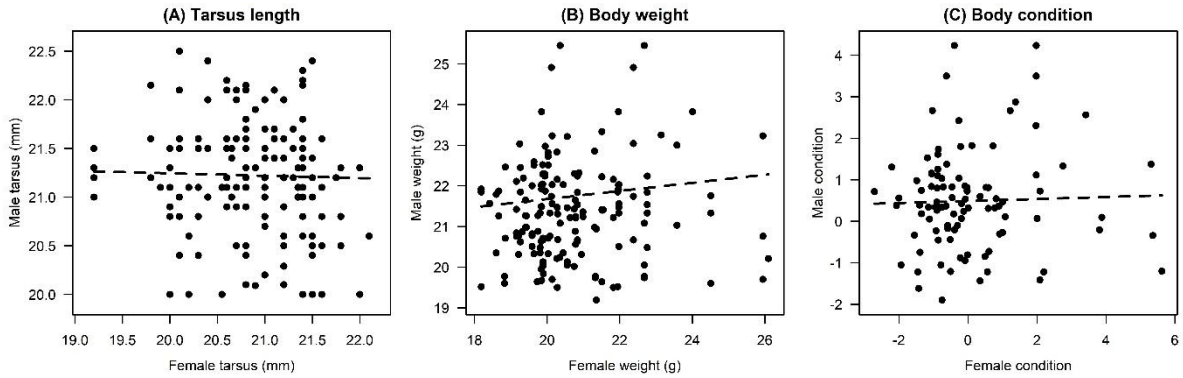

Figure 1. Absence of an assortative mating pattern based on tarsus length (A), body weight (B), or body condition (C) for dunnocks. Figures combine data from all three breeding seasons. Each data point represents a mating pair. Dashed lines show the slope of each linear regression, and no slope is different from zero.

3.1.2 Trait-fitness relationships

None of the three predictor variables explained variation in female or male reproductive success (both early and late measures) across all sampled individuals. Female tarsus length never predicted the total number of offspring produced by females (Table 1A). When it comes to males, tarsus length did not predict the total number of offspring produced by males in all scenarios but Season C, when larger males sired more offspring than smaller males (Table 1A). These results remained the same for both sexes when solely focusing on the production of fledged offspring (Table 2A).

Female body weight did not predict the total number of offspring produced by females in all scenarios but Season A, when larger females produced more offspring than smaller females (Table 1B). Male body weight predicted the total number of offspring produced by males when combining all seasons and when analysing Season C separately, but no relationship between body weight and reproductive success was found in Seasons A and B (Table 1B). For both females and males, no relationship was found between body weight and the number of fledged offspring produced (Table 2B).

Finally, female body condition did not predict the total number of offspring produced by females in all scenarios but Season A, when high-quality females produced more offspring than low-quality females (Table 1C). Male body condition never predicted the total number of offspring produced by males (Table 1C). For both females and males, no relationship was found between body condition and the number of fledged offspring produced (Table 2C).

Table 1. Least squares regressions of reproductive success (early measure: i.e., number of embryos, number of fertilized eggs, and/or number of hatchlings) on tarsus length (A), body weight (B), and body condition (C). For each predictor variable, there are four models: one that combines all three breeding seasons and one for each breeding season. For each model, the slope, the standard error (SE), the confidence interval (95% CI), the sample size (n), and the *p* value (whenever $p \leq 0.05$, the slope differs from zero: underlined results) are provided. For models combining all breeding seasons, the number of individuals is accompanied by the total number of measures. For models on single breeding seasons, the total number of individuals equals the total number of measures.

