



Females pair with males larger than themselves in a socially monogamous songbird

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Mate choice is a key driver of evolutionary phenomena such as sexual dimorphism. Social mate choice is studied less often than reproductive mate choice, but for species that exhibit biparental care, choice of a social mate may have important implications for offspring survival and success. Many species make pairing decisions based on size that can lead to population-scale pairing patterns such as assortative and disassortative mating by size. Other size-based pairing patterns, such as females pairing with males larger than themselves, have been commonly studied in humans, but less often studied in nonhuman animal systems. Here we show that sexually size-dimorphic mountain chickadees, *Poecile gambeli*, appear to exhibit multiple self-referential pairing patterns when choosing a social mate. Females paired with males that were larger than themselves more often than expected by chance, and they paired with males that were slightly larger than themselves more often than they paired with males that were much larger than themselves. Preference for slightly larger males versus much larger males did not appear to be driven by reproductive benefits as there were no statistically significant differences in reproductive performance between pairs in which males were slightly larger and pairs in which males were much larger than females. Our results indicate that self-referential pairing beyond positive and negative assortment may be common in nonhuman animal systems.

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Mate choice is often studied in the context of reproductive or genetic partner choice because reproductive decisions can influence evolution when some individuals sire more offspring than others (e.g. reproductive skew; Johnstone, 2000). However, for species that form breeding pairs, choice of a social partner may be just as important for determining individual fitness (Rueger et al., 2016; Schaedelin et al., 2015). Individuals in socially monogamous pairings can obtain reproductive success by mating with their social partner or with extrapair partners, resulting in pairs typically raising offspring sired by one female and multiple males (Cockburn, 2006). Males typically sire at least some of the offspring they raise with their social mate (Brouwer & Griffith, 2019), so when biparental care is required to raise young, theory suggests that both males and females should contribute to raising offspring to maximize their individual fitness (Trivers, 1972). Furthermore, both

males and females should also experience strong selection to pair with a high-quality social mate to maximize their offspring's genetic quality and survival through high-quality parental care (Burley, 1983; Kokko & Johnstone, 2002; Trivers, 1972; but see Wang, Forstmeier, et al., 2017). Such preference for high-quality social mates is observed in multiple species of mouth-brooding cardinalfish where females preferentially pair with large males that can brood heavy clutches of eggs, and males preferentially pair with large females than can produce large eggs (Kolm, 2001, 2002; Rueger et al., 2016). Given the possibility for social mate choice to influence individual fitness, identifying the mechanisms that shape pairing decisions and measuring the consequences of these decisions have been two common themes in behavioural ecology (Bateson & Healy, 2005; Davies & Halliday, 1977).

One of the most common traits known to influence social partner choice is body size (Jiang et al., 2013). Larger body size is often associated with fecundity (Dittrich et al., 2018; Honěk, 1993; Kamler, 2005), competitive ability (Funghi et al., 2015; Haley et al., 1994; Tokarz, 1985) and quality (Backwell & Passmore, 1996; Ellis &

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Bercovitch, 2011; Vanpé et al., 2007), which can generate direct and indirect benefits for an individual who pairs with a large social mate. When individuals in a population share similar mate choice preferences for size, a population level pairing pattern can arise, such as positive or negative assortment (Arnqvist et al., 1996; Burley, 1983; Jiang et al., 2013). Positive assortment is characterized by a positive correlation between a male and female trait within pairs, such as large males paired with large females and small males paired with small females (Arnqvist et al., 1996; Rueger et al., 2016), whereas negative assortment is characterized by a negative correlation between a male and female trait within pairs (Jönsson, 1987; Petrie, 1983).

Assortative pairing patterns can arise through a multitude of preference and nonpreference mechanisms. Some species appear to exhibit mutual self-referential mate choice in which males and females prefer social mates similar to their own size (Rueger et al., 2016; Stulp et al., 2013; but see Burley, 1983), but assortment can also occur due to a combination of preferences for size and competitive ability (Crespi, 1989). For example, if males prefer large females, and large males exhibit the greatest competitive ability, this can result in positive assortment for size within pairs when large males outcompete small males to pair with large females (Davies & Halliday, 1977; Harari et al., 1999; Ridley, 1983). Alternatively, assortative pairing patterns may not reflect active mate choice but instead may be the result of confounding effects that are unrelated to mate choice (Holtmann & Dingemanse, 2021; Wang et al., 2019). For example, a recent analysis revealed that the strength of positive assortment in multiple systems was greatly reduced when controlling for observer effects and spatial and temporal autocorrelation in measurements of size (Wang et al., 2019). Further analyses have revealed that initial appearances of assortative mating in the wild can instead be driven by phenotypic plasticity to shared environments or processes that result in similar individuals settling in the same habitats (Edelaar et al., 2008; Holtmann & Dingemanse, 2021). Together, studies of wild populations and captive experiments have recently cast doubt on the abundance of assortative pairing patterns in animal mating systems, suggesting that many of these patterns might be over-exaggerated and susceptible to publication bias towards observations of positive and negative assortment rather than null results (Wang, Forstmeier, et al., 2017; Wang et al., 2019).

Less studied in nonhuman animal systems is the idea that males and females choose social mates based on self-referential rules beyond similarity and dissimilarity. For example, while humans often exhibit preferences for similar-sized mates, resulting in positive assortment for height (Courtiol et al., 2010; Stulp et al., 2013), humans also typically follow two additional self-referential pairing norms: the 'male-taller' norm and the 'male-not-too-tall' norm. The male-taller norm describes the tendency for women to prefer men taller than themselves and for men to prefer women shorter than themselves (Fink et al., 2007; Gillis & Avis, 1980; Stulp et al., 2013). The male-not-too-tall norm describes the further tendency for women to prefer men who are taller, but not too much taller, than themselves and vice versa (Salska et al., 2008; Stulp et al., 2013). Combined, these preferences result in a widespread pairing pattern in which tall men pair with tall women and short men pair with short women, and men are typically taller, but not too much taller, than women in heterosexual romantic relationships (Stulp et al., 2013).

Similar patterns appear in nonhuman animal systems in both male-larger (Dechaume-Moncharmont et al., 2013) and female-larger forms (Johannesson et al., 2008; Ng et al., 2019; Robertson, 1990), but understanding the mechanisms driving these patterns requires further investigation beyond identification of a pattern. For example, experimentation has revealed that male-larger and

female-larger patterns in nonhuman animals can be driven by preferences for slightly larger mates, similar to the male-not-too-tall norm in humans (López-Cortegano et al., 2020; Ng & Williams, 2014). However, preference for slightly larger mates is not the only mechanism that can lead to a male-larger or female-larger pattern. A male-larger pattern could also be driven by female preference for large males regardless of the female's body size. Fisherian-like female preferences for large males is common in reproductive partner choice (Backwell & Passmore, 1996; Ellis & Bercovitch, 2011; Vanpé et al., 2007), and if female preference for the largest male also occurs in social mate choice, this process could lead to patterns with the appearance of pairing relative to self without true self-referential choice. Furthermore, the importance of confounding effects in driving the appearance of self-referential choice has not been considered nearly as often as in relation to assortment, but confounding effects such as measurement error and plasticity to shared environments could also influence detection of self-referential pairing patterns beyond assortment. However, if self-referential pairing patterns are driven by mate choice and not confounding effects, then they could have important implications for the evolution and continuation of sexual size dimorphism in a population (López-Cortegano et al., 2020; Ng et al., 2019). These mechanisms may also influence the maintenance of sexual size dimorphism if reproductive performance differs in relation to how closely pairs follow the pattern (Robertson, 1990; Tryjanowski & Šimek, 2005). Comparing the reproductive performance of pairs that do and do not follow a specific pairing pattern may help reveal why such patterns persist (Kolm, 2002).

