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How sexual and natural selection shape sexual size dimorphism: Evidence from multiple evolutionary scales

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Abstract

1. Sexual size dimorphism (SSD) is pervasive across taxa and reflects differences in the effects of sexual and natural selection on body size between the sexes. However, disentangling the complex eco-evolutionary interactions between these two mechanisms remains a major challenge for biologists.
2. Here, we combine macro-evolutionary (between-species), local evolutionary (between-population) and fine-scale evolutionary (within-population) patterns of SSD to explore how sexual and natural selection interact and shape the evolution of SSD in Australian agamid lizards. Australian agamid lizards show substantial variation in SSD, ecological traits and species density making them an ideal study system to address this question.
3. At the between-species level, population density, ecological generalism and mean species size significantly predict SSD variation; however, only ecological generalism was found to significantly explain variation in larger-than-average male-biased SSD. At the population level, density positively correlated with SSD in native habitats, but not city park habitats. Last, agonistic behaviour acted as the primary driver of SSD at the within-population level.
4. Our results indicate how sexual and natural selection can interact at different evolutionary scales, and show the importance of considering both selective mechanisms when investigating patterns of SSD.

KEYWORDS
agamid lizards, city landscapes, eastern water dragon, eco-evolutionary interactions, natural selection, sexual selection, sexual size dimorphism

1 | INTRODUCTION

Sexual size dimorphism (SSD) is common in nature and often reflects the conflicting demands and selective pressures operating on the sexes (Wikelski & Trillmich, 1997). Many vertebrate taxa display male-biased SSD (Abouheif & Fairbairn, 1997), which is usually attributed to sexual selection (Darwin, 1981), but can also result from natural selection through ecological divergence (Darwin, 1859). Although these mechanisms (natural and sexual selection) are often studied in isolation, they are not necessarily mutually exclusive, with their interaction often being complex (Andersson, 1994; Krüger, 2005; Krüger, Davies, & Sorenson, 2007) and underappreciated. This has resulted in the evolution of male-biased SSD remaining poorly understood for most taxa.

Male-biased SSD is primarily associated with sexual selection since larger male body size can confer an advantage for territory defence and mate acquisition (Andersson, 1994; Carothers, 1984; Cox, Butler, & John-Alder, 2007; Cox, Skelly, John-Alder, & Jr Garland, 2003; Stamps, 1983). Larger males, therefore, obtain a greater lifetime reproductive success (Baird, Fox, & McCoy, 1997; Clutton-Brock, Major, Albon, & Guinness, 1987; Isaac, 2005; McElligott et al., 2001; Owen-Smith, 1993). Both mating system and mating competition have been shown to positively influence SSD (Dunn, Whittingham, & Pitcher, 2001; Szekely, Lislevand, & Figuerola, 2007), indicated by correlations between male-biased SSD and the sex ratio of the population (Poulin, 1997; Stamps, 1983), and the frequency of agonistic behaviour (Carothers, 1984; Cox et al., 2003; Stamps, 1983). In terrestrial turtles, for example, male-biased SSD is predominantly determined by male–male combat (Berry & Shine, 1980), whilst in ungulates and cervids, SSD is largely driven by adult sex ratio (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Clutton-Brock, Albon, & Harvey, 1980). However, a growing body of literature suggests that natural selection through ecological niche partitioning between the sexes may also result in the evolution of SSD (Clutton-Brock, Harvey, & Rudder, 1977; Fairbairn, 1997; Fisher, 1958; Lande, 1980; Ralls, 1977; Shine, 1989; Slatkin, 1984). Ecological niche partitioning can occur in order to reduce resource competition between the sexes (Butler, Sawyer, & Losos, 2007; Losos, Butler, & Schoener, 2003; Pearson, Shine, & How, 2002; Schoener, 1967; Shine, 1991), or can occur due to differences in life histories between males and females (Wikelski & Trillmich, 1997). Quality, dispersion and density of food have also been shown to influence SSD as food often determines whether territorial mating systems are energetically feasible (Jarman, 1974). Furthermore, habitat type can be an important ecological factor influencing SSD (Kaliontzopoulou, Carretero, & Adams, 2015) as habitats can vary in food availability, visibility and density of competitors (Selander, 1966). *Anolis* lizards in Puerto Rico and Jamaica, for instance, exhibit habitat-specific SSD (Butler, Schoener, & Losos, 2000).

Although the influences of sexual and natural selection on the evolution of SSD are commonly tested in isolation, they are likely to interact in multiple ways (Krüger, 2005; Krüger et al., 2007; Shine, 1989). First, the proliferation of "good genes" via strong sexual selection not only drives traits that confer a reproductive advantage (e.g. larger male body sizes), but also traits that improve viability (Proulx, 1999). For example, species that occur in a variety of environments (ecological generalists) often display greater SSD (Östman & Stuart-Fox, 2011). Second, natural selection can constrain the evolution of exaggerated sexual traits, including body size (Hosken & House, 2011). Third, effects of sexual and natural selection on SSD may be mediated by population density. Population density can result in, and intensify, male sexual selection (Emlen & Oring, 1977; Ghiselin, 1974; Kokko & Rankin, 2006), where larger male size is favoured at high density (increased male–male competition) due to the fitness advantage larger size confers (Ghiselin, 1974; Stamps, 1983). However, at extremely high population densities, competition for mates may become too great, resulting in the evolution of alternative reproductive tactics (Gross, 1996), where larger males guard females and defend territories whilst smaller males sneak copulations (Berard, Nurnberg, Epplen, & Schmidtke, 1994; Eadie & Fryxell, 1992; Forsyth & Montgomerie, 1987; Lucas & Howard, 1995; Reichard, Smith, & Jordan, 2004; Tomkins & Brown, 2004; Wirtz, 1982; Zimmerer & Kallman, 1989). The evolution of alternative reproductive tactics within a population results in greater variation in male body size and thus SSD. High population densities can also exacerbate competition for food, favouring niche partitioning of the sexes by natural selection (Wikelski & Trillmich, 1997). Resource density and habitat type ultimately modulate population density and can therefore, in turn, influence the degree of competition over mates (Kokko & Rankin, 2006). However, effects of population density on SSD have rarely been examined.