		(A) Tarsus length					(B) Body weight					(C) Body condition				
Sex	**Seasons**	**Slope**	**SE**	**95% CI**	**n**	***p***	**Slope**	**SE**	**95% CI**	**n**	***p***	**Slope**	**SE**	**95% CI**	**n**	***p***
females	All	-0.31	0.52	-1.32–0.70	57/81	0.55	0.02	0.19	-0.35–0.41	57/80	0.90	0.04	0.19	-0.33–0.43	57/80	0.82
	A	1.23	1.31	-1.53–3.99	19	0.36	0.90	0.38	0.10–1.70	19	0.03	0.86	0.39	0.03–1.69	19	0.04
	B	-0.94	0.93	-2.83–0.95	32	0.32	0.48	0.33	-0.19–1.15	32	0.15	0.53	0.33	-0.14–1.20	32	0.12
	C	-1.35	0.73	-2.84–0.15	30	0.08	-0.24	0.30	-0.86–0.39	29	0.44	-0.14	0.31	-0.78–0.50	29	0.66
males	All	0.70	0.36	-0.02–1.42	85/126	0.06	0.44	0.20	0.03–0.84	85/125	0.03	0.37	0.22	-0.06–0.79	85/125	0.09
	A	-0.31	0.88	-2.12–1.49	34	0.72	0.17	0.39	-0.62–0.95	33	0.67	0.24	0.39	-0.56–1.04	33	0.54
	B	0.13	0.53	-0.94–1.21	48	0.80	0.49	0.40	-0.31–1.30	48	0.22	0.52	0.43	-0.34–1.37	48	0.23
	C	1.46	0.49	0.47–2.45	44	< 0.01	0.62	0.29	0.04–1.20	44	0.04	0.29	0.35	-0.41–0.98	44	0.41

Table 2. Least squares regressions of reproductive success (late measure: i.e., fledged offspring) on tarsus length (A), body weight (B), and body condition (C). For each predictor variable, there are four models: one that combines all three breeding seasons and one for each breeding season. For each model it is informed the slope, the standard error (SE), the confidence interval (95% CI), the sample size (n), and the *p* value (whenever $p \leq 0.05$, the slope differs from zero: underlined results). For models combining all breeding seasons, the number of individuals is accompanied by the total number of measures. For models on single breeding seasons, the total number of individuals equals the total number of measures.

		(A) Tarsus length					(B) Body weight					(C) Body condition				
Sex	**Seasons**	**Slope**	**SE**	**95% CI**	**n**	***p***	**Slope**	**SE**	**95% CI**	**n**	***p***	**Slope**	**SE**	**95% CI**	**n**	***p***
females	All	-0.19	0.31	-0.81–0.43	57/81	0.55	0.03	0.12	-0.20–0.26	57/80	0.81	0.04	0.12	-0.19–0.28	57/80	0.73
	A	0.88	0.78	-0.78–2.53	19	0.28	0.32	0.25	-0.21–0.86	19	0.22	0.28	0.26	-0.27–0.83	19	0.30
	B	-0.80	0.39	-1.61–0.01	32	0.052	0.05	0.15	-0.26–0.36	32	0.73	0.09	0.15	-0.22–0.40	32	0.57
	C	-0.36	0.51	-1.41–0.69	30	0.49	-0.01	0.20	-0.42–0.41	29	0.97	0.03	0.20	-0.39–0.45	29	0.88
males	All	0.09	0.16	-0.23–0.41	85/126	0.58	0.08	0.09	-0.10–0.27	85/125	0.37	0.08	0.10	-0.12–0.27	85/125	0.44
	A	-0.52	0.43	-1.40–0.35	34	0.23	-0.09	0.20	-0.49–0.31	33	0.64	-0.05	0.20	-0.46–0.36	33	0.80
	B	-0.16	0.21	-0.57–0.25	48	0.44	0.10	0.16	-0.22–0.41	48	0.54	0.16	0.17	-0.18–0.49	48	0.35
	C	0.68	0.26	0.15–1.20	44	0.01	0.28	0.15	-0.03–0.58	44	0.07	0.12	0.18	-0.24–0.48	44	0.50

3.2 Metrics of sexual selection (Hypotheses 3, 4, and 5)

The I_s estimates were usually higher among males than among females, with one exception, because the magnitudes of I_s estimates were similar in Season A (Table 3). When it comes to $I_{fss,}$ I and Jones index estimates, males faced a higher selection strength in all breeding seasons (Table 3). Finally, both sexes have positive Bateman gradients (when including all sampled individuals), but the confidence intervals for females and males consistently overlapped (Table 3). When excluding individuals with zero mating success, Bateman gradients were positive for females only in Season B, and for males in all seasons (Table 3).