Here we investigated the presence of size-based pairing patterns in the mountain chickadee, *Poecile gambeli*, a small montane songbird native to the western United States and Canada. This species forms breeding pairs in the autumn, which persist through the winter and into the following breeding season (Ekman, 1989). Breeding pairs exhibit biparental care of young and are socially monogamous, meaning both males and females mate within their social pairing as well as outside of their social pair, resulting in around 30% of offspring being sired by extrapair matings (C. L. Branch, personal observation). Thus, most offspring in a nest are sired by one male and one female. Mountain chickadees exhibit male-biased sexual size dimorphism with overlapping male–female size distributions (Harrap & Quinn, 1995), meaning that any of the prior-mentioned size-based pairing patterns could occur. After confirming male-biased sexual size dimorphism in our population, we investigated whether mountain chickadees exhibit positive or negative assortment for size within breeding pairs and whether they exhibit additional self-referential pairing patterns. Given male-biased sexual size dimorphism, we predicted that females would pair with males larger than themselves and that this could lead to positive assortment for size if the largest females paired with the largest males, thus avoiding males smaller than themselves. Furthermore, we predicted that the presence of any size-referential pairing patterns may have arisen due to a reproductive advantage and therefore we expected pairings that followed the observed pattern, if any, to nest earlier, produce larger clutches and broods, and fledge heavier nestlings than those that did not follow the pattern. In each analysis we controlled for confounding effects that could bias measurements and influence pairing decisions when possible.

METHODS

Study System

We studied mountain chickadees over seven breeding and nonbreeding periods (years 2015–2021) at Sagehen Experimental

Forest (Sagehen Creek Field Station, University of California, Berkeley, CA, U.S.A.) in the Sierra Nevada Mountains, California, U.S.A. We classified seasons as running from September (postnatal dispersal and formation of winter social groups) through August and conducted research at two elevational sites (low: 1900 m; high: 2400 m; Kozlovsky et al., 2018). Adults and juveniles were captured from September through March using mist nets at established feeders, and breeding birds were captured by hand at nestboxes during the breeding season, which typically extends from May through August. We defined juveniles as individuals in their first year of life, including their first season as a breeder, and adults as any individuals older than 1 year (Branch et al., 2019). At the time of capture, we banded each bird with two coloured plastic bands and a coloured passive integrated transponder (PIT) tag. We banded nestlings 16 days posthatch with a metal U.S. Geological Survey numbered band, and if nestlings were recaptured after fledging, we banded them with an additional plastic colour band and a coloured PIT tag. At each individual's first postfledging capture, we measured wing length to the nearest 0.5 mm using flattened wing length (hereafter wing length) and aged birds that were not initially banded as nestlings as juvenile or adult using multiple plumage characteristics (Pyle, 1997). For all analyses of body size, we used wing length as a measure of size. We did not measure mass or tarsus length.

We sexed individuals through observations of breeding behaviours (e.g. only females incubate) and breeding physiology (e.g. males have large cloacal protuberances and females have brood patches). We identified breeding pair composition through observations of colour bands at nestboxes and PIT-tag reads at nestboxes equipped with radiofrequency identification (RFID) antennas (Bridge et al., 2019). Mountain chickadees included in our analyses paired only once within a breeding season, but pair membership sometimes changed between breeding seasons due to partner death or re-pairing with different mates (Pitera et al., 2021). We tracked the reproductive performance of pairs by monitoring first egg dates, clutch size, brood size and nestling mass during breeding using ca. 400 nestboxes across both elevations (e.g. Kozlovsky et al., 2018; Pitera et al., 2021). Brood size was defined as the number of nestlings that survived to day 16, and mean nestling mass was the mean mass of all nestlings in a nest at day 16. We also calculated the coefficient of variation of nestling mass within nests to obtain a proxy of variation in nestling quality as higher mass is often associated with increased survival probability in songbirds (Cleasby et al., 2010; Magrath, 1991).

Sexual Size Dimorphism

We quantified sexual size dimorphism at both the population level and within breeding pairs. At the population level, we compared wing lengths of male and female breeders using a linear model with wing length as the response variable, and sex, elevation and season banded as fixed effects. To quantify sexual size dimorphism within breeding pairs, we ran the same linear model but included pair identity as a random effect to constrain comparisons of wing length to within pairs using the 'lmer' command in the R package 'lme4' (Bates et al., 2015). In both models, we included season banded as a fixed effect because different climate conditions across seasons might lead to variation in wing length (Potti, 2000), and different observers across seasons could lead to variation in wing length measurements (Wang et al., 2019). We did not record the identity of the researcher conducting each measurement, so we cannot directly control for observer identity. For these analyses and those in the Pairing Based on Size section below, each breeding pair was represented only once in our data set, even if they paired together in multiple years. Individual birds could be present in the

data set multiple times if they switched mates across years, but we associated each pair with the first year we detected them breeding together, likely the first year they paired. Our data set included 466 pairs, including 326 males and 316 females.

Pairing Based on Size

We tested for positive and negative assortment for size using two methods. First, we correlated male and female wing length within pairs using a Pearson's correlation to match the methods of classic studies of assortment (reviewed in Jiang et al., 2013). Second, we constructed a linear model with male wing length as the response variable and female wing length and the season the male was banded as fixed effects. We also controlled for seasonal variation in the female's wing length measurement by centering the female wing length fixed effect on the season the female was banded using within-subject centering (Van de Pol & Wright, 2009). We ran the reverse of this model with female wing length as the response variable as well. Elevation (site) was not an important predictor of wing length for either sex in the sexual size dimorphism models (Appendix), so we did not include it as a fixed effect here. We calculated an R^2 value for the linear model using the 'performance' package in R (Lüdtke et al., 2021).

We tested for the presence of additional size-based pairing patterns by comparing our observed pairing relationships to permutations of the observed data that represented pairing scenarios that were random with respect to wing length. Preliminary analyses suggested that females tended to pair with males larger than themselves, so we first tested whether this male-larger pattern occurred more often than expected by chance. We calculated the difference in wing length within pairs by subtracting the female's wing length from the male's wing length, then we permuted the observed data set by swapping the identities of males and females across pairs. We conducted these permutations in a stepwise fashion by employing increasingly restrictive randomizations that account for possible confounds. We first restricted swaps to within sex, then added season banded, elevation (site), season bred and age at banding (juvenile, adult, unknown) categories, resulting in five separate permutation analyses. We restricted swaps to within season banded because previous analyses showed that average wing length varied across seasons (Appendix) and we restricted swaps to within elevations because no individuals have ever been recorded breeding at both elevations at our site. Both restrictions reduced the possibility that differences in scale could influence our results (Moura et al., 2021; Rolán-Alvarez et al., 2015). Restricting swaps to within the season that pairs bred meant that our permutations represented possible pairings that could have taken place when pairs were forming but did not, and restricting swaps to within the age at banding reduced the possibility that any undetected age effect influenced wing length. Including this final category greatly reduced our pool of possible swaps for many individuals, so we report results below from the fourth permutation step that limited swaps to within sex, season banded, elevation and season bred categories. Results from the remaining permutations can be found in the Appendix. We ran each permutation 1000 times to create 1000 randomized data sets, then compared the percentage of female-larger pairings in the observed data to the distribution of the percentage of female-larger pairings in the randomized data sets. We calculated a P value for each comparison by determining the number of times the observed percentage was greater than the randomized values, then divided by the number of randomizations (Farine, 2017).

After finding support for the male-larger pattern, we tested whether female preference for a slightly larger male (male-not-too-large pattern) or the largest male was responsible for the male-

larger pattern. For this test we focused specifically on pairs where the male was larger than the female. We first split the observed data in half based on the median difference in wing length of pairs in which the male was larger than the female (4 mm) and categorized any value less than or equal to the median as male slightly larger than the female ($N = 234$ pairs), and any value greater than the median as male much larger than the female ($N = 181$ pairs). Splitting the data in the opposite way, including pairs less than the median in the male slightly larger category and pairs greater than or equal to the median in the male much larger category, returned the same results. We repeated the same stepwise permutation procedure as above but removed pairs in which the female was larger than the male and pairs with equal wing lengths from each randomized data set before comparing the percentage of pairs in which the male was slightly larger and much larger than the female to the percentage of pairs in the same categories in the randomized data sets. We calculated P values as above.