Here, we investigate the interaction between sexual selection (mating interactions) and natural selection (ecological interactions) on the evolution of SSD in agamid lizards across different evolutionary scales (species, populations and individuals). We focus on effects of density and habitat on SSD at each scale using (a) 43 Australian agamid species (1,069 individuals), (b) nine populations of a single species, the eastern water dragon (*Intellagama lesueurii*; 264 individuals), and (3) 137 eastern water dragon individuals from a single population. In addition, to further investigate the mechanisms influencing the evolution of SSD, we examine the effect of agonistic behaviour and sex ratio on SSD at the within-population level. Agamid lizards show substantial variation in SSD, ecological traits and density within and between species making them an ideal system in which to study the evolution of SSD. Specifically, eastern water dragons show male-biased SSD and occur at varying densities in a broad range of riparian and human-dominated landscapes. By integrating multiple evolutionary scales, our study provides empirical insights into the ways sexual and natural selection interact to drive the evolution of male-biased SSD in agamid lizards.

2 | MATERIALS AND METHODS

2.1 | Study design

Table 1 shows the number of males and females that ecological and morphological data were collected for at each evolutionary level. Supporting Information Table S1, Figures S1 and S2 show the sex differences between morphological traits at the between-species, between-population and within-population level analyses.

2.1.1 | Between-species level

Morphological data were compiled using museum specimens and published literature for 43 agamid species (Littleford-Colquhoun, Clemente, Whiting, Ortiz-Barrientos, & Frère, 2017; Thompson, Clemente, Withers, Fry, & Norman, 2009; Thompson & Withers, 2005). Where possible, data were collected for at least five individuals of each sex, for each species (see Supporting information Table S2 for species numbers).

2.1.2 | Between-population level

At the between-population level, ecological and morphological data were collected for nine genetically independent (Littleford-Colquhoun et al., 2017) populations of the eastern water dragon. The eastern water dragon is a semi-aquatic arboreal agamid lizard that is native to Australia. They are found in abundance both across their native riparian habitat (ranging from northern Queensland to north-eastern Victoria) and across human-dominated landscapes (including urban and suburban locations (Baird, Baird, & Shine, 2012; Gardiner, Doran, Strickland, Carpenter-Bundhoo, & Frère, 2014). Eastern water dragons display male-biased sexual dimorphism with males having larger heads and jaws and displaying red ventral coloration (Baird, Baird, & Shine, 2013; Cuervo & Shine, 2007; Thompson, 1993). In addition, males exhibit alternative mating strategies by either aggressively defending a territory or assuming satellite behaviour (Baird et al., 2012), whilst female dragons are polyandrous (Frère, Chandrasoma, & Whiting, 2015). Both male and female dragons display agonistic behaviours including tail slapping and arm waving; however, males also display head bobbing and push-ups (Baird et al., 2012). Eastern water dragons are regarded as an omnivorous generalist species, with their diet including insects, native/exotic flowers, fruits and seeds which can extend to anthropogenic food sources within the city. They show no niche differentiation.

Here, we sampled four city park populations and five isolated native habitat (hereafter native habitat) populations. The four city park populations were enclosed habitats surrounded by an impermeable/impenetrable urban matrix. These city parks were man-made and highly curated spaces located within or adjacent to the central business district of Brisbane, Queensland (QLD), Australia (CP1: −27.474366, 153.029116; CP2: −27.475915, 152.978495; CP3: −27.462811, 153.019148; CP4: −27.482239, 153.029533). Supporting information Figure S3 shows the location of all city park populations within the central business district of Brisbane. City Park 1 (CP1; 18 ha), CP2 (52 ha) and CP3 (16 ha) are botanical showcases, and CP4 (17.5 ha) is a manicured leisure space. The five native habitat populations were found along unfragmented native (without human modification) riverside habitats in south-east QLD (INH1: −27.525913, 152.92557; INH2: −26.622728, 152.960120; INH3: −26.564226, 152.973053; INH4: −26.759938, 152.852996; INH5: −26.674471, 153.114576). See Supporting information Table S3 for sample sizes for each city park and native habitat population. Satellite images of all city park and native habitat populations are displayed in Supporting information Supporting information Figure S4. Only adult eastern water dragons were used in between-population SSD analyses (male SVL >226 mm, female SVL >187 mm). As we do not currently have growth trajectories for the eastern water dragon, we used SVL cut-offs to differentiate between adult and subadult dragons. These cut-offs were verified using known age records and hatchling data from a larger longitudinal morphological dataset on CP3. All individuals (male and female) with SVL <150 mm were considered juveniles, whilst the mean SVL of all individuals with SVL >150 mm was used to differentiate between subadult and adult eastern water dragons. This mean SVL was calculated separately for males and females.

2.1.3 | Within-population level

Ecological and morphological data were collected for 102 adult individuals (51 males, 51 females) as part of an ongoing behavioural and genetic study of CP3 eastern water dragons. Only adult individuals which had been sighted a minimum of 25 times were used in the analysis at this evolutionary scale. City Park 3 comprises a range of discrete microhabitats (Supporting information Figure S5), including a lake area (Lake), rainforest area (Rainforest), a tropical bromeliad garden (Broms), a baobab garden (Baobabs), a children's playground area (Playground) and a densely planted ornamental garden named the Spectacle Garden (Spec). It accommodates a large population of dragons, estimated at 336 individuals (Strickland et al., 2017). City Park 3 is an enclosed population, surrounded by residential and commercial buildings, busy roads and a train line (Strickland, Gardiner, Schultz, & Frère, 2014). This prevents the immigration and emigration of eastern water dragons from the parkland (Gardiner et al., 2014). Behavioural surveys were conducted twice daily (between 07.30 and 10.30 hr and between 13.00 and 15.00 hr) between August and April (2014–2016). Methodology for how dragons were identified and how behavioural surveys were conducted can be found in Gardiner et al. (2014) and Strickland et al. (2014).

