Sex-specific associations between social behaviour, its predictability and fitness in a wild lizard

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Elements:

1) Table 1: Estimates (median and 95% credible intervals) from double hierarchical mixed models fitting social distance in males and females separately.
2) Table 2: Estimates (median and 95% credible intervals) from double hierarchical mixed models fitting social distance in both sexes.
3) Figure 1: Posteriors of mean social distance, intra-individual variation (IIV) in social distance, and their relationship in 386 eastern water dragons.
4) Figure 2: Full posterior distributions of the effects of individual social distance (mean and IIV) on fitness measures in each sex.
5) Figure 3: Predicted lifetime reproductive success and reproductive success as a function of individual standardized values for mean social distance and IIV in males and females.
6) Figure 4: Predicted survival as a function of individual mean social distance and IIV in males and females.

Abstract

Social environments impose a number of constraints on individuals' behaviour. These constraints have been hypothesized to generate behavioural variation among individuals, social responsiveness, and within-individual behavioural consistency (also termed 'predictability'). In particular, the social niche specialization hypothesis posits that higher levels of competition associated with higher population density should increase among-individual behavioural variation and individual predictability, as a way to reduce conflicts. Being predictable should hence have fitness benefits in group-living animals. However, to date, empirical studies on fitness consequences of behavioural predictability remain scarce. In this study, we investigated the associations between social behaviour, its predictability and fitness in the eastern water dragon (*Intellagama lesueurii*), a wild gregarious lizard. Since this species is sexually dimorphic, we examined these patterns both between sexes and among individuals. Although females were more sociable than males, there was no evidence for sex-differences in among-individual variation or predictability. However, females exhibited positive associations between social behaviour, its predictability and survival while males only exhibited a positive association between mean social behaviour and fitness. These findings hence partly support predictions from the social niche specialization hypothesis and suggest that the function of social predictability may be sex-dependent.

Introduction

For many organisms, group living implies repeatedly interacting with the same social partners over time, which often requires dealing with conflict. For sociality to evolve, individuals must therefore adapt ways to minimise conflict and to maximise received fitness benefits. Behaviourally, individuals can do this in multiple ways. First, they can partition their behavioural (and/or ecological) niche (i.e., adopt different roles) such that conflicts do not arise as frequently (Bergmüller & Taborsky, 2010). Second, they may learn to respond to a partner's behaviour by altering their own behaviour (i.e., be socially responsive) (Johnstone, 2001). Third, they may become "predictable" in their behaviour (i.e., behave consistently), allowing conflict to be avoided by allowing social partners to learn an optimal behavioural response (Wolf et al., 2011). These principles could explain why we often observe dominance hierarchies, spatio-temporal segregation or cooperation in group-living animals. The implication, therefore, is that for social evolution to occur, there needs to be both heritable variation in, and selection for social behaviours, social responsiveness and behavioural predictability within populations. Such variation is expected to be maintained by natural selection, via frequency-dependent mechanisms (Wolf & McNamara, 2013).

Heritable social behaviours should manifest as consistent behavioural differences among individuals. In the past two decades, animal personality research has uncovered a variety of ways in which individuals consistently differ in their behaviour. Importantly, consistent differences may not only concern average levels of repeatedly expressed behaviours (e.g., some individuals are bolder than others, Bell et al., 2009), but also the way individuals plastically adjust their behaviour to environmental conditions (e.g., some individuals are more plastic than others, Dingemanse et al., 2010) and their behavioural predictability (e.g., some individuals behave more consistently than others, Stamps et al., 2012). Although less studied than among-individual variation in behaviours and plasticity, among-individual variation in predictability has been reported in an increasing number of species (see Mitchell et al., 2021), has been shown to be determined by additive genetic effects (Martin et al., 2017; Prentice et al., 2020) and may have fitness benefits. For instance, behaving unpredictably has been suggested to decrease predation risks (Briffa, 2013; Humphries & Driver, 1970; Richardson et al., 2018), and shown to increase fitness when foraging under unpredictable environmental conditions (Patrick et al., 2021).