Reproductive Consequences of Size Differences within Pairs

We investigated the potential adaptive benefits of the male-not-too-large pattern by comparing the reproductive performance of pairs in which the male was slightly larger and much larger than the female. Our sample size of reproductive performance data for pairs in which the female was larger than the male was small compared to the other categories ($N = 22$ pairs for female larger than male with all breeding data versus 266 pairs for male slightly larger and 198 pairs for male much larger than female), so we did not include female-larger pairs in these analyses. We tested whether pairs in which the male was slightly larger and much larger than the female differed in five breeding performance variables: first egg date, clutch size, brood size, mean nestling mass and the coefficient of variation of nestling mass. We modelled each breeding variable separately and included pair difference in wing length as a categorical fixed effect (two levels: male slightly larger and male much larger) in each model. We also included elevation (two levels: high and low), season (seven levels) and parent age (four levels: both adults, adult male and juvenile female, juvenile male and adult female, both juveniles) as fixed effects in each model because each of these variables are associated with breeding performance in this system (Pitera et al., 2021). We included an interaction between elevation and season, as the difference in reproductive performance between elevations sometimes varies across seasons (Kozlovsky et al., 2018). We also tested for an interaction between pair difference in wing length and elevation and an interaction between pair difference in wing length and season by comparing models with and without these interactions using the 'anova' command in base R (R Core Team, 2021). Neither of the interactions including the pair difference in wing length variable improved upon the model without the interaction ($P > 0.05$), so we report results from models without these interactions. We included pair identity (ID) as a random effect to control for pairs that bred in multiple years.

We employed linear mixed models to model first egg date, mean nestling mass and the coefficient of variation of nestling mass in the R package 'lme4' (Bates et al., 2015). Coefficient of variation of nestling mass was log-transformed prior to modelling to improve residual fit. For both clutch size and brood size, we used a generalized linear mixed model with a generalized Poisson distribution and log link in the R package 'glmmTMB' to account for underdispersion in both data sets and to improve residual fit (Brooks et al., 2017; Joe & Zhu, 2005). When modelling clutch size, we ran models with and without including first egg date as a fixed effect as clutch size is sometimes associated with lay date in this species (Kozlovsky et al., 2018). These models returned the same

significance of results, so we report results from the model with first egg date as a fixed effect. We tested the residual fit of all models using the R package 'DHARMA' (Hartig, 2018).

Wing Length as a Measure of Body Size

For some species, wing length is known to change with age (Merom et al., 1999; Pienkowski & Minton, 1973). We have not conducted a longitudinal study on the relationship between age and wing length in this system, but when we ran both sexual size dimorphism models with wing length as the response variable and age (juvenile versus adult) as a fixed effect, we found no significant effect of age (Appendix). Therefore, we report results from sexual dimorphism models without age, which allowed us to use a larger data set that included individuals with unknown ages. To further control for the possibility that wing length can change with time, we also ran the sexual size dimorphism and pairing analyses on a more conservative subset of data that only included pairs in which both individuals were measured for wing length in the same season they paired. This ensured that wing length and pair identities were recorded during the same moult period, as adult mountain chickadees moult once per year following the breeding season in August and September and juveniles retain their flight feathers grown in the nest until after their first adult breeding season (Pyle, 1997). Analyses on this subset of data produced the same results as those using the full data set. We report results from the full data set in the main text and report results from the conservative analysis in the Appendix. All analyses were conducted in R version 4.1.1 (R Core Team, 2021).

We took a female-centric view when describing analyses and results because social mate choice is likely more important for females than for males in this species (e.g. Branch et al., 2015, 2019). In contrast to many frogs (Davies & Halliday, 1977; Fan et al., 2013), insects (Honek, 1993) and fish (Kamler, 2005), fecundity of female birds is less often explained by size (Wang, Kempnaers, et al., 2017) and more often explained by other factors, such as breeding date, food availability and experience (Kozlovsky et al., 2018; Mills et al., 2008; Pitera et al., 2021), so we think it is unlikely males would benefit greatly from pairing with a female of a specific size (but see Johnston & Johnson, 1989).

Ethical Note

All methods and procedures were approved by the University of Nevada Reno (UNR) Institutional Animal Care and Use Committee (IACUC) in accordance with UNR IACUC protocols 20-11-1103, 20-06-1014 and 20-08-1062, under California Department of Fish and Wildlife Permit SC-193630001-20007-001. We banded both adults and nestlings in the field and reduced stress by removing birds quickly from mist nets and releasing them immediately after minimal measurements were completed. We banded nestlings near nestboxes to limit handling time. We have used these methods previously with no adverse effects (Kozlovsky et al., 2018; Pitera et al., 2021).

RESULTS

Male mountain chickadees exhibited significantly longer wing lengths than females at the population level ($N = 642$ individuals; mean $\pm$ SE wing length: males: 71.5 ± 0.14 mm; females: 67.9 ± 0.18 mm; $F_{1,633} = 598.47$, $P < 0.001$; Fig. 1a, Appendix, Table A1) and within breeding pairs ($N = 466$ pairs; mean $\pm$ SE wing length: males: 71.5 ± 0.12 mm; females: 67.9 ± 0.15 mm; $F_{1,469} = 947.16$, $P < 0.001$; Fig. 1a, Appendix, Table A1), but male and female wing length distributions did overlap (Fig. 1a). We found no

evidence of positive or negative assortment for size within pairs when using a Pearson's correlation ($r_{464} = 0.05$, $P = 0.269$) or when using a linear model with either male wing length as the response variable ($F_{1,458} = 0.14$, $P = 0.712$; Fig. 1b, Appendix, Table A2) or female wing length as the response variable ($F_{1,458} = 0.34$, $P = 0.562$; Appendix, Table A2). However, we did observe a pairing pattern that indicated pairing relative to self: out of 466 unique pairs, we observed 21 pairs where the female had a longer wing length than the male, 30 pairs where the female and male were equal in wing length and 415 pairs where the male had a longer wing length than the female. When controlling for sex, season banded, elevation (site) and season bred, our permutation analysis testing the male-larger pattern revealed that the observed number of female-larger pairings was significantly fewer than expected if males and females paired randomly with respect to wing length (observed = 4.5% of pairings; expected = 6.6% of pairings; $P = 0.004$; Fig. 2a, b, Appendix, Table A4). Within male-larger pairs, our permutation analysis testing the male-not-too-large pattern revealed more pairs in which the male was slightly larger than the female than expected (observed = 56.4% of male-larger pairings, expected = 49.7%, $P < 0.001$; Fig. 2a, c, Appendix, Table A5) and fewer pairs in which the male was much larger than the female than expected if males and females paired randomly (observed = 43.6% of male-larger pairings, expected = 50.3%, $P < 0.001$; Fig. 2a, d, Appendix, Table A5). All other permutation analyses returned nearly the same results no matter the restrictions we placed on swaps, and the level of significance did not exhibit an obvious directional shift as we increased the number of restrictions in each permutation (Appendix, Tables A4, A5, Figs A1, A2). Furthermore, the conservative analyses run on pairs that were measured in the same year they paired returned the same results for the sexual dimorphism model (Appendix, Table A6), the assortment analysis (Appendix, Table A7) and the pairing permutations (Appendix, Fig. A3) when controlling for sex, season banded, elevation and season bred. We found no statistically significant differences in any of the measured reproductive

parameters between pairs that followed the male-not-too-large pattern and those that did not (Table 1, Appendix, Fig. A4).

DISCUSSION

We investigated the presence of size-based pairing patterns in mountain chickadees to better understand the mechanisms underlying social mate choice related to size in animal systems. Social mate choice in this species was not consistent with positive or negative assortment for size based on wing length, but mountain chickadees did appear to exhibit a different form of self-referential mate choice where females paired with males larger than themselves more often than expected by statistical chance. This pattern is similar to the male-taller norm in humans (Gillis & Avis, 1980; Stulp et al., 2013) and the male-larger pairing pattern in other animals (Dechaume-Moncharmont et al., 2013). Further comparison of natural pairings to those possible under random pairing scenarios revealed that the male-larger pattern was consistent with the hypothesis that females prefer pairing with a slightly larger male rather than a much larger male, similar to the male-not-too-tall pattern also commonly observed in humans (Salska et al., 2008; Stulp et al., 2013) and the male slightly larger than female pairing pattern in other animals (López-Cortegano et al., 2020; Ng & Williams, 2014). Preferences for slightly larger individuals can at times secondarily result in positive assortment for size (López-Cortegano et al., 2020), but our study matches previous reports that suggest mating preferences can exist in the absence of assortative mating (Wang et al., 2019). Our observed lack of positive assortment for size also suggests that the male-not-too-large pattern we observed was not likely driven by Fisherian-like preferences for large mates. A female preference for large males without self-referential choice could result in a male-not-too-large pattern if large females can outcompete small females to pair with large males, but such a phenomenon would also presumably result in positive assortment for size. Instead, female mountain chickadees exhibited a statistical tendency to pair less often with males