We detected male-biased operational sex ratios in the three breeding seasons (A: 1.27; B: 1.47; C: 1.33). The breeding season showing the most skewed male bias (i.e., Season B) is associated with the higher selection estimates for both sexes in all scenarios (Table 3).

Table 3. Estimates of selection strength for females and males of a dunnock population, through three breeding seasons (A, B, and C). Four indices of selection are shown: the opportunity for sexual selection (I_s), the opportunity for pre-fertilisation sexual selection (I_{fss}), the opportunity for selection (I), the Bateman gradient (in its traditional form and excluding individuals with zero mating success), and the Jones index. The Bateman gradients are presented as slopes with standard errors (± SE) and 95% confidence intervals (inside parentheses). For Bateman gradients, when $p \leq 0.05$, the slope differs from zero. Females (Season A): mating success (ms) – 1.51 ± 0.96 SD; fertilization success (fs) – 1.14 ± 0.95 SD; reproductive success (rs) – 3.76 ± 3.23 SD; n = 37 (30 obtained at least one mate). Females (Season B): ms – 1.51 ± 0.98 SD; fs – 1.10 ± 1.01 SD; rs – 3.10 ± 3.21 SD; n = 49 (39 obtained at least one mate). Females (Season C): ms – 1.74 ± 1.02 SD; fs – 1.28 ± 0.97 SD; rs – 3.10 ± 2.49 SD; n = 39 (32 obtained at least one mate). Males (Season A): ms – 1.19 ± 0.77 SD; fs – 0.87 ± 0.80 SD; rs – 2.91 ± 3.02 SD; n = 47 (39 obtained at least one mate). Males (Season B): ms – 0.97 ± 0.77 SD; fs – 0.72 ± 0.84 SD; rs – 2.00 ± 2.72 SD; n = 72 (53 obtained at least one mate). Males (Season C): ms – 1.21 ± 0.85 SD; fs – 1.08 ± 0.86 SD; rs – 1.65 ± 2.22 SD; n = 52 (40 obtained at least one mate).

	Females			Males		
Index	**Season A**	**Season B**	**Season C**	**Season A**	**Season B**	**Season C**
I_s	0.40	0.42	0.34	0.41	0.63	0.49
I_{fss}	0.70	0.83	0.57	0.84	1.36	0.64
I	0.74	1.07	0.64	1.07	1.85	1.80
Bateman gradient	1.64 ± 0.50 SE, 0.64–2.65	2.00 ± 0.38 SE, 1.24–2.76	1.32 ± 0.34 SE, 0.63–2.00	2.12 ± 0.49 SE, 1.13–3.11	2.26 ± 0.32 SE, 1.62–2.91	1.55 ± 0.30 SE, 0.95–2.15
Bateman (no zeros)	0.41 ± 0.82 SE, -1.26–2.08	1.91 ± 0.69 SE, 0.51–3.31	0.44 ± 0.61 SE, -0.81–1.68	1.79 ± 0.77 SE, 0.24–3.34	2.55 ± 0.59 SE, 1.38–3.73	1.85 ± 0.56 SE, 0.73–2.98
Jones index	1.04	1.30	0.77	1.37	1.79	1.08

4. Discussion

We found no evidence of assortative mating patterns in dunnocks. Large females do not pair more often with large males than expected by chance, thus refuting Hypothesis 1. Similarly,

294 females in better body condition (hereafter, high-quality females) do not pair more often with
295 males in better body condition (high-quality males), thereby refuting Hypothesis 2. In addition,
296 we found that males almost always faced higher sexual selection than females, corroborating
297 Hypothesis 3. When considering only individuals that mate at least once, additional matings
298 consistently increased male fitness, whereas they had little influence on females, thus
299 corroborating Hypothesis 4. Finally, the season with the most skewed sex ratio (more males
300 per female) was the one in which both sexes experienced stronger sexual selection, thus
301 supporting Hypothesis 5. Below, we discuss all these results.