In contrast, and as mentioned earlier, higher predictability should be favoured in social contexts that involve repeated interactions (Johnstone, 2001; Wolf et al., 2011). Individual variation in social behaviour and social responsiveness has been widely studied (Aplin et al., 2015; Chervet et al., 2011; Watson et al., 2018) and social behaviour has been shown to correlate with fitness (Brent et al., 2013; Delmé et al., 2023; Kohn, 2017; Silk, 2007). At the same time, social behaviours and responsiveness have also been shown to be heritable (Bailey & Desjonquères, 2022; Godoy et al., 2022; Lea et al., 2010). In contrast, predictability has seldom been studied in social traits and the association between social predictability and fitness has, to our knowledge, never been reported.

In the present study, we take advantage of a unique behavioural dataset collected in wild eastern water dragons (*Intellagama lesueurii*) to estimate individual predictability in social behaviour and investigate its correlation with individual mean social behaviour and fitness. Here, we focus on social distance, a proxy for social tolerance, which refers to non-aggressive physical proximity between individuals and represents a fundamental first step for the evolution of affiliative behaviour (Smith & Ivins, 1984). The eastern water dragon is a territorial and long-lived agamid lizard, which exhibits long-term social associations and avoidances (Strickland et al., 2017). In this sexually dimorphic species, sexes differ in their spatial and social behaviour. In particular, females are generally more sociable than males and occur in smaller territories which they largely share with other individuals (Baird et al., 2012). Previous research has also shown that dragons vary consistently in social behaviours (e.g., degree, social tendency, choosiness, centrality, density, Delmé et al., 2023; Strickland & Frère, 2018) and in their social plasticity (e.g., how they adjust their social tendency to local density, Strickland & Frère, 2019).

In particular, we test predictions from the social niche specialization hypothesis (Bergmüller & Taborsky, 2010) between and within sexes. This hypothesis, which is derived from ecological niche theory, posits that individuals within a population should adopt different behavioural niches to reduce the costs of intraspecific competition, which drives among-individual variation. Under higher densities or when competition intensifies, populations are hence expected to exhibit more among-individual variation and individuals to be more predictable. In dragons, individuals of both sexes compete for resources (e.g., food, shelter and basking sites) and the costs of such competition increase with density

(Baxter-Gilbert & Whiting, 2019). Males show alternative mating strategies associated with body size, territory exclusiveness, and agonistic displays (i.e., territorial to satellite, Baird et al., 2012; Piza-Roca et al., 2020 but see Ball et al., 2023) due competition for access to females. This additional source of intra-sexual competition in males may drive a higher among-individual variation and a higher predictability in their social behaviour compared to females. Alternatively, male mating strategies may be unrelated to social tolerance, and we could find the opposite pattern between sexes. Indeed, females are more often found in the vicinity of each other (Baird et al., 2012; Strickland & Frère, 2019), which may drive a higher level of competition for resources. The latter would be supported by a recent finding that females are slightly more repeatable than males in several social traits (i.e. social tendency and association strength in same-sex interactions and density Delmé et al., 2023).

Predictions from the social niche specialization hypothesis could also be extended to the individual level as social environments often vary within populations. That is, we would expect more socially tolerant individuals, which consistently occur in denser environments (be it by choice or not, see Webber & Vander Wal, 2018), to be more predictable than individuals that are less socially tolerant and occur in sparser environments. If predictability is an adaptation to reduce the costs of social conflicts, we would expect it to be positively associated with fitness. Alternatively, unpredictability could be favoured if it reflects individuals being more opportunistic and better at appropriately adjusting their behaviour to every situation (Briffa & Lane, 2017). Using double-hierarchical generalized linear models and >30000 observations made over 4 years in >300 individuals, we provide rare estimates of predictability in social behaviour and its association with mean social behaviour and fitness in the wild.