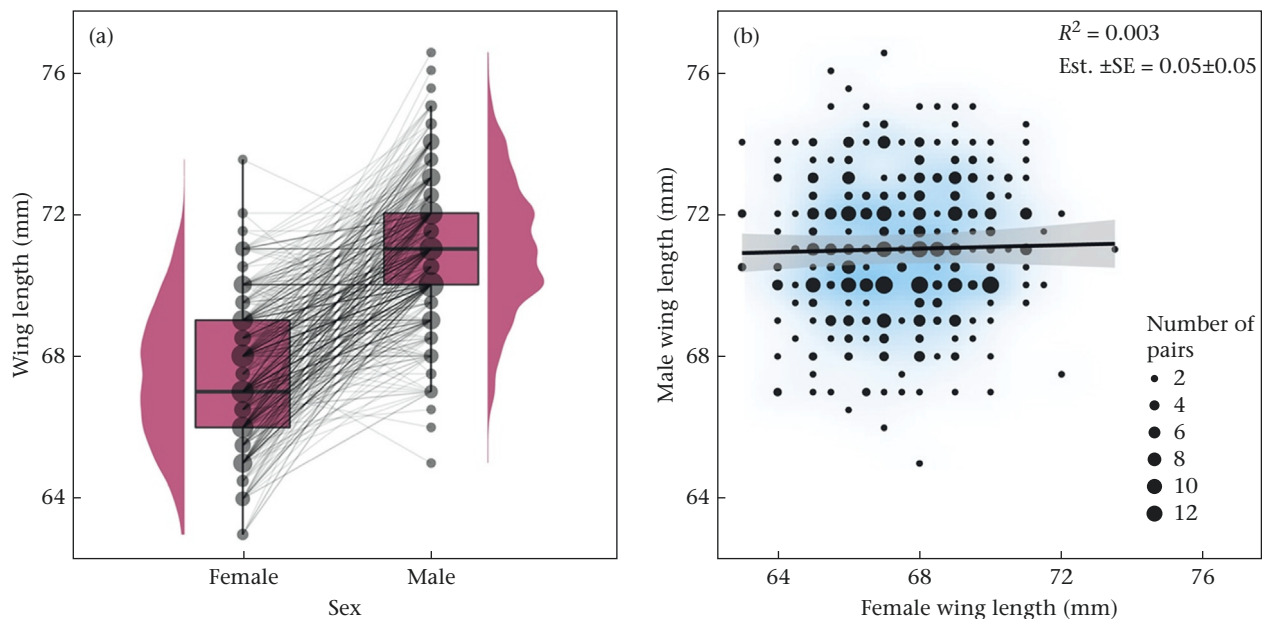


Figure 1. Wing length relationships within mountain chickadee breeding pairs. (a) Sexual size dimorphism and comparison of wing lengths within breeding pairs. Box plots show female and male wing lengths, sizes of points show relative sample sizes for each wing length, and lines across box plots connect breeding pairs. (b) Correlation of male and female wing length within breeding pairs. Line shows model prediction for a linear model where female wing length was not centred on season banded and shading shows 95% confidence intervals. Points show raw data and are sized relative to the number of pairs at each value. Background shows density of pairs, with darker regions containing more pairs at those values. R^2 , estimate and SE values are presented for the female wing length fixed effect.

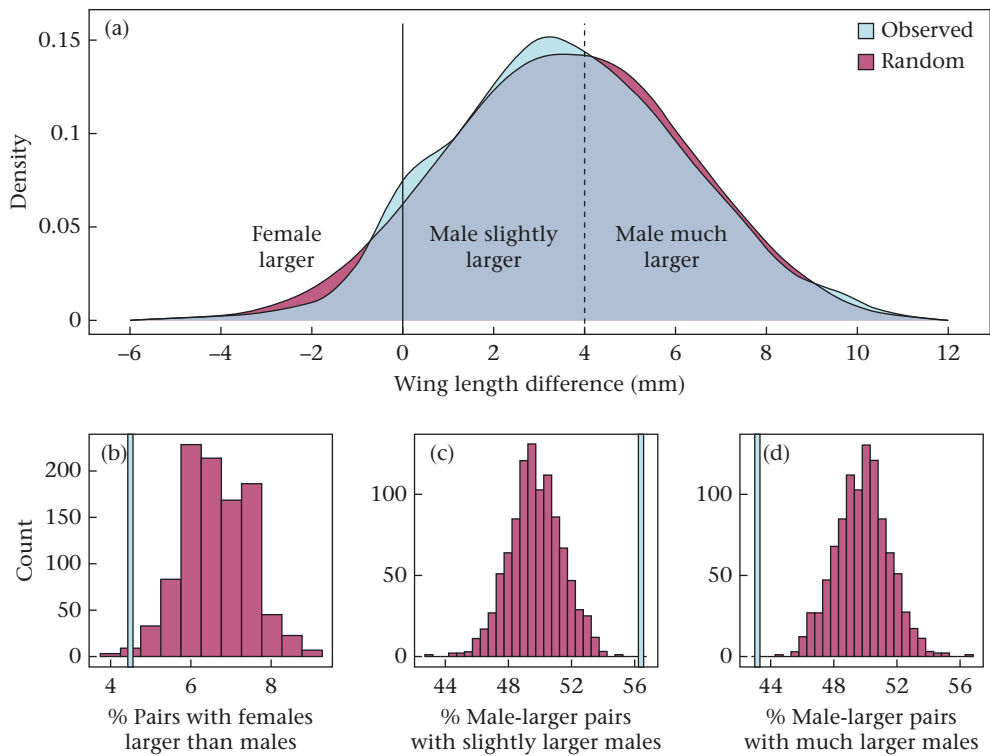


Figure 2. Results from permutation tests to test the male-larger and the male-not-too-large pairing patterns in mountain chickadees. (a) Density plot for the distribution of observed differences in wing length within pairs in relation to the average random distribution from the permutation tests. The dashed line shows the median wing length difference for male-larger pairs. (b) Observed percentage of female-larger pairs (blue line) in relation to the distribution of percentages from the permutations ($P = 0.004$). (c) Observed percentage of pairs in which the male was slightly larger than the female (blue line) in relation to the distribution of percentages from the permutations ($P < 0.001$). (d) Observed percentage of pairs in which the male was much larger than the female (blue line) in relation to the distribution of percentages from the permutations ($P < 0.001$). Note (d) is the mirror image of (c).

Table 1
Analysis testing whether mountain chickadee pairs that followed the ‘male not too large’ pattern (male slightly larger than the female) and pairs that did not (male much larger than the female) differed in reproductive performance

Breeding performance response variable	N (pairs)	Pair type fixed effect			
		Estimate	SE	χ^2	P
First egg date (days)	296 male slightly larger	0.42	0.51	0.67	0.412
	223 male much larger				
Clutch size (eggs)	294 male slightly larger	0.01	0.01	0.27	0.604
	219 male much larger				
Brood size (chicks)	272 male slightly larger	0.01	0.02	0.44	0.507
	201 male much larger				
Mean nestling mass (g)	267 male slightly larger	0.01	0.08	0.01	0.962
	198 male much larger				
Coefficient of variation of nestling mass	266 male slightly larger	−0.02	0.04	0.46	0.498
	198 male much larger				

Sample sizes differ for each breeding performance response variable due to nest failure and mortality during nesting. Parameter estimates are presented for each breeding performance response variable and represent the modelled mean difference between pairs in which the male was slightly larger than the female and pairs in which the male was much larger than the female. See Fig. A4 for plots of each breeding performance variable. Chi-square statistics come from type III Wald chi-square tests run in the R package ‘car’ (Fox & Weisberg, 2019).

that were much larger than themselves and did not exhibit positive assortment for size within pairs. Importantly, both the male-larger pattern and the male-not-too-large pattern remained when controlling for multiple confounding factors. Despite the statistical strength of the male-larger pattern and the male-not-too-large pattern we observed, it is less clear how biologically significant these patterns are, especially since there were many pairs that did not follow these norms (Fig. 2a). For species such as the Australian frog, *Uperoleia laevis*, self-referential mate choice has likely been selected for due to the reproductive benefits females gain by pairing with males slightly

smaller than themselves. Females of this species who paired with a male that was 70% of their size had more eggs fertilized than females that paired with a larger male (Robertson, 1990). We observed no obvious reproductive differences between pairs that did and did not follow the male-not-too-large pattern, indicating that size-based pairing patterns are unlikely to be driven by a reproductive advantage in mountain chickadees. This may be unsurprising because fecundity is likely less related to size in birds (Wang, Kempnaers, et al., 2017; but see Johnston & Johnson, 1989), compared to other taxa such as insects and fish, where fecundity is often directly proportional to body size (Dittrich et al., 2018; Honěk,

1993; Kamler, 2005). Furthermore, most fecundity-based hypotheses for mate choice suggest males should pair with large females (e.g. Davies & Halliday, 1977), but the patterns we observed involved females pairing with larger males. It is possible that females obtain nonreproductive benefits by pairing with a larger male, but the presence of the male-not-too-large pattern suggests females may experience costs when paired to a male who is too large. Alternatively, the patterns we observed could be driven by unmeasured confounding effects that could lead to suboptimal mate choice. We speculate on the identity of these potential benefits and costs and other confounding effects below to help guide possible future research directions into the size-based pairing decisions of birds.