2.2 | Morphology, sexual dimorphism index (SDI) and sexual size dimorphism (SSD)

Morphological measurements taken for all individuals in this study included jaw width (JW), jaw length (JL), upper forelimb length (UFL), lower forelimb length (LFL), upper hindlimb length (UHL), lower hindlimb length (LHL) and snout–vent length (SVL) as described in Littleford-Colquhoun et al. (2017).

To estimate overall SSD, a sexual dimorphism index (SDI) was first calculated for each of the seven morphological measurements taken. The SDI was calculated as: *[(larger sex/smaller sex) − 1]*, arbitrarily set to positive when males are larger and negative when females are larger (Lovich & Gibbons, 1992). Whilst there are multiple ways in which the above calculation can be applied to morphological data (SDI can be calculated for each of the seven morphological traits using all female–male pairs of a species/population/territory, or SDI can be calculated for each of the seven morphological traits using male and female averages for each species/population/territory), we found a high correlation between these two methodologies (Supporting information Figure S6) and therefore all female–male pairs were used to calculate overall SSD rather than using male and female averages.

At the between-species level, for each species, SDI measurements were calculated for each male to every female. The mean SDI for each morphological measurement was then used in a

TABLE 1 Table outlining models used in sexual size dimorphism (SSD) analyses

Evolutionary scale	Testing	No. species	No. populations	No. microhabitats	No. males	No. females	Calculation of SDI and SSD	No. SSD measurements
Between-species	SSD	43	NA	NA	502	499	For each species, SDI measurements were calculated for each male to every female. Then for each species, the mean SDI measurement for each morphological trait was used to generate overall species SSD	43
Between-populations	SSD	1	9	NA	124	121	SDI for each morphological measurement calculated for every male to every female within each population. All SDI measures used in PCA to generate overall SSD measurement for every male–female pair-wise comparison within each population	1913
	Coefficient of variation (CV) of body size	1	9	NA	124	121	NA	NA
Within-population	SSD	1	1	6	51	51	SDI for each morphological measurement calculated for each focal male to every female within its 95% home range. SDI measures used to generate overall SSD measurements for each male–female pairwise comparison	1,423
	Agonistic behaviour	1	1	6	51	51	NA	NA
	Male and female body size	1	1	6	51	51	NA	NA

phylogenetic principal component analysis (pPCA; corrects for non-independence among observations; Revell (2009)). Species principal component (PC) scores from the first axis of the pPCA were used as a measure of overall SSD between males and females. The pPCA was carried out using the *phyl.pca* function in R package *phytools* (Revell, 2012) and utilized the phylogeny of Pyron and Burbrink (2014) which was pruned to only include the 43 agamid species used in this study. In our dataset, sample sizes per species were highly variable; however, we did not find that subsampling significantly influenced mean SDI measurements (correlation between subsampled and full dataset: $R^2 = 0.99$), and therefore, the full dataset was used in subsequent analyses.

At the between-population level, SDI measurements were calculated for every male to every female within each population. All pairwise SDI measurements were used in a principal component analysis (PCA) with the PC scores from the first axis used as a measurement of overall SSD between males and females (similar methods used in Östman & Stuart-Fox, 2011).

At the within-population level, SDI measurements were calculated for each focal male (minimum of 25 sightings) to every female within its 95% home range. Home range size of each individual was calculated following the methodology outlined in Gardiner et al. (2014). The size of the home range was calculated using kernel utilization distribution methods in the adehabitat package (Calenge, 2006) in R version 3.3.1 (R Development Core Team, 2013), estimating contours of 95% to represent an individual's outermost boundary. The smoothing factor was visually selected, $h = 7$, to control for variation around density estimates (Strickland et al., 2017). It should be noted that all males, regardless of mating tactic (territorial or satellite behaviour), occupy a home range. All pairwise SDI measurements were used in a PCA with the PC scores from the first axis used as a measurement of overall SSD between males and females.

For each evolutionary scale (between-species, between-population and within-population), a PC score of zero was indicative of the average SSD, whereas a more positive SSD PC score was indicative of a larger-than-average male-biased SSD, whilst a more negative PC score was indicative of a smaller-than-average male-biased SSD, which also included female-biased SSD. Table 1 outlines how SDI and SSD were calculated at each evolutionary scale (see Supporting information Table S4 for pPCA/PCA loadings for each evolutionary level). SSD values were used in subsequent analyses.

2.3 | Predictor variables

2.3.1 | Density

Between-species level

To estimate species density (number of individuals per square kilometre), we used the Atlas of Living Australia (ALA) records for each species (ALA website at http://www.ala.org.au, accessed 28 July 2017) divided by the species' Australian geographical range in square kilometres (calculated in Stuart-Fox & Owens, 2003). Whilst we acknowledge there are caveats using this estimate, unfortunately

Calculation of body size	% variance PC1 explained	Type of model used	Dependent variable	Predictor variables	Random effects	Model weighted
Morphological measurements for all individuals from all 43 species were used in a PCA. First PC used to calculate species size as [(mean male PC1 + mean female PC1)/ 2] for each species	89%	Phylogenetic generalized least squares (PGLS)	SSD	logDensity + Number climate zones + Species size	NA	NA
NA	55%	REML-based linear mixed-effect models (LME)	SSD	logDensity * Habitat	Male ID Female ID Population	NA
Morphological measurements for all individuals used in PCA. First PC (PC1) defined as body size. PC scores then split by sex. Absolute difference between PC scores calculated for every male–male and female–female pair within each population. Coefficient of variation (CV) then calculated for each sex in each habitat type	86%	Linear models (LM)	CV of body size	logDensity * Habitat	NA	NA
NA	41%	LME	SSD	logDensity * Microhabitat + Sex ratio + Agonistic frequency	Male ID Female ID	Home range overlap
Morphological measurements for all individuals used in PCA. First PC (PC1) defined as body size.	86%	LME	Agonistic frequency	logDensity + male body size	Microhabitat	NA
	84%	LM	Male body size	Mean female size + *SD* female size + number of males + number of females	Microhabitat	NA

there are no current density estimates available for these species. We therefore acknowledge that this estimate of species density can only be used as a coarse proxy measure.