302 We found no evidence of assortative mating in dunnocks (whether based on body size
303 or body condition). This result runs counter to the overall pattern of a positive, moderate
304 correlation between female and male size across animal species (Moura et al., 2021). However,
305 when focusing only on Avian species, Moura et al. (2021) and another meta-analysis (Wang et
306 al., 2019) show that, while positive, the average correlation between female size and male size
307 is small. Accordingly, studies on several avian species (other than the dunnocks studied here)
308 found no evidence of size-assortative mating patterns, for instance: the common tern (*Sterna*
309 *hirundo*) (Apanius & Nisbet, 2006), the great tit (*Parus major*) (Kölliker et al., 1999, Holtmann
310 & Dingemanse 2022), the mute swan (*Cygnus olor*) (Włodarczyk et al., 2016), and the rufous
311 hornero, *Furnarius rufus* (Diniz et al., 2016). Consequently, the result shown here does not
312 diverge much from the overall Avian pattern of little correlation between female size and male
313 size in mating pairs.

314 The absence of assortativity in dunnocks probably occurs because, as shown here, body
315 size and body condition have little effect on reproductive success, at least in the three sampled
316 reproductive seasons. For females, tarsus length does not influence reproductive success, and
317 body weight and body condition only increased reproductive success in Season A. This result
318 is surprising as large females are traditionally expected to produce more offspring than smaller

319 females (Darwin, 1871; Shine, 1988; Székely et al., 2007), and a recent meta-analysis has
320 shown that larger females do produce more offspring across animal taxa (Macedo-Rego, 2020).
321 Among males, a positive influence on reproductive success was found only for body size in
322 Season C and for body weight when combining all seasons. With little to no influence of body
323 size and condition on reproductive success, females and males seem to gain little or no benefit
324 from mating with large and/or high-quality partners compared with other potential partners.
325 Given this and knowing that mate search, preference for specific mates, and mate choice can
326 be costly (Cotton et al., 2006; Waffender & Henshaw, 2023), it is not surprising that we found
327 no assortativity in dunnocks' mating patterns.
328 However, why did we find a positive association between size or condition and
329 reproductive success in some (few) analyses, but not in all of them? There are two possibilities.
330 First, these positive correlations may be spurious. If one conducts several analyses, some are
331 expected to refute the null hypothesis (Bland & Altman, 1995). The second possibility is that
332 body size and/or condition do influence reproductive success in dunnocks, but environmental
333 changes from one season to the other often attenuate or even preclude such influence from
334 occurring. For instance, if a large body size or a good body condition helps in obtaining
335 territories or resources (Piper et al., 2000; Sergio et al., 2009), but the availability or quality of
336 those vary through time (Carnicer et al., 2009; Lurz et al., 2000), the relevance of body
337 size/condition might accordingly vary.
338 This demonstrates that when resource or territory availability varies, it has meaningful
339 effects. For example, in an area in the United Kingdom where food was scarce, females'
340 territories were larger. This made it more difficult for males to guard females, leading to
341 increased polyandry and decreased polygyny (Davies & Lundberg, 1984). However, when the
342 authors increased food availability, females' living areas shrank, male mate-guarding became
343 more feasible, and some males managed to obtain more sexual partners (Davies & Lundberg,

344 1984). When it comes to the New Zealand population we studied, we have no data on the
345 availability or quality of territories. However, if environmental instability diminishes the
346 hypothetical advantages of size or condition in gaining territory, such instability may be enough
347 to prevent a preference for larger or higher-quality individuals and hinder the development of
348 assortative mating.

349 Regarding the intensity of sexual selection, in 14 of 15 scenarios (five sexual selection
350 indexes × three breeding seasons), we found higher estimates for males than for females.
351 Similarly, we found that each additional mating (for those with more than one mating partner)
352 is more beneficial for males. These results indicate that, compared with females, male dunnocks
353 face stronger selection and benefit more from polygamy, which corroborates the Darwin-
354 Bateman paradigm (Dewsbury, 2005) and aligns with the pattern observed in animals in
355 general (Janicke et al., 2016). This pattern is hypothesized to occur because females typically
356 exhibit higher parental investment than males. Specifically, females produce large, nutritious
357 gametes, carry and nurture eggs, and care for the young in several taxa, while males invest
358 more in seeking additional mates (Trivers, 1972). It has also been proposed that males face
359 stronger selection because they tend to have higher reproductive potential, as they produce
360 gametes faster than females, thereby replenishing their gamete stores sooner (Clutton-Brock &
361 Parker, 1992). According to these hypotheses, when males show lower parental investment
362 and/or a higher reproductive rate than females, the standardized variation in male
363 mating/fertilization/reproductive success should be higher (Andersson, 1994a), as found here.