Benefits and Costs of Social Mate Choice

There are many possible benefits a female may gain by pairing with a male larger than herself. Size is often associated with intraspecific dominance and competitive ability (Funghi et al., 2015; Haley et al., 1994; Tokarz, 1985), which can result in larger individuals obtaining the highest quality territories (Candolin & Voigt, 2001; Fretwell, 1969). If a female pairs with a male larger than herself, she may gain access to a higher quality breeding territory than she could gain by pairing with a male smaller than herself. Furthermore, in larger bird species, differences in male and female size can benefit both sexes when a pair's difference in size is great enough that they are able to specialize on different prey items (Tryjanowski & Šimek, 2005). However, mountain chickadees weigh only 10–13 g (Harrap & Quinn, 1995), and the largest difference in wing length we observed within a pair was 11 mm. Due to this comparatively minor difference in wing length for an already small bird, we think it is unlikely that size differences within pairs allowed male and female mountain chickadees to focus on different food sources. A different possibility is size may be a signal of individual quality or condition (Burley, 1983; Crespi, 1989; Kolm, 2001; Rueger et al., 2016) or be correlated with another signal of individual quality (Johnstone et al., 1996), and thus females that pair with males larger than themselves may obtain indirect genetic benefits through their offspring. However, while most of these hypotheses could be viable explanations for the male larger pattern, each would also suggest a female could maximize her direct or indirect benefits by pairing with the largest possible male, which is contrary to the pattern we observed. Instead, we observed that females exhibit a tendency to pair with males slightly larger than themselves rather than the largest possible male, suggesting that pairing with a much larger male may be costly.

Sexual conflict, such as traumatic insemination in some insects (Morrow & Arnqvist, 2003; Tataric et al., 2014) and forced copulation in many waterfowl (Brennan et al., 2010), could make mating with a much larger male harmful to a female in some species. However, songbirds mate via a 'cloacal kiss' that requires no intromission and is unlikely to cause any internal or external damage, no matter the male's size (Briskie & Montgomerie, 2001; Herrera et al., 2013). Furthermore, we have never observed male mountain chickadees attacking females, so sexual conflict is unlikely to explain the presence of the male-not-too-large pattern in this species. Alternatively, the process of searching for the best possible male could be costly due to time and energy invested in searching or increased predation risk when travelling through potentially unfamiliar habitats (Bonte et al., 2012; Yoder et al., 2004). This hypothesis also seems unlikely to apply to mountain chickadees because dispersal in our population occurs over fairly short distances (ca. 1 km on average; C. L. Branch & V. V. Pravosudov, personal observations), meaning there may be little energetic cost to searching for a mate. However, while dispersal distance

appears to be short, mountain chickadees may experience selection to disperse quickly and early to pair prior to the beginning of winter.

Mountain chickadees in our population are highly sedentary, even during harsh winter conditions (Kozlovsky et al., 2018). To survive this harsh environment, they cache seeds of various pine species on a territory throughout the autumn and use these caches during the winter (e.g. Pravosudov & Roth, 2013). Pairs form in the autumn and then spend the winter on a territory together where they have cached seeds (Ekman, 1989), meaning juveniles pairing for the first time and older individuals replacing their previous mate may need to pair quickly to establish a winter territory with their mate where they can cache. Once pine cones open and chickadees have access to the seeds, many other animals also compete for the seeds (Vander Wall, 1990). Thus, an individual that pairs late and begins caching late might not have enough food to last the winter during a season when cone abundance is low. This potential push to disperse and pair quickly could influence the optimality of an individual's search efforts if chickadees are rushed in selecting a social mate, meaning males and females may settle for a suitable social mate, rather than an optimal social mate if dispersal timing overlaps with timing of pine cone opening and food caching. Rushed pairing decisions could also occur in the spring for individuals that lost a mate over the winter, or in the autumn if winter flocks contain few juveniles or adults without a mate, meaning a new bird joining a flock may have few pairing options, which could also influence the optimality of pairing. Similar patterns of less-than-optimal pairing have been observed in fish where the ecological importance of being paired is thought to outweigh optimal mate choice (Taborsky et al., 2009). The fact that we did observe pairing patterns in relation to size despite the possibility for limited mate choice opportunities is interesting because size does not appear to influence social mate choice in all bird species (Wang, Kempenaers, et al., 2017; Wang et al., 2022). Further research investigating the timing of dispersal and its influence on mate choice opportunities may provide helpful insights into the mechanisms driving the pairing patterns we observed.

Rationality of Social Mate Choice

Thus far we have assumed that both female and male mountain chickadees behave rationally when choosing a social mate, even if it is possible that they are somewhat rushed in making mate choice decisions. However, in a crowded environment, it is possible for both sexes to behave irrationally. In mate choice experiments, rationality is often investigated as transitivity, represented by this relationship: if $A > B$ and $B > C$, then $A > C$ (Lea & Ryan, 2015; Tversky, 1969). While this pattern has been observed in some animal systems when individuals are presented with only two mates to choose from (Arbuthnott et al., 2017; Dechaume-Moncharmont et al., 2013), transitivity can break down when females are simultaneously presented with three or more males that differ on multiple axes, possibly due to the decoy effect (Lea & Ryan, 2015). The decoy effect describes the phenomenon in which the presence of a third option can lead to an irrational choice of a low-quality option even when a high-quality option is available (Tsetsos et al., 2010; Tversky, 1969). For example, a female mountain chickadee may value large size over plumage traits when choosing a social mate. If presented with a much larger male that has low-quality plumage and a slightly larger male with high-quality plumage, the female, valuing large size over plumage, should select the larger of the two males. However, when a third male is introduced that is smaller than the female and has medium-quality plumage, this may cause the female to reconsider her initial decision even though she has no interest in the third male. As a result, she might choose the second

male, which appears a much better choice than the third male, even though the first male matches her preferences more closely than the other two.

Similar examples of the decoy effect have been observed in Túngara frogs, *Physalaemus pustulosus*, in a mate choice context (Lea & Ryan, 2015), in rufous hummingbirds, *Selasphorus rufus*, in a foraging context (Bateson et al., 2003) and in humans in a gambling context (Tversky, 1969). Mountain chickadees form breeding pairs in the autumn when they also form social groups that last through the winter (Ekman, 1989), meaning females and males could be searching for mates in a crowded environment with many options, creating the setting for both males and females to potentially behave irrationally due to the decoy effect. This possibility for irrationality could explain why some females pair with males who are only slightly larger than themselves, rather than pairing with the largest available male. Alternatively, size might be a less valued trait in relation to plumage or cognitive traits, resulting in less selective preferences for the most optimally sized males. Further research including mate choice experiments would be required to determine whether transitivity and the decoy effect occur in this species and whether females value size differently from other traits.

Conclusion

We found statistical support for two self-referential pairing patterns in mountain chickadees: the male-larger pattern describes the tendency for females to pair with a male larger than themselves, and the male-not-too-large pattern shows the tendency for females to pair with a male who is not too much larger than themselves. Combined, these patterns suggest there may be benefits to a female pairing with a larger male, but costs, or at least a lack of a benefit to a female pairing with a much larger male. We found no significant differences in reproductive performance between pairs where the male was slightly larger versus much larger than the female, suggesting these preferences may not be driven by differences in reproductive performance. Identifying the adaptive benefits of these patterns is difficult without targeted experiments, but one possibility is that females gain access to higher-quality territories by pairing with a larger male because size is often associated with dominance and territory quality. This benefit to females could lead to higher overwinter survival for females that pair with a high-quality male in the autumn. Alternatively, multiple factors of this species' biology may result in less-than-optimal mate choice, such as the decoy effect when searching for a mate in a potentially crowded environment, or a rush to pair as soon as possible and settle on a territory quickly in order cache enough pine seeds to survive the winter.