Between-population level

Population density was estimated as the number of individuals per square metre and was calculated by slowly walking transects through each population, recording all lizards encountered (Anderson, Laake, Crain, & Burnham, 1979; de Infante Anton, Ruiz, Igual, & Tavecchia, 2014; Kacoliris, Berkunsky, & Williams, 2009). Lizards were not captured during density transects. At least three 30-metre (m) transects were walked in each population, with each transect replicated three times. Population density was then calculated as the average of these transect densities. At least a 30-min gap was kept between transect replications so dragons could return to the area if disturbed. Only dragons that occurred within 7–10 m (depending on habitat) of transect were recorded. The total searched area of each transect was then calculated, with the number of individuals recorded divided by the transect area. In native habitat populations, transects were walked along river banks, and hence very linear. In city park populations, which are nonlinear, transects were walked within a defined plot, with the area of each plot calculated for density estimates.

Within-population level

Home range density was calculated as the number of individuals (adult males and adult females) that occurred within the focal male's 95% home range, divided by its home range size (i.e. individuals per m^2).

2.3.2 | Habitat

Between-species level

Climate zones were measured at the between-species level. Here, the number of discrete climate zones (equatorial, tropical, subtropical, desert, grassland or temperate) each species' range extends across was tallied using ALA presence records mapped over the Köppen major climate classifications of Australia (acquired from the Bureau of Meteorology, Australia).

Between-population level

At the between-population level, habitat type was classified as city park (CP) or native habitat (INH) for each individual.

Within-population level

At the within-population level, microhabitat was recorded as lake area (Lake), rainforest area (Rainforest), tropical bromeliad garden (Broms), baobab garden (Baobabs), children's playground area (Playground) or Spectacle Garden (Spec).

2.3.3 | Size

Size was used as a predictor variable at the between-species level analysis to test for allometry in SSD (Rensch, 1959). Morphological measurements for all individuals from all 43 species were used in a PCA. We used the first PC (95% of variance; see Supporting information Table S5 for PCA loadings) to calculate species size as *[(mean male PC1 + mean female PC1)/2]* for each species.

2.3.4 | Agonistic displays

The frequency of agonistic displays (per male) was used as a predictor variable at the within-population level analysis and was calculated as the number of times a focal male was sighted during the behavioural surveys displaying agonistic behaviours (head bob, tail slap, arm wave, push-ups; Baird et al., 2012), divided by his total number of sightings. Therefore, agonistic display frequencies represent an average over the entire field season.

2.3.5 | Sex ratio

Sex ratio within a male's home range was used as a predictor variable at the within-population level analysis only. Of the total number of adult individuals that occurred within a focal male's 95% home range, the sex ratio was calculated by dividing the number of adult males by the number of all adult individuals.

2.4 | Statistical analyses

Table 1 outlines the statistical tests and model structures used at each evolutionary scale to test for associations between SSD and predictor variables. Prior to all analyses, at all evolutionary scales, density was log10-transformed (logDensity) so that the distribution of density better approximated normality. At each level, collinearity among predictor variables was visually assessed prior to analysis; however, none of the variables were strongly correlated. Model residuals were checked for assumptions of normality and homoscedasticity. All statistical analyses were performed in R 3.3.1 (R Development Core Team, 2013).

At the between-species level, we first checked for a phylogenetic signal in SSD PC scores using the *phylosig* function in R package *phytools* to obtain a value of Pagel's λ (Pagel, 1999) and its corresponding *p* value. Pagel's λ is a parameter that estimates the size of phylogenetic signal in trait data, where low λ (close to zero) indicates a weak phylogenetic signal and a high λ (close to one) indicates a strong phylogenetic signal. The significance of λ was assessed based on comparison of the likelihood a model accounting for the observed λ with the likelihood of a model that assumes complete phylogenetic independence using 1,000,000 simulations. We then ran a phylogenetic generalized least squares regression (PGLS) to determine the predictors of SSD (Table 1). A PGLS was run regardless of whether a phylogenetic signal was detected in SSD PC scores as it is important to check whether a phylogenetic signal is present in the residuals of the regression as well as the dependent variable itself. In addition, the PC scores provided by pPCA are in the original, phylogenetically dependent state (not in a phylogenetically independent state); therefore, subsequent analyses using these scores should be analysed using phylogenetic methods (Revell, 2009). In the PGLS, we used the maximum likelihood value of λ to adjust the strength of phylogenetic non-independence, implemented in the R package *caper* (Orme, 2013). In addition to the PGLS models ran for all 43 agamid species, individual PGLS models were run for (a) those species which showed a smaller-than-average male-biased SSD (negative PC scores), including species which displayed female-biased SSD (species which displayed female-biased SSD are shown with an asterisks (*) in Supporting information Table S2 and were identified using raw morphology data), and (b) those species which displayed a larger-than-average male-biased SSD (positive PC scores).

At the between-population and within-population level analyses, REML-based linear mixed-effect models (LME) were used to test for associations between SSD and predictor variables (Table 1) using the lmer function of the lme4 package (version 1.1-1.4). To deal with the non-independent nature of pairwise data points (all male-to-female pairs used to calculate SDI measurements and thus SSD PC scores), significance was assessed using a randomized null model. We randomly shuffled observed SSD PC scores across male–female pairs at each level, regardless of habitat or population at the between-population level, and home range or microhabitat at the within-population level. We repeated this randomization procedure 1,000 times to generate a distribution of random *t* values. We estimated the significance of the effect of predictor variables by calculating a *p* value as the proportion of times the random *t* estimate of each predictor variable was larger (if positive estimate) or smaller (if negative estimate) than the observed (Ruxton & Neuhäuser, 2013).

