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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

Sexual size dimorphism, natural selection, sexual selection, Agamid lizards, eastern water dragon, city landscapes, eco-evolutionary interactions.

Introduction

Sexual size dimorphism (SSD) is common in nature and often reflects the conflicting demands and selective pressures operating on the sexes (Wikelski and Trillmich 1997). Many vertebrate taxa display male-biased SSD (Abouheif and Fairbairn 1997), which is usually attributed to sexual selection (Darwin 1883), 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, and 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 (Stamps 1983, Carothers 1984, Andersson 1994, Cox et al. 2003, Cox, Butler, and John-Alder 2007). Larger males, therefore, obtain a greater lifetime reproductive success (Clutton-Brock et al. 1987, Owen-Smith 1993, Baird, Fox, and McCoy 1997, McElligott et al. 2001, Isaac 2005). Both mating system and mating competition have been shown to positively influence SSD (Dunn, Whittingham, and Pitcher 2001, Szekely, Lislevand, and Figuerola 2007), indicated by correlations between male-biased SSD and the sex ratio of the population (Stamps 1983, Poulin 1997), and the frequency of agonistic behaviour (Stamps 1983, Carothers 1984, Cox et al. 2003). In terrestrial turtles, for example, male-biased SSD is predominantly determined by male-male combat (Berry and Shine 1980), whilst in ungulates and cervids, SSD is largely driven by adult sex ratio (Alexander et al. 1979, Clutton-Brock, Albon, and 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 (Fisher 1958, Clutton-Brock, Harvey, and Rudder 1977, Ralls 1977, Lande 1980, Slatkin 1984, Shine 1989, Fairbairn 1997). Ecological niche partitioning can occur in order to reduce resource competition between the sexes (Schoener 1967, Shine 1991, Pearson, Shine, and How 2002, Losos, Butler, and Schoener 2003, Butler, Sawyer, and Losos 2007), or can occur due to differences in life histories between males and females (Wikelski and 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, and 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, and 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 (Shine 1989, Krüger 2005, Krüger, Davies, and Sorenson 2007). 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 and Stuart-Fox 2011). Second, natural selection can constrain the evolution of exaggerated sexual traits, including body size (Hosken and 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 (Ghiselin 1976, Emlen and Oring 1977, Kokko and Rankin 2006), where larger male size is favoured at high density (increased male-male competition) due to the fitness advantage larger size confers (Ghiselin 1976, 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 (Wirtz 1982, Forsyth and Montgomerie 1987, Zimmerer and Kallman 1989, Eadie and Fryxell 1992, Berard et al. 1994, Lucas and Howard 1995, Reichard, Smith, and Jordan 2004, Tomkins and Brown 2004). 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 and Trillmich 1997). Resource density and habitat type ultimately modulate population density, and can therefore, in turn, influence the degree of competition over mates (Kokko and 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 i) 43 Australian agamid species (1069 individuals), ii) nine populations of a single species, the eastern water dragon (*Intelegama lesueurii*; 264 individuals), and iii) 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.

Materials and Methods

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, Fig. S1 and S2 show the sex differences between morphological traits at the between-species, between-population and within-population level analyses.

i. Between-species level

Morphological data were compiled using museum specimens and published literature for 43 agamid species (Thompson and Withers 2005, Thompson et al. 2009, Littleford - Colquhoun et al. 2017). Where possible, data were collected for at least five individuals of each sex, for each species (see Table S2 for species numbers).

ii. 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 across both their native riparian habitat (ranging from Northern Queensland to north eastern Victoria) and across human-dominated landscapes (including urban and suburban locations (Baird, Baird, and Shine 2012, Gardiner et al. 2014)). Eastern water dragons display male-biased sexual dimorphism with males having larger

heads and jaws and displaying red ventral colouration (Baird, Baird, and Shine 2013, Thompson 1993, Cuervo and Shine 2007). In addition, males exhibit alternative mating strategies by either aggressively defending a territory or assuming satellite behaviour (Baird, Baird, and Shine 2012), whilst female dragons are polyandrous (Frère, Chandrasoma, and 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, Baird, and Shine 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 manmade 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). Fig. 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 un-fragmented 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 Table S3 for sample sizes for each city park and native habitat populations. Satellite images of all city park and native habitat populations are displayed in Fig. S4. Only adult eastern water dragons were used in between-population SSD analyses (male SVL > 226mm, female SVL > 187mm). As we do not currently have growth trajectories for the eastern water dragon, we used SVL cut offs to differentiate between adult and sub adult 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 < 150mm were considered juveniles, whilst the mean SVL of all individuals with SVL > 150mm was used to differentiate between sub adult and adult eastern water dragons. This mean SVL was calculated separately for males and females.

iii. 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 (Fig. 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 Spectacular 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 et al. 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 0730 and 1030 hours and between 1300 and 1500 hours) between August and April (2014 to 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).