364 However, because (i) male dunnocks provide costly parental care (in terms of energy
365 and time) before and after egg-hatching (Byle, 1990; Santos & Nakagawa, 2013), (ii) sperm
366 varies in quality among male dunnocks (Lara et al., 2020) and sperm is not as cheap as once
367 thought (Dewsbury, 1982; Parker & Pizzari, 2010), male reproductive investment per offspring
368 is increased, which should reduce male reproductive rates. Accordingly, while sexual selection

estimates are higher for males, they are not substantially higher than those for females in the studied population.

Finally, we found that both sexes faced stronger selection when the operational sex ratio (OSR) was more male-biased; however, we stress that this result should be interpreted with caution, given our sample size of only three breeding seasons. Nevertheless, regarding males, the result aligns with traditional expectations (Emlen & Oring, 1977; Shuster, 2009). Males under male-biased OSR have fewer mating opportunities; some will remain unmated, while others will obtain one or more mating partners, thereby increasing variance in male success. However, in this same scenario, (almost) all females should mate at least once, thus reducing variance in female success. Why was this not the case here? One possibility is that, even if most females mate, they vary in their ability to attract mates, and some attract and mate with more males. In fact, dunnock females compete for males through complex vocalizations (Langmore & Davies, 1997). If these vocalizations are highly energy-demanding, time-consuming, or attract predators, high-quality females should better face these costs (see Zahavi, 1975) and thus attract more males. Because polyandry benefits females (Jennions & Petrie, 2000; Kvarnemo & Simmons, 2013) and polyandrous females can cryptically favour sperm from high-quality males (Eberhard, 1996; Thornhill, 1983), attracting more males could promote an increased variation in female fitness.

In summary, while our results corroborate long-standing hypotheses within the theory of sexual selection, they also align with the most recent perspective that females often mate multiply (Jennions & Petrie, 2000; Kvarnemo & Simmons, 2013) and may thus face selective pressures similar to those faced by males. While some of our selection indexes (I_s, I_{fss}, and I) only set upper limits to selection strength (Klug et al., 2010), and part of the variation can be stochastic, the pattern we found was the same when using the index that seems to better quantify sexual selection intensity *per se* (the Jones index; Henshaw et al., 2016). With this,

future studies should investigate which traits (whether behavioural, morphological, or physiological) most influence female and male success in dunnocks. In fact, by identifying these traits, we might open avenues of investigation to determine how females and males in the studied population choose mates, which might shed light on the absence of assortative mating patterns. After all, even if mating with a large partner occasionally confers fitness benefits, depending on environmental conditions, both females and males might exhibit traits other than body size (or condition) that better describe the fitness return these individuals provide to their partners.

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CRediT authorship contribution statement

Grazieli da Silva Cerqueira: Conceptualization; Data curation; Investigation; Validation; Visualization; Writing - original draft; and Writing - review & editing. **Eduardo S. A. Santos:** Data curation, Investigation; Funding acquisition; and Writing - review & editing. **Benedikt Holtmann:** Data curation, Investigation, Formal analysis, Writing - review & editing. **Carlos Esteban Lara:** Data curation, Investigation, Formal analysis, Writing - review & editing. **Shinichi Nakagawa**: Data curation, Writing - review & editing and Funding acquisition. **Renato C. Macedo-Rego:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Supervision; Validation; Visualization; Writing - original draft; and Writing - review & editing.

Declaration of Competing Interest

The authors have no competing interests.

Data availability

The raw data collected in the field have been archived within the SPI-Birds data hub (Culina et al., 2020) and are available upon request.

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