A wide range of species exhibit sexual size dimorphism, but identifying the underlying mechanism driving one sex to be larger than another is often difficult (Blanckenhorn, 2005; Janicke & Fromonteil, 2021; Ng et al., 2019). Our observation of the male-larger pattern and the male-not-too-large pattern could help explain the presence of male-biased sexual size dimorphism in mountain chickadees. While we did observe some female-larger pairs, the overall pattern of females pairing with males larger than themselves suggests that small males may be at a disadvantage in obtaining a mate. If small males are less able to find a mate, female preference for males larger than themselves could help to maintain male-biased sexual size dimorphism in this population, but further research would be required to resolve this hypothesis.

Our study focused on a natural population of birds making pairing choices in an undisturbed habitat over 7 years, meaning our observations are likely as true to natural systems as possible. However, our study is also limited because we were not able to

control all possible confounds, meaning some questions remain about the importance of confounding factors and their influence on pairing decisions in birds. Further experimental research assessing these pairing patterns through presentation of individuals of alternating sizes could help reveal the underlying mechanisms, the confounds influencing these decisions and the evolutionary implications of these patterns.

Author Contributions

Joseph F. Welklin: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Roles/Writing – original draft. **Carrie L. Branch:** Conceptualization, Data curation; Formal analysis; Investigation; Methodology; Writing – review & editing. **Angela M. Pitera:** Data curation; Investigation; Writing – review & editing. **Benjamin R. Sonnenberg:** Data curation; Investigation; Writing – review & editing. **Lauren M. Benedict:** Data curation; Investigation; Writing – review & editing. **Virginia K. Heinen:** Data curation; Investigation; Writing – review & editing. **Dovid Y. Kozlovsky:** Data curation; Investigation; Writing – review & editing. **Vladimir V. Pravosudov:** Conceptualization, Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Writing – review & editing.

Data Availability

All data and scripts are available through Figshare: https://figshare.com/articles/dataset/Code_and_data_for_Females_pair_with_males_larger_than_themselves_in_a_socially_monogamous_songbird/21382281.

Declaration of Interest

None.

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Appendix

Table A1

Analysis of sexual dimorphism in wing length at the population level and within mountain chickadee breeding pairs

Comparison	N	Fixed effect	Estimate	SE	t	P
Population level	642 individuals	Intercept	67.92	0.18	376.42	<0.001
		Sex (Male)	3.49	0.14	24.25	<0.001
		Elevation (Low)	<0.01	0.15	0.01	0.997
		Season banded 2015–2016	0.18	0.25	0.72	0.474
		Season banded 2016–2017	−1.18	0.24	−4.91	<0.001
		Season banded 2017–2018	−0.55	0.24	−2.34	0.020
		Season banded 2018–2019	−0.78	0.26	−3.04	0.003
		Season banded 2019–2020	0.072	0.27	0.27	0.789
		Season banded 2020–2021	−0.33	0.27	−1.22	0.222
		Intercept	67.88	0.15	459.33	<0.001
Within pairs	446 pairs	Sex (Male)	3.59	0.12	468.21	<0.001
		Elevation (Low)	−0.19	0.12	−1.63	0.103
		Season banded 2015–2016	0.32	0.21	1.57	0.117
		Season banded 2016–2017	−1.24	0.19	−6.64	<0.001
		Season banded 2017–2018	−0.47	0.19	−2.54	0.011
		Season banded 2018–2019	−0.70	0.21	−3.33	0.001
		Season banded 2019–2020	0.24	0.24	0.993	0.321
		Season banded 2020–2021	−0.21	0.25	−0.812	0.417
		Random effects	Variance	SD		
		Pair ID	0.05	0.21		
		Residual	3.13	1.77		

Results from two linear models are shown, one analysing difference in wing length (mm) at the population level and one analysing differences in wing length within pairs using pair identity (ID) as a random effect. Estimates are presented for the low-elevation site. Season banded is in comparison to the 2014–2015 season. Seasons run from September through August.

Table A2

Test of whether mountain chickadees exhibit positive or negative assortment for size within pairs

Response variable	N	Fixed effect	Estimate	SE	t	P
Male wing length	446 pairs	Intercept	71.33	0.16	444.56	<0.001
		Female wing length	0.01	0.04	0.22	0.826
		Season banded 2015–2016	0.68	0.27	2.50	0.013
		Season banded 2016–2017	−1.29	0.25	−5.18	<0.001
		Season banded 2017–2018	−0.33	0.26	−1.24	0.214
		Season banded 2018–2019	−1.08	0.27	−4.04	<0.001
		Season banded 2019–2020	0.19	0.31	0.60	0.551
		Season banded 2020–2021	0.27	0.36	0.73	0.465
Female wing length	446 pairs	Intercept	67.89	0.19	360.35	<0.001
		Male wing length	0.01	0.05	0.22	0.826
		Season banded 2015–2016	−0.16	0.30	−0.55	0.586
		Season banded 2016–2017	−1.30	0.27	−4.77	<0.001
		Season banded 2017–2018	−0.68	0.27	−2.55	0.011
		Season banded 2018–2019	−0.35	0.32	−1.09	0.276
		Season banded 2019–2020	0.242	0.35	0.69	0.491
		Season banded 2020–2021	−0.67	0.35	−1.92	0.055

Results from two linear models are shown, one with male wing length (mm) as the response variable and one with female wing length as the response variable. The opposite-sex fixed effect was centred on season to remove across-season variation. The season banded fixed effect shows the comparison of each season to the 2014–2015 season. Seasons run from September through August.

Table A3

Analysis of sexual dimorphism in wing length at the population level and within mountain chickadee breeding pairs, with age included as a fixed effect

Comparison	N	Fixed effect	Estimate	SE	t	P
Population level	409 individuals	Intercept	67.87	0.21	328.48	<0.001
		Sex (Male)	3.55	0.17	20.43	<0.001
		Age (Juvenile)	−0.08	0.23	−0.35	0.730
		Elevation (Low)	0.11	0.18	0.61	0.538
		Season banded 2015–2016	−0.10	0.28	−0.35	0.725
		Season banded 2016–2017	−1.52	0.32	−4.73	<0.001
		Season banded 2017–2018	−0.59	0.28	−2.14	0.033
		Season banded 2018–2019	−0.72	0.37	−1.95	0.052
		Season banded 2019–2020	0.85	0.40	2.15	0.033
		Season banded 2020–2021	0.03	0.39	0.08	0.936
Within pairs	196 pairs	Intercept	67.86	0.21	325.50	<0.001
		Sex (Male)	3.55	0.17	20.49	<0.001
		Age (Juvenile)	−0.06	0.26	−0.24	0.812
		Elevation (Low)	−0.20	0.19	−1.02	0.311
		Season banded 2015–2016	0.15	0.28	0.53	0.598
		Season banded 2016–2017	−1.49	0.30	−4.92	<0.001
		Season banded 2017–2018	−0.36	0.27	−1.33	0.183
		Season banded 2018–2019	−0.62	0.40	−1.56	0.119
		Season banded 2019–2020	0.79	0.45	1.77	0.078
		Season banded 2020–2021	−0.48	0.46	−1.03	0.303
		Random effects	Variance	SD		
		Pair ID	0.13	0.35		
		Residual	2.79	1.67		

Results from two linear models are shown, one analysing difference in wing length (mm) at the population level and one analysing differences in wing length within pairs, using pair identity (ID) as a random effect. The season banded fixed effects are shown in comparison to the 2014–2015 season. Seasons run from September through August. A similar analysis without age as a fixed effect is presented in the main text and in [Table A1](#) with a larger sample size.

Table A4

Results from the permutation analysis used to test whether the number of pairings in which the female was larger than the male differed from expected by chance

Permutation	Restrictions	Range of random values	P	Difference of observed from expected percentage
1	Sex	3.65–9.87%	0.004	−2.34%
2	Sex, season banded	4.29–9.87%	0.003	−2.14%
3	Sex, season banded, elevation	3.86–9.23%	0.004	−2.15%
4	Sex, season banded, elevation, season bred	3.86–9.23%	0.004	−2.14%
5	Sex, season banded, elevation, season bred, age banded	4.08–9.66%	0.005	−1.96%

The observed percentage of pairings in which the female was larger than the male was 4.5%. See [Fig. A1](#) for histograms from each permutation.