In order to assess whether the body size of a particular sex was driving variation in SSD PC scores, at the between-population level, we tested for associations between predictor variables and variability around the mean (coefficient of variation; CV) of male and female body size using linear regressions (lm; Table 1). Identifying whether male or female body size (or both) is driving SSD variation allows us to better understand the mechanisms underpinning SSD. For example, the increased frequency of alternative reproductive tactics in males would translate into a higher coefficient of variation in male body size compared to female body size. In addition, we also tested for associations between predictor variables and body size at the within-population level using linear regressions (Table 1). At both the between-population and within-population level, all morphological measurements for all individuals were used in PCA. We used the first PC as a measure of body size (86% of variance for between-population and 84% for within-population level; see Supporting information Table S5 for PCA loadings).

3 | RESULTS

3.1 | Between-species level

We assessed the effect of species' density (number of individuals per km^2 estimated from locality records), ecological generalism (the number of climate zones occupied) and species mean size on the extent and direction of SSD among 43 Australian agamid species. Overall, we found variation in SSD PC scores among species (2.7E-06 ± 0.31;

mean ± *SD*), ranging from negative PC scores which were indicative of species with smaller-than-average male-biased SSD, including those species which displayed female-biased SSD (species which displayed female-biased SSD are identified with an asterisks (*) in Supporting information Table S2), to positive PC scores which were indicative of species with larger-than-average male-biased SSD. We found a lack of phylogenetic signal in SSD PC scores at the species level (Pagel's $\lambda = 0.00072$, $p = 1$; Supporting information Figure S7). All 43 species occupied more than one Australian climate zone (3.93 ± 1.44), with a mean species' density of 0.003 ± 0.003 individuals per km^2, and an average body size PC score of −1.12 ± 1.86 (negative scores represent smaller species, whilst positive scores represent larger species).

The full PGLS model accounted for 31% of interspecies variation in SSD, with density, number of climate zones and species size all found to be significant predictors (Table 2a, Figure 1a and Supporting information Figure S8). Phylogenetic analysis of the regression parameters suggested that there was no phylogenetic effect in the residual error of the regression model (Pagel's $\lambda = 0$; Table 2a; Figure 1ai). When split by species with a larger-than-average male-biased SSD and a smaller-than-average male-biased SSD (including those species which displayed female-biased SSD), only the number of climate zones a species inhabits was a significant predictor of species with a larger-than-average male-biased SSD ($p = 0.009$; Table 2b; Figure 1aii). Conversely, no variables significantly predicted smaller-than-average male-biased SSD and female-biased SSD (Table 2c).

3.2 | Between-population level

At the between-population level, we assessed the extent and effect of habitat type and density on male-biased SSD in eastern water dragons using nine distinct populations. The nine populations comprised four city park populations (CP1, CP2, CP3 and CP4) found in enclosed human-engineered habitats and five native habitat populations (INH1, INH 2, INH 3, INH 4 and INH 5) found in continuous native habitats. On average, city park populations displayed larger male-biased SSD (0.064 ± 1.972; mean ± *SD*; Figure 1bi) than native habitat populations (−0.168 ± 1.949). Overall, city park populations and native habitat populations showed similar density estimates (city park populations: 0.029 ± 0.013, native habitat populations: 0.027 ± 0.018); however, it should be noted that INH1 and INH3 had a lower population density than INH2 and INH4.

We found a significant interaction between habitat type and density (logDensity:Habitat: $p = 0.007$; Table 3a; Figure 1bii), indicating that the effect of density on male-biased SSD differed between habitat types. Male-biased SSD PC scores were positively associated with density in native habitat but not city park populations (Figure 1bii). To check that this trend was not primarily driven by smaller SSD PC scores in the two low-density native habitat populations (INH1 and INH3), we also ran LME models using populations with logDensity greater than −1.8. Regardless of the number of populations used, we found a significant interaction between habitat type and density (logDensity:Habitat: $p = 0.028$). Moreover, for populations with a high density (greater than −1.8 logDensity), we found that city park populations displayed smaller SSD PC scores (0.064 ± 1.972; mean ± *SD*) than native habitat populations (0.071 ± 1.736).

In addition, the interaction between habitat type and density predicted male but not female body size variation (Table 3b,c). For native habitat populations, male body size variation decreased with density, whilst variation increased with density for city park populations.

TABLE 2 Results from phylogenetic least squares regressions (PGLS) using Pagel's lambda transformation for (a) overall between-species sexual size dimorphism (SSD) for 43 agamid species, (b) 20 agamid species that showed larger-than-average male-biased SSD PC scores and (c) 23 agamid species that showed smaller-than-average male-biased SSD/female-biased SSD. In all tables, t_{obs} represents the observed *t* value for each variable in the model. Significant results in bold

	Parameter	Estimate	*SE*	t_{obs}	*p* value	Adjusted R^2	λ
(a) Between-species—all species							
SSD ~ Climate zones + logDensity + Species size	Intercept	0.29	0.27	1.10	0.280	0.31	0
	Climate_zones	**0.059**	**0.03**	**2.08**	**0.045**		
	logDensity	**0.16**	**0.08**	**2.18**	**0.035**		
	Species size	**0.05**	**0.02**	**2.23**	**0.032**		
(b) Between-species—larger-than-average SSD							
SSD ~ Climate zones + logDensity + Species size	Intercept	0.14	0.25	0.57	0.575	0.29	0
	Climate_zones	**0.07**	**0.03**	**2.55**	**0.022**		
	logDensity	0.06	0.08	0.77	0.450		
	Species size	0.03	0.02	1.53	0.145		
(c) Between-species—smaller-than-average SSD							
SSD ~ Climate zones + logDensity + Species size	Intercept	0.06	0.22	0.28	0.784	−0.00	0
	Climate_zones	−0.01	0.02	−0.40	0.692		
	logDensity	0.09	0.05	1.69	0.107		
	Species size	−0.01	0.03	−0.29	0.777		