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 and 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 (Fig. S6), and therefore used all female-male pairs 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 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 utilised 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 utilisation 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-populations 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 Table S4 for pPCA/PCA loadings for each evolutionary level). SSD values were used in subsequent analyses.

Predictor variables

1. Density

i. 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 and Owens 2003). Whilst we acknowledge there are caveats using this estimate, unfortunately 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.

ii. Between-population level

Population density was estimated as the number of individuals per square meter and was calculated by slowly walking transects through each population, recording all lizards encountered (Anderson et al. 1979, Kacoliris, Berkunsky, and Williams 2009, de Infante Anton et al. 2014). 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-minute gap was kept between transect replications so dragons could return to the area if disturbed. Only dragons that occurred within seven to 10m (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 non-linear, transects were walked within a defined plot, with the area of each plot calculated for density estimates.

iii. 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 m²).

2. *Habitat*

i. *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).

ii. *Between-population level*

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

iii. *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 Spectacled Garden (Spec).

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 Table S5 for PCA loadings) to calculate species size as $[(\text{mean male } PC1 + \text{mean female } PC1) / 2]$ for each species.

4. *Agonistic displays*

The frequency of agonistic displays (per male) were 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.

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.

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 the 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 generalised least square 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 1) 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 Table S2 and were identified using raw morphology data), and 2) 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 randomised 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 randomisation procedure 1000 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 and Neuhauser 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 Table S5 for PCA loadings).

Results

Between-species level

We assessed the effect of species' density (number of individuals per km² 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 ($2.7\text{E-}06 \pm 0.31$; mean $\pm$ s.d), 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 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 $\lambda = 0.00072$, $P = 1$; Fig. 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 km², 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 inter-species variation in SSD, with density, number of climate zones and species size all found to be significant predictors (Table 2a, Fig 1a and Fig. 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; Fig. 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; Fig. 1 aii). Conversely, no variables significantly predicted smaller than average male-biased SSD and female-biased SSD (Table 2c).

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 of 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 $\pm$ s.d; Fig. 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; Fig. 1 bii), 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 (Fig. 1 bii). 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 > -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 (> -1.8 logDensity), we found that city park populations displayed smaller SSD PC scores (0.064 ± 1.972 ; mean $\pm$ s.d) 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.

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 ($2.11E-12 \pm 1.687$; mean $\pm$ s.d; see Fig. 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; Fig. 1 cii), 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).

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’ (Proulx 1999, Östman and Stuart-Fox 2011) or as a by-product of density (Borregaard and 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), while 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; Ghiselin 1976, Emlen and Oring 1977, Kokko and 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 urbanised versus more rural locations).

At the between-population level, we found that the relationship between density and SSD was influenced by habitat type (Fig. 1 bii). Similar to other lizard species and pseudo-scorpions (Stamps 1983, Zeh 1987, Stamps, Losos, and Andrews 1997), we found that, in native habitat, SSD was positively correlated with population density. Further, for high density populations ($> -1.8 \log \text{Density}$), 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, Baird, and Shine 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, Baird, and Shine 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), and had a larger overall body size compared to other males, displayed a higher frequency of agonistic displays than smaller males (Fig. 1 cii). 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, Baird, and Shine 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 depends on habitat. Furthermore, in agamid lizards, density can drive the directionality of SSD between species (female-biased to male-biased) while ecological generalism predicts the extent of male-biased SSD between species. These results highlight 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.

Author contributions

BLLC collected data, GT and DSF provided additional field data. BLLC performed statistical analyses. CHF, KS and CC contributed to statistical analyses. RC and NP contributed to metadata analysis, and DSF contributed to the study design of this work. BLLC wrote the manuscript, with advice from CHF and all co-authors.

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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

Table S1. Mean (μ) and standard deviation (s) of seven morphological traits for 43 agamid species.

Table S2. Sample sizes used at the between-species level analyses.

Table S3. Population sample sizes, mean and standard deviation (stdev) of SSD PC scores used for between-population level analyses.