Table A5

Results from the permutation analysis used to test whether females paired with slightly larger males more often than expected by chance

Permutation	Restrictions	Range of random values	P	Difference of observed from expected percentage
1	Sex	44.74–55.75%	<0.001	+6.40%
2	Sex, season banded	45.24–55.64%	<0.001	+6.17%
3	Sex, season banded, elevation	44.79–55.56%	<0.001	+5.79%
4	Sex, season banded, elevation, season bred	43.23–55.05%	<0.001	+6.64%
5	Sex, season banded, elevation, season bred, age banded	44.79–56.14%	<0.001	+6.38%

The observed percentage of pairings in which the male was slightly larger than the female was 56.4%. Results from permutations for pairings in which the male was much larger than the female were the mirror image of these results. See [Fig. A2](#) for histograms from each permutation.

Table A6

Analysis of sexual dimorphism within mountain chickadee breeding pairs using the conservative data set that only included individuals paired in the same year their wing length was measured

Comparison	N	Fixed effect	Estimate	SE	t	P
Within pairs	162 pairs	Intercept	57.99	0.22	304.73	<0.001
		Sex (Male)	3.39	0.20	16.51	<0.001
		Elevation (Low)	−0.07	0.24	−0.31	0.758
		Season banded 2015–2016	−0.04	0.35	−0.12	0.902
		Season banded 2016–2017	−1.45	0.34	−4.27	<0.001
		Season banded 2017–2018	−0.51	0.33	−1.54	0.124
		Season banded 2018–2019	−1.02	0.42	−2.40	0.017
		Season banded 2019–2020	−0.32	0.47	−0.67	0.502
		Season banded 2020–2021	−0.76	38	−2.01	0.045
		Random effects	Variance	SD		
		Pair ID	0.00	0.00		
		Residual	3.42	1.85		

Pair identity (ID) was included as a random effect to restrict comparisons to within pairs. The season banded fixed effects are shown in comparison to the 2014–2015 season. Seasons run from September through August.

Table A7

Test of whether mountain chickadees exhibit positive or negative assortment for size using the conservative data set that only included individuals paired in the same year their wing length was measured

Response variable	N	Fixed effect	Estimate	SE	t	P
Male wing length	162 pairs	Intercept	71.22	0.25	288.47	<0.001
		Female wing length	−0.01	0.08	−0.16	0.872
		Season banded 2015–2016	0.05	0.49	0.10	0.917
		Season banded 2016–2017	−1.53	0.46	−3.30	0.001
		Season banded 2017–2018	−0.05	0.46	−0.11	0.914
		Season banded 2018–2019	−1.45	0.58	−2.52	0.013
		Season banded 2019–2020	−0.01	0.67	−0.01	0.998
		Season banded 2020–2021	−0.10	0.53	−0.19	0.852
Female wing length	162 pairs	Intercept	68.09	0.24	286.13	<0.001
		Male wing length	−0.01	0.08	−0.16	0.872
		Season banded 2015–2016	−0.19	0.47	−0.42	0.679
		Season banded 2016–2017	−1.44	0.45	−3.23	0.002
		Season banded 2017–2018	−1.01	0.45	−2.26	0.025
		Season banded 2018–2019	−0.67	0.56	−1.21	0.229
		Season banded 2019–2020	−0.65	0.66	−1.00	0.318
		Season banded 2020–2021	−1.47	0.51	−2.87	0.005

Results from two linear models are shown, one with male wing length (mm) as the response variable and one with female wing length as the response variable. The opposite-sex fixed effect was centred on season to remove across-season variation. The season banded fixed effects are shown in comparison to the 2014–2015 season. Seasons run from September through August.

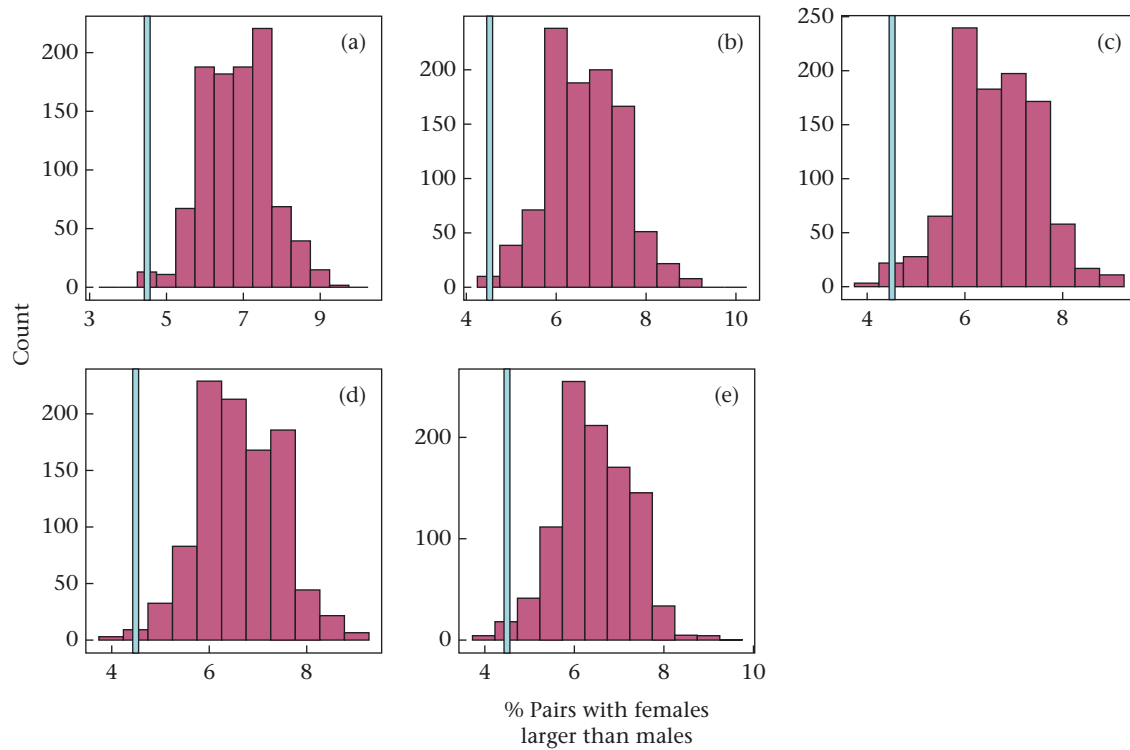


Figure A1. Results from permutation tests examining whether the observed percentage of female-larger pairings (blue lines) differed from the percentage expected by chance. (a) Permutation 1, with swaps restricted to within sex only. (b) Permutation 2, with swaps restricted to within sex and season banded categories. (c) Permutation 3, with swaps restricted to within sex, season banded and elevation categories. (d) Permutation 4, with swaps restricted to within sex, season banded, elevation and season bred categories. (e) Permutation 5, with swaps restricted to within sex, season banded, elevation, season bred and age categories. Figures correspond to the results in [Table A4](#).