3.3 | Within-population level

Previous observational studies suggested that population density may vary between microhabitats within study site CP3. We therefore assessed the effect of microhabitat, home range density (density of adult individuals sighted within a focal male's 95% home range), the interaction between microhabitat and density, sex ratio and the frequency of agonistic displays (agonistic frequency) on within-population SSD, estimated for each focal male relative to females within his home range. On average, CP3 dragons showed large variation in SSD PC scores (2.11E-12 ± 1.687; mean ± *SD*; see Figure 1ci for an example of the variation in SSD PC scores for two different focal males and the females that occur within their 95% home range); however, only frequency of agonistic displays (per male) significantly correlated with within-population male-biased SSD PC scores ($p < 0.001$; Table 3d; Figure 1cii), where the frequency of agonistic displays increased with overall male-biased SSD. Microhabitat, home range density (number of individuals within each focal male's home range), their interaction and sex ratio did not show a significant correlation with SSD PC scores. In addition, the frequency of male agonistic displays was not significantly associated with home range density ($p = 0.089$) but was significantly associated with male body size ($p = 0.001$). Larger agonistic males were also found to have, on average, smaller females within their home range ($p = 0.047$). Male body size was not significantly associated with the number of males or females within a male's home range, or variation in female body size (standard deviation of female size).

4 | DISCUSSION

Here, we combine macro-evolutionary (between-species), local evolutionary (between-population) and fine-scale evolutionary (within-population) patterns of SSD to provide insight into the ways by which sexual and natural selection interact to drive and shape the evolution of SSD in agamid lizards. At the between-species level, we found that density, ecological generalism (the number of climate zones a species inhabits) and mean species size all significantly predict variation in SSD; however, only ecological generalism significantly explained variation in larger-than-average male-biased SSD. At the between-population level, we found that density influences the extent of male-biased SSD in eastern water dragons, but the effect of density on SSD depends on habitat type. Specifically, SSD was positively associated with population density in native but not city park habitats. Furthermore, within a single city park population (within-population level), males that were larger relative to females within their home range (higher SSD) showed a higher frequency of agonistic displays but did not have relatively more females or a higher density within their home range. Overall, this study highlights that the interacting effects of sexual and natural selection on SSD can shift depending on evolutionary scale.

Density, ecological generalism and mean species size significantly influenced SSD at the between-species level. However, the relationship between SSD and ecological generalism was primarily driven by species with a larger-than-average male-biased SSD. This suggests that ecological generalism may predict the extent of male-biased SSD. This relationship may arise through the proliferation of "good genes" (Östman & Stuart-Fox, 2011; Proulx, 1999) or as a by-product of density (Borregaard & Rahbek, 2010), although we found no correlation between density and ecological generalism. In addition, our results suggest that density may influence the overall directionality of SSD at the between-species level, with SSD switching from female-biased SSD (and smaller-than-average male-biased SSD) to larger-than-average male-biased SSD at higher densities. Shine (1989) proposed that sexual selection drives the directionality of SSD (female-biased to male-biased), whilst natural selection may influence the extent of the SSD. Our results are consistent with this hypothesis, given that higher densities generally result in stronger sexual selection (i.e. competition over mates; Emlen & Oring, 1977; Ghiselin, 1974; Kokko & Rankin, 2006). However, the influence of natural selection cannot be discounted since higher density can also increase competition over other resources. Additionally, we interpret our data cautiously because species density estimates from locality records may be biased towards certain species and/or certain parts of their distribution (e.g. more urbanized vs. more rural locations).

At the between-population level, we found that the relationship between density and SSD was influenced by habitat type (Figure 1bii). Similar to other lizard species and pseudo-scorpions (Stamps, 1983; Stamps, Losos, & Andrews, 1997; Zeh, 1987), we found that in native habitat, SSD was positively correlated with population density. Further, for high-density populations (greater than −1.8 logDensity),

FIGURE 1 Predictors of sexual size dimorphism (SSD) at (a) the between-species, (b) between-population and (c) within-population level. (ai) shows between-species SSD PC scores mapped onto the agamid phylogeny; (aii) boxplot showing the PC scores of smaller-than-average male-biased and female-biased SSD species (red) and larger-than-average (blue) male-biased SSD species for each number of climate zones inhabited (Table 1a-c). The boxes show the median and first and third quartiles, and whiskers represent the 95% CI. (aiii) Scatterplot of logDensity against SSD PC scores for smaller-than-average male-biased and female-biased SSD species (red) and larger-than-average (blue) male-biased SSD species (Table 2a–c). (bi) shows the average SSD PC scores for each eastern water dragon population mapped onto the phylogeny (phylogeny is based on ND5 subunits of CP1-4 and INH1-3; however, INH4 and INH5 have been added to the phylogeny arbitrarily, and therefore, this phylogeny is an approximation); (bii) scatterplot showing the interaction between logDensity and every population pairwise SSD PC score depending on habitat (city park; blue and native habitat; green; Table 3a). (ci) Representation of the SSD PC scores between a focal male eastern water dragon (blue dragon) and the females (red dragons) present in his 95% home range (phylogeny is a graphical representation only); (bii) scatterplot showing the relationship between SSD PC scores and the frequency of agonistic displays (Table 3d)