Table S4. Loadings from the first PC of a phylogenetic PCA at the between-species level and a standard PCA at the between-population and within-population levels.

Table S5. Loadings from the first PC of a morphological PCA.

Fig. S1. Boxplots showing variation in morphology at the between-population level analyses.

Fig. S2. Boxplots showing variation in morphology at the within-population level analyses.

Fig. S3. Map showing locations of all four city park populations.

Fig. S4. Satellite images showing land use and vegetative cover of isolated native habitat populations and city park populations.

Fig. S5. Map of CP3 study site.

Fig. S6. Graph showing high correlation between two different calculations of sexual dimorphism index.

Fig. S7. Between-species measures of SSD PC scores plotted next to the agamid phylogeny.

Fig. S8. Scatterplot of species size against SSD PC scores.

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Figure legend

Fig. 1. Predictors of sexual size dimorphism (SSD) at the a) 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, 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 2). (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 4).

814 **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	Calculation of body size	% variance PC1 explained	Type of model used	Dependent variable	Predictor variables	Random effects	Model weighted
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	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 Generalised Least Squares (PGLS)	SSD	logDensity + Number climate zones + Species size	NA	NA
	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 pairwise comparison within each population	1913	NA	55%	REML based linear-mixed models (LME)	SSD	logDensity * Habitat	Male ID Female ID Population	NA
Between-populations	Coefficient of variation (CV) of body size	1	9	NA	124	121	NA	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

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	1423	NA	41%	LME	SSD	logDensity * Microhabitat + Sex ratio + Agonistic frequency	Male ID Female ID	Home range overlap
	Agonistic behaviour	1	1	6	51	51	NA	NA	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
	Male and female body size	1	1	6	51	51	NA	NA		84%	LM	Male body size	Mean female size + stdev female size + number of males + number of females	Microhabitat	NA

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.

a) Between-species – all species	Parameter	Estimate	SE	t_{obs}	P value	Adjusted R^2	λ
SSD ~ Climate zones + logDensity + Species size						0.31	0
	Intercept	0.29	0.27	1.10	0.280		
	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	Parameter	Estimate	SE	t_{obs}	P value	Adjusted R^2	λ
SSD ~ Climate zones + logDensity + Species size						0.29	0
	Intercept	0.14	0.25	0.57	0.575		
	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	Parameter	Estimate	SE	t_{obs}	P value	Adjusted R^2	λ
SSD ~ Climate zones + logDensity + Species size						-0.00	0
	Intercept	0.06	0.22	0.28	0.784		
	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		

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

a) Between-population - overall SSD	Parameter	Estimate	SE	df	t_{obs}	95% t_{rand}	P value	Adjusted R ²
SSD ~ logDensity * Habitat								NA
	Intercept	11.00	3.71	234.37	2.96	-0.02 - 0.10	0.002	
	logDensity	7.60	2.34	232.91	3.25	-0.02 - 0.10	0.001	
	Habitat	-6.47	2.62	231.10	-2.47	-0.11 - 0.01	0.010	
	logDensity:Habitat	-4.44	1.66	230.31	-2.67	-0.11 - 0.01	0.007	
b) Between-population - Female CV of body size	Parameter	Estimate	SE	df	t_{obs}	95% t_{rand}	P value	Adjusted R ²
CV of body size ~ logDensity * Habitat								-0.65
	Intercept	0.78	0.51	NA	1.52	NA	0.203	
	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	Parameter	Estimate	SE	df	t_{obs}	95% t_{rand}	P value	Adjusted R ²
CV of body size ~ logDensity * Habitat								0.90
	Intercept	-0.16	0.33	NA	-0.49	NA	0.648	
	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	Parameter	Estimate	SE	df	t_{obs}	95% t_{rand}	P value	Adjusted R^2
SSD ~ logDensity * Microhabitat + Sex ratio + Agonistic frequency								NA
	Intercept	-5.82	5.36	50.77	-1.09	-0.04 – 0.12	0.194	
	logDensity	-4.29	3.27	50.66	-1.31	-0.06 – 0.10	0.151	
	Microhabitat	1.52	0.97	50.65	1.57	-0.10 – 0.06	0.089	
	Sex ratio	-4.67	4.27	50.80	-1.09	-0.11 – 0.04	0.180	
	Agonistic frequency	9.03	2.34	50.67	3.85	-0.09 – 0.04	< 0.001	
	logDensity:Microhabitat	0.89	0.60	50.65	1.48	-0.10 – 0.06	0.108	