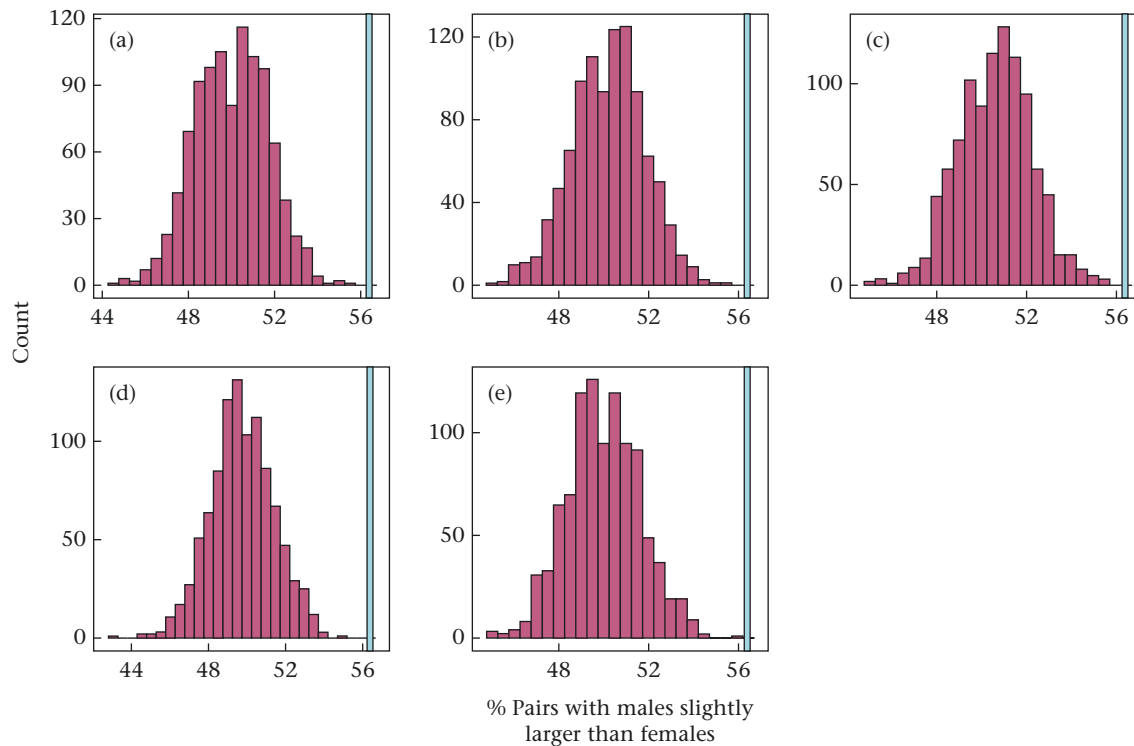


Figure A2. Results from the permutation tests examining whether the observed percentage of pairings in which the male was slightly larger than the female (blue lines) differed from the percentage expected by chance. (a) Permutation 1, with swaps restricted to within sex only. (b) Permutation 2, with swaps restricted to within sex and season banded categories. (c) Permutation 3, with swaps restricted to within sex, season banded and elevation categories. (d) Permutation 4, with swaps restricted to within sex, season banded, elevation and season bred categories. (e) Permutation 5, with swaps restricted to within sex, season banded, elevation, season bred and age categories. Figures correspond to the results in [Table A5](#). Results from permutations for pairings in which the male was much larger than the female were the mirror image of these results.

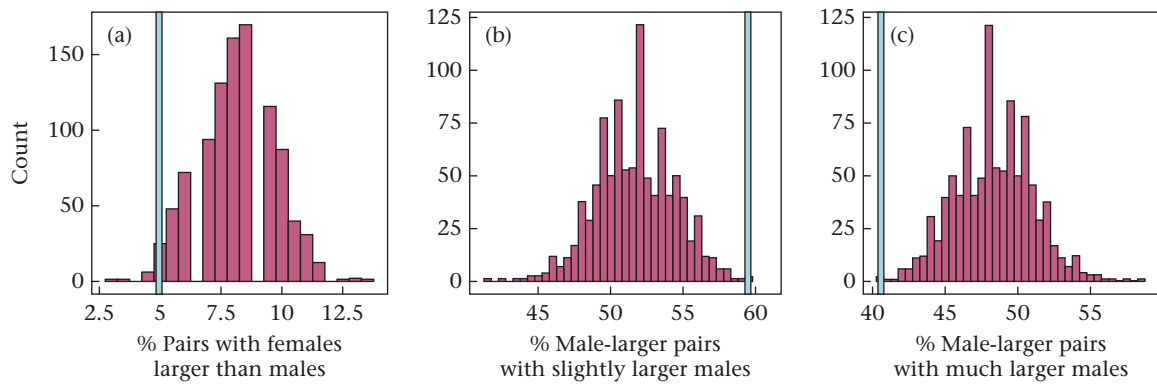


Figure A3. Results from permutation tests used to test the male-larger and the male-not-too-large pairing patterns in mountain chickadees using the conservative data set that only included individuals that paired in the same year their wing length was measured. Permutation swaps were restricted to within sex, season banded, elevation and season bred categories. (a) Observed percentage of female-larger pairs (blue line) in relation to the distribution of percentages from the permutations ($P = 0.008$). (b) Observed percentage of pairs in which the male was slightly larger than the female (blue line) in relation to the distribution of percentages from the permutations ($P < 0.001$). (c) Observed percentage of pairs in which the male was much larger than the female (blue line) in relation to the distribution of percentages from the permutations ($P < 0.001$). Note (c) is the mirror image of (b).

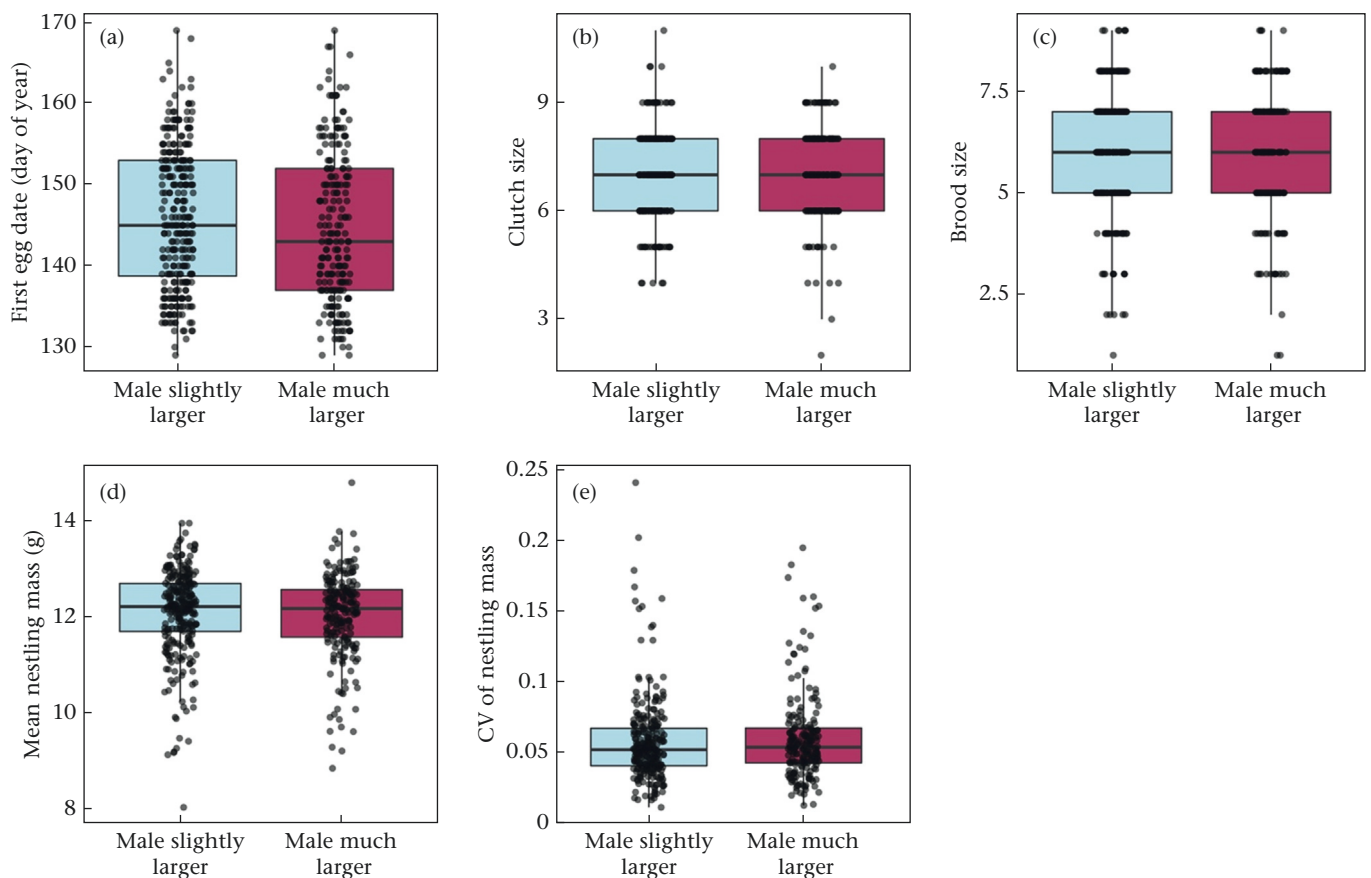


Figure A4. Plots of reproductive performance in relation to whether a pair followed the male-not-too-large norm or not. Points show raw data and box plots show median and first and third quartiles.