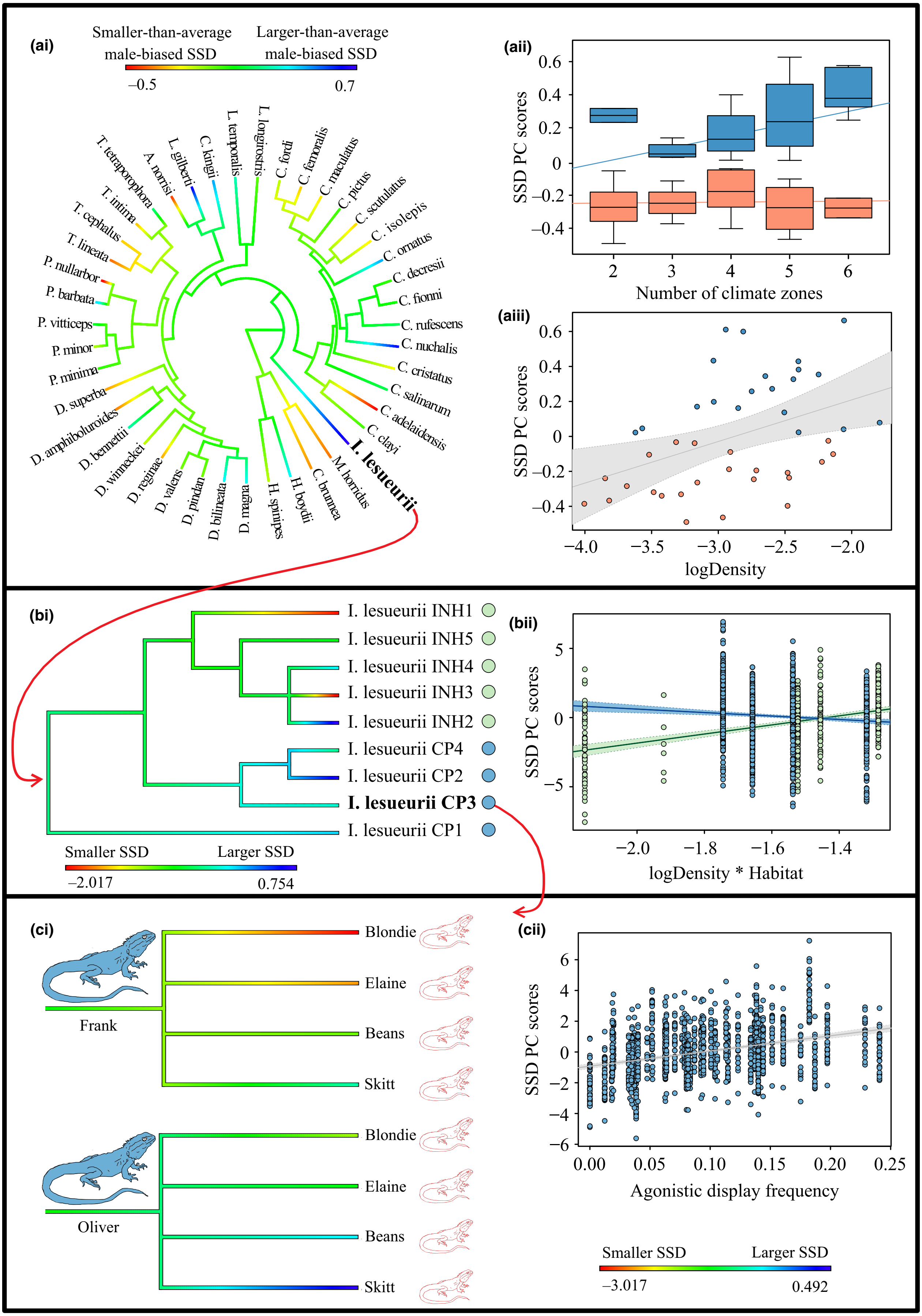
(ai)
Smaller-than-average male-biased SSD
Larger-than-average male-biased SSD
–0.5
0.7
T. tetraporophora
A. norrisi
L. gilberti
C. kingii
L. temporalis
L. longirostris
C. fordi
C. femoralis
C. maculatus
C. pictus
C. scutulatus
C. isolepis
C. ornatus
C. decresii
C. fionni
C. rufescens
C. nuchalis
C. cristatus
C. salinarum
C. adelaidensis
C. clayi
I. lesueurii
M. horridus
C. brunnea
H. boydii
H. spinipes
D. magna
D. bilineata
D. pindan
D. valens
D. reginae
D. winneckei
D. bennettii
D. amphiboluroides
D. superba
P. minima
P. minor
P. vitticeps
P. barbata
P. nullarbor
T. lineata
T. cephalus
T. intima
(aii)
SSD PC scores
0.6
0.4
0.2
0
–0.2
–0.4
2
3
4
5
6
Number of climate zones
(aiii)
SSD PC scores
0.6
0.4
0.2
0
–0.2
–0.4
–4.0
–3.5
–3.0
–2.5
–2.0
logDensity
(bi)
I. lesueurii INH1
I. lesueurii INH5
I. lesueurii INH4
I. lesueurii INH3
I. lesueurii INH2
I. lesueurii CP4
I. lesueurii CP2
I. lesueurii CP3
I. lesueurii CP1
Smaller SSD
Larger SSD
–2.017
0.754
(bii)
SSD PC scores
5
0
–5
–2.0
–1.8
–1.6
–1.4
logDensity * Habitat
(ci)
Frank
Blondie
Elaine
Beans
Skitt
Oliver
Blondie
Elaine
Beans
Skitt
(cii)
SSD PC scores
6
4
2
0
–2
–4
–6
0.00
0.05
0.10
0.15
0.20
0.25
Agonistic display frequency
Smaller SSD
Larger SSD
–3.017
0.492

TABLE 3 Results of (a) REML linear mixed-model testing for associations between predictor variables and between-population sexual size dimorphism (SSD), (b) linear model testing for associations between predictor variables and coefficient of variation (CV) in female body size, (c) linear model testing for associations between predictor variables and coefficient of variation (CV) in male body size between populations and d) REML linear mixed-model testing for associations between predictor variables and within-population sexual size dimorphism (SSD). In all tables, t_{obs} represents the observed *t* value for each variable in the model, and 95% t_{rand} represents the 95% confidence intervals of the random *t* values generated by the randomized null model which shuffled SSD PC scores to assess the significance of observed *t* values. *p* values were calculated as the proportion of times the randomized *t* value was larger than the observed. Significant results in bold