Methods

Study species

The eastern water dragon is a long-lived (lifespan of 28–40 years, Harlow and Harlow 1997, Griffiths 2006) agamid lizard exhibiting male-biased sexual dimorphism (Thompson, 1993), polyandry (Frère et al., 2015) and alternative mating strategies (Baird et al., 2012). In this species, individuals hold territories, which vary in size and exclusiveness between females, territorial males and non-territorial males (Baird et al., 2012; Gardiner et al., 2014). While females' territories are smaller and largely overlap with each other, male territories generally overlap with females' and either exclude (for territorial males) or overlap with other male's (non-territorial males) (Baird et al., 2012). In this species, spatial proximity between individuals has been used as a proxy for affiliative interactions. Previous research has established that individuals remaining within 1.85m of each other without exhibiting agonistic behaviours (e.g., head bobbing, arm waiving, tail slapping) express social tolerance towards each other (Strickland et al., 2014). However, this distance represents a small percentile of all social distances and individuals can adjust their social behaviour depending on their location within their entire home range (which are larger than 4200m^2 for males and 2700m^2 for females, Piza-Roca et al., 2018). Therefore, variation in social tolerance likely encompasses a larger range of distances. Previous research in this population has also shown that dragons form non-random associations with other individuals (e.g., as preferences and avoidances, see Strickland et al., 2014, 2017) and that sexes differ in their average levels of sociality. Indeed, females are generally more social than males and form stronger associations with females and males than males do with each other (Strickland et al., 2014). Sexes differ in their repeatability, males being more repeatable in social network metrics (Strickland & Frère, 2018) and females being more repeatable in density (Delmé et al., 2023). Sexes were also found to differ in their social plasticity (Strickland & Frère, 2019). Indeed, while both sexes increase social tendency and non-random associations in response to local density, females plastically respond to their social environments (e.g., sex ratio, number of avoidances) more than males (Strickland et al., 2018; Strickland & Frère, 2019). Finally, recent research has shown a positive association between reproductive success and social behaviour (degree and social tendency) towards opposite-sex partners in males, while no such association was found in females (Delmé et al., 2023).

Data collection

Behavioural data was collected as part of an ongoing long-term study (started in 2010) of a wild urban population of eastern water dragons at the Roma Street Parkland, Brisbane, Australia (27° 270 4600 S, 153° 10 1100 E). This population, which has an average estimated size of 336 individuals, has been monitored through frequent behavioural surveys (most of them from September to April when individuals are most active). As with many other long-term studies, data was collected by a number of researchers (including authors of this study) and students and was used in independent research projects. Behavioural surveys were conducted once or twice a day (am and pm) on average three times a week. Observers walked along a defined transect of the parkland, which covers 85% of the population (Strickland et al., 2014), and collected data for all the individuals encountered. Individuals in this population are recognizable thanks to their unique facial scale and colouration patterns (Gardiner et al., 2014). Head profile photographs of each individual were taken upon encounter (using a Canon EOS 600 digital camera) to allow their later identification using the I3S Manta software package (Van Tienhoven et al., 2007). Each individual's behaviour was also recorded (e.g., aggression or mating behaviours), along with its GPS coordinates (using a Garmin eTrex 10 handheld device, with a 3m resolution). Sex determination was based on sexual dichromatism and dimorphism present in the species, males being larger, with wider jaws, and presenting red colouration on their chest (Thompson, 1993).The behavioural data used in this study was collected between August 2016 and August 2020. During this period, individuals had on average at least 41 observations per field season. Data was collected under animal ethics approval through Animal Ethics Committee of the University of the Sunshine Coast (ANA1487) and Scientific Purposes Permit (WISP17696616).