	Parameter	Estimate	*SE*	*df*	t_{obs}	95% t_{rand}	*p* value	Adjusted R^2
(a) Between-population—overall SSD								
SSD ~ logDensity * Habitat	**Intercept**	**11.00**	**3.71**	**234.37**	**2.96**	**−0.02 to 0.10**	**0.002**	NA
	logDensity	**7.60**	**2.34**	**232.91**	**3.25**	**−0.02 to 0.10**	**0.001**	
	Habitat	**−6.47**	**2.62**	**231.10**	**−2.47**	**−0.11 to 0.01**	**0.010**	
	logDensity:Habitat	**−4.44**	**1.66**	**230.31**	**−2.67**	**−0.11 to 0.01**	**0.007**	
(b) Between-population—female CV of body size								
CV of body size ~ logDensity * Habitat	Intercept	0.78	0.51	NA	1.52	NA	0.203	−0.65
	logDensity	0.01	0.32	NA	0.02	NA	0.985	
	Habitat	−0.04	0.40	NA	−0.09	NA	0.930	
	logDensity:Habitat	−0.01	0.25	NA	−0.03	NA	0.976	
(c) Between-population—male CV of body size								
CV of body size ~ logDensity * Habitat	Intercept	−0.16	0.33	NA	−0.49	NA	0.648	0.90
	logDensity	−0.38	0.20	NA	−1.85	NA	0.123	
	Habitat	**0.99**	**0.27**	**NA**	**3.74**	**NA**	**0.014**	
	logDensity:Habitat	**0.48**	**0.17**	**NA**	**−2.90**	**NA**	**0.034**	
(d) Within-population—overall SSD								
SSD ~ logDensity * Microhabitat + Sex ratio + Agonistic frequency	Intercept	−5.82	5.36	50.77	−1.09	−0.04 to 0.12	0.194	NA
	logDensity	−4.29	3.27	50.66	−1.31	−0.06 to 0.10	0.151	
	Microhabitat	1.52	0.97	50.65	1.57	−0.10 to 0.06	0.089	
	Sex ratio	−4.67	4.27	50.80	−1.09	−0.11 to 0.04	0.180	
	Agonistic frequency	**9.03**	**2.34**	**50.67**	**3.85**	**−0.09** to **0.04**	**< 0.001**	
	logDensity:Microhabitat	0.89	0.60	50.65	1.48	−0.10 to 0.06	0.108	

we found that city park populations, on average, displayed smaller SSD with larger variation than native habitat populations. In addition, compared to native habitat populations, we found that male body size variation increased with density for city park populations. Together, these results suggest that these trends within the city may be linked to an increased frequency of alternative male reproductive tactics (previously described in the eastern water dragon (Baird et al., 2012)), where both large and small males coexist. This could be because, unlike native habitat populations, city park populations are enclosed habitats where males are unable to disperse and are therefore faced with a limited number of available territories. In these highly competitive environments (high density and limited territories), larger males may be better able to hold and maintain territories, compared with smaller males. Smaller males are then left to either forgo reproduction or adopt satellite mating tactics and sneak copulations in order to reproduce (Baird et al., 2012). The presence of alternative male reproductive tactics, and thus the existence of both large and small males (increased male body size variation), creates variation in the extent of male-biased SSD, thus "diluting" the extent of SSD we observe.

Our analyses of a single city park population suggest that sexual selection is the primary driver of within-population male-biased SSD. We found a significant positive relationship between SSD and agonistic frequency. Agonistic behaviour is often a sexually selected trait as it is tightly linked to an individual's fitness since it plays an important role in territory defence and male–male competition (Carpenter, 1978; Trivers, 1976). Consistent with alternative reproductive tactics, male eastern water dragons that were larger relative to females within their home ranges (larger SSD), had a larger overall body size compared to other males, and displayed a higher frequency of agonistic displays than smaller males (Figure 1cii). In larger territorial males, agonistic behaviours are displayed in order to defend females and/or resources, whereas smaller satellite males do not defend territories and therefore tend to display fewer agonistic behaviours (Baird et al., 2012). This aligns with previous studies in other lizard species, where male-biased SSD has been linked to male agonistic behaviour (Carothers, 1984). For instance, using 497 lizard populations representing 302 species and 18 families, Cox et al. (2003) found that as predicted by the intrasexual selection hypothesis (sexual selection arises from variance in mating success and can act via intrasexual processes, e.g. male aggression), agonistic male behaviour was significantly correlated with male-biased SSD. We expected that larger agonistic males may have more females or males within their home range and potentially a higher home range density. However, this was not the case, possibly because the frequency of a male's agonistic behaviour largely depends on his reproductive tactic (dominance or satellite tactics) rather than the number of individuals that occur within his home range (home range density). In addition, we found that larger agonistic males have, on average, smaller females within their home range compared to other smaller less agonistic males. Whilst further research is required to better understand this result, it highlights that SSD at the within-population level is driven by relatively larger (agonistic) males having relatively smaller females within their home range (increased SSD).

Overall, our results suggest that although sexual selection may drive SSD at the within-population level, effects of density on variation in SSD between populations depend on habitat. Furthermore, in agamid lizards, density can drive the directionality of SSD between species (female-biased to male-biased) whilst ecological generalism predicts the extent of male-biased SSD between species. These results highlight that that the interaction between natural and sexual selection in the evolution of SSD can result in different patterns at differing evolutionary levels. By combining macro-evolutionary and fine-scale evolutionary patterns to better understand patterns of SSD, this study serves as a template for future comparative analyses across other taxa. In order to extend between-population and within-population level analyses, it would be insightful to compare this study with patterns found in female-biased size dimorphic agamid species. Moreover, our results suggest that human-engineered environments can lead to the increased frequency of alternative male reproductive tactics when population density exceeds a particular threshold, thus reversing the direction of the effect of sexual selection on male-biased SSD. This suggests that city landscapes, in addition to altering genetic and morphological patterns (Littleford-Colquhoun et al., 2017), can also influence the relationship between natural and sexual selection.

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AUTHORS' CONTRIBUTIONS

B.L.L.-C. collected data, and G.T. and D.S.-F. provided additional field data. B.L.L.-C. performed statistical analyses. C.H.F., K.S. and C.C. contributed to statistical analyses. R.H.C. and N.P. contributed to metadata analysis, and D.S.-F. contributed to the study design of this work. B.L.L.-C. wrote the manuscript, with advice from C.H.F. and all co-authors.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.jm8r78r (Littleford-Colquhoun et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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