Response variable

For each observation of each individual, we used the minimum distance (in m) to other individuals present within the same survey as a proxy for social tolerance such that the higher the distance, the less socially tolerant an individual was. Importantly, we excluded observations during which individuals were engaged in agonistic or mating interactions from the analyzed dataset. This measure is hereafter referred to as "social distance". Previous work on social behaviour in this population focused on the occurrence of social proximity between individuals, to capture social tolerance or gregariousness (Strickland et al., 2014). However, the distribution of such sociality measure (binary) did not allow fitting DHGLMS, which is why we chose a distance variable. Note that social distance was perfectly correlated (r=-1) to this previously used binary index and to the number of individuals present within 9.25 m (the average dragon territory size, see Strickland & Frère, 2019) at the among-individual level

(Text S1, Tables S1-S4). Hence, these measures capture the same aspect of an individual's social environment (Webber & Vander Wal, 2018). Individual variation in social environments can be driven by individuals establishing their territories in habitats that have varying densities or by seeking or avoiding the proximity of other individuals. We note that both processes cannot be disentangled because dragons, which are free to express habitat choice, can disperse to any suitable area of this urban park.

Parentage analyses

To determine reproductive success, we conducted annual sampling between 2010 and 2020. We caught all possible adult individuals using a lassoing technique and collected tail tip tissue or blood through caudal venepuncture (Littleford-Colquhoun et al., 2017). We further measured snout-vent length and captured head profile images to match individuals to behavioural data using the previously described facial scale identification method (Gardiner et al., 2014). We extracted DNA from blood and tissue using DNeasy Blood and Tissue extraction kits (Qiagen) as per manufactures instructions. The extracted DNA was then sequenced at Diversity Arrays Technology, Canberra, using DArTcap^{TM} technology (Feutry et al., 2020). This resulted in a total of 6,425 SNP loci prior to filtering, across 1285 individuals for which 775 were adults with behavioural survey data. As per Delmé et al., 2023, we restricted homozygote genotype calls to those with a minimum read depth of 5 to account for false homozygote genotype calls. Using the dartR package (Mijangos et al., 2022), SNPs were further filtered for an individual call rate of 80% or greater, a locus call rate of 99% or greater, removal of monomorphic loci, the proportion of technical replicates assay pairs of at least 99%, and only one locus per short read tag was retained. We used plink to filter for linkage disequilibrium with locus pairs exhibiting an $r^2 \geq 0.7$ removed from the dataset (Chang et al., 2015).To determine the optimal minor allele frequency (MAF) filtering we conducted a sensitivity analysis by using a range of MAF values (0.3-0.4). Each subsequent dataset was then used to assign parentage using the R package Sequoia (Huisman, 2017). We selected the MAF filtering parameters by the highest assignment rate of known mothers and lowest number of misassignments to known mothers (Jackson et al., 2019) and cross validated these using relatedness estimates (See Delmé et al., 2023, for which parentage data herein overlaps). The best performing filtering used a MAF $\geq$0.43 producing a resultant data set of 179 high quality loci were then used to assign parentage with the R package, Sequoia (Huisman, 2017). From the 775 adult individuals included in the parentage assignment, 77 dams and 82 sires were assigned at least one offspring. A total of 535 offspring assignments were made to 239 dams and 296 sires.

Fitness metrics

We defined three fitness metrics: lifetime reproductive success, reproductive success, and survival. Lifetime reproductive success was the total number of adult offspring produced by individuals during their entire lifetime. This metric was hence only available for individuals assumed to be dead (not seen during the 2022-2023 field season). In this rather closed population (Littleford-Colquhoun et al., 2017), 99% of consecutive sightings of individuals occurred within 27 days and 97.6% of multi-season sightings of individuals occurred in consecutive field seasons. Lifetime reproductive success was corrected (using fixed effects, see section below) for the year of appearance to account for the fact that individuals that appeared later during the study (particularly after 2017) were less likely to have offspring that would be caught as adults (i.e., at least 2-3 years old) before the end of 2020 (end of the sampling, see above). For similar reasons, a new recruit can be assigned to a parent several years after its parent died. We tested whether the year of disappearance was associated with a decline in lifetime reproductive success but found no evidence for such association. Lifetime reproductive success data was available for 125 females and 134 males.

Our second fitness proxy, age-corrected reproductive success, was the total number of adult offspring of individuals (regardless of whether they were dead or still alive), corrected by the number of years individuals had been in the population and year of appearance (using fixed effects, see section below). This proxy therefore measures the average number of offspring an individual has at a given age. Reproductive success data was available for 177 males and 188 females.

Our third fitness proxy, survival, was the number of years an individual had been seen in the population (data from March 2023) and was corrected for its year of appearance and detectability (the median time between its successive observations). This metric therefore indicated whether for a given year of appearance and detectability level, an individual lived longer than another. Survival data was available for 180 males and 196 females and included individuals that were still alive and that were not genotyped.

In this dataset, 10 individuals severely infected with the recently emerged fungal pathogen *Nannizziopsis barbatae* (Peterson et al., 2020) were euthanized between 2018 and 2021. These individuals were excluded from the lifetime reproductive success and survival analyses. Although a substantial (>30%) proportion of the population now exhibits symptoms concordant with *N.barbatae* infection, most cases are relatively mild and a previous study did not detect any impact of the disease on dragons' social behaviour (Tacey et al., 2023). These individuals therefore remained in the social behaviour analyses.

Statistical analyses

The recent introduction of double-hierarchical generalized linear models (DHGLMs, Cleasby et al., 2015) in ecological research and the availability of statistical tools (e.g., brms, Bürkner, 2017) have allowed the investigation of increasingly complex aspects of behavioural variation such as the relationship between average levels of behaviours and their predictability (Hertel et al., 2020). Here, we performed our statistical analyses in R (R Core Team, 2022) using the package brms (Bürkner, 2017). We fitted all models in males and females separately. A DHGLM is a mixed model which includes a mean model and a dispersion model. While the mean model of a DHGLM allows estimating how fixed and random effects impact the response (here social distance), the dispersion model fits residuals from the former as a function of the same or different fixed and random effects to test how these effects impact deviations in the response relative to the population mean. Among-individual variation in the mean model hence captures individual differences in the average value of the response while among-individual variation in the dispersion model captures individual differences in the average value of deviations (i.e., predictability). Importantly, these deviations include random "noise" but also plastic responses to unknown external factors (Stamps et al., 2012; Westneat et al., 2015). The higher these deviations, also termed intra-individual variation (IIV) are, the more unpredictable or plastic an individual is.

Fixed effects in both models included: i) a measure of body size (snout-vent length, measured during annual captures, Littleford-Colquhoun et al., 2017) to account for individual differences due to age and/or dominance (Baird et al., 2012; Piza-Roca et al., 2020), ii) quadratic seasonal effects (day since the 1st of August), iii) field season (4 years, factorial) and iv) time of the day (morning vs. afternoon surveys). Random effects in both models included individual identity (ID) to estimate long-term individual variation in intercepts, a within-season individual component (a combination of ID and Field Season, Araya-Ajoy et al., 2015) to account for consistent individual variation driven by short-term environmental factors, and date of observation. The parameters of interest for this study were therefore the long-term individual variance in observed behaviour (mean model), in deviations (dispersion model) and their correlation. A similar model was run for the total population dataset, and included sex as a fixed effect to test for sex differences in mean sociability and predictability.

In all models, social distance was fitted using a lognormal distribution. However, the distribution of social distances included zeros (8% of the records), most of which were probably not true zeros (two individuals touching) but distances lower than the detection threshold (the minimum non-zero distance recorded), here 1.64 m, which is roughly two dragon lengths. To be able to fit a lognormal distribution on our model, we therefore, needed to add a constant to these zeros, the value of which was determined using simulations (Text S2). These simulations showed that a constant equal to 80% of our detection threshold combined with left-censoring allowed retrieving unbiased parameter estimates (Figures S1-S2). We note that zeros represent a small proportion of our data and that our detection threshold of 1.64m is lower than the distance previously established for social tolerance (1.85m) in this study system (Strickland et al., 2014). Therefore, most variation in social behaviour in this study species is expected to occur at a larger scale.

All models used default uninformative priors, 4 chains and thinning intervals of 4. Univariate models were run for 5000 iterations (1000 warmups). More informative priors were also fitted and yielded similar results (Table S5). All models had an effective sample size above 1000 and model performance was assessed based on R-hat values being under 1.01, and visualizing trace plots and posterior predictive plots. Model fit was also assessed by calculating R^2, which was 0.19 for males and 0.21 for females.

Raw-scale estimates of individual repeatability (Rp) and coefficients of variation (CV, the ratio of standard deviation on mean) were computed for each sex. These two metrics, which are variance-standardized for the former and mean-standardized for the latter, facilitate between-studies comparisons and meta-analyses. Their calculation followed the procedures described in O'Dea et al., 2022, which involve computing the variance of fixed effects, and back-transforming variance estimates to the original data scale for the mean and dispersion models. Finally, to assess sex-bias in variability we computed the natural logarithm of the ratio of male and female CVs (lnCVR, see Nakagawa et al., 2015; Zajitschek et al., 2020), positive values indicating a male bias.

To investigate how social distance and its predictability were associated with fitness, our three fitness measures were fitted as a function of individual-specific values derived from the model (best linear unbiased predictors, BLUPs). More specifically, each fitness measure was either fitted as a function of individual values in mean social distance or individual values for IIV in social distance. We modelled reproductive success responses with zero-inflated Poisson distributions (using the pscl package, Jackman, 2010; Zeileis et al., 2008), and survival with a Cox proportional-hazards model (using the R package survival, Therneau, 2024). These models included additional fixed effects such as year of appearance, number of years in the population (for reproductive success) and detectability (for survival). Each model was run for each individual posterior value (i.e., 4000 times) and we stored each coefficients to later calculate their median and 95% credible intervals. Caution has been raised against the use of BLUPs in subsequent analyses when such procedure does not consider uncertainty around each BLUP, which can result in spurious results (Hadfield et al., 2010). However, we here used their entire posterior distribution and checked using simulations (Text S3, Figure S3) that this approach generated little to no bias for estimating selection when fitness has a zero-inflated Poisson distribution and the phenotype is moderately repeatable. Individual-level correlations between traits and fitness have been shown to estimate selection more accurately than do phenotypic correlations (Dingemanse et al., 2021). While multi-response models would have been preferable for these analyses, we could not satisfactorily implement a multivariate DHGLM for traits that do not have the same number of repeats (fitness being measured once), and different distributions (number of offspring being zero-inflated) in the package brms. This prompted our decision to use a 2-step approach, after carefully verifying that this approach would yield unbiased results.

Results

Summary statistics

The entire dataset included 30475 records from 189 males and 197 females. Individuals were observed on average 41 times per field season. Approximately 46% of all individuals were recorded for more than one field season. Regarding sex-specific trait distributions, males seemed to be less social than females. Indeed, the raw social distance was on average 7.1 m (sd=6.8) in males and 5.9 m (sd = 6.4) in females. As a result, females experienced higher conspecific densities than males (6.5×10^{-3} [6.1×10^{-3}; 6.9×10^{-3}] and 5.6×10^{-3} [5.2×10^{-3}; 6.0×10^{-3}] individuals per m^2, respectively, Text S4). Social distance also seemed to be slightly more variable phenotypically in females than in males (lnCVR = -0.11). Regarding fitness proxies, the reproductive success of individuals known to be dead was similar between sexes (1.01 for males and 1.04 for females), although males exhibited more variability than females (sd=2.55 for males and 1.63 for females, lnCVR =0.48). In the entire population, males and females also had on average the same number of offspring (0.87 for males and 0.85 for females), and males also exhibited more variability than females (sd=2.34 for males and 1.46 for females, lnCVR = 0.44). In contrast, males had an average survival of 3.39 years (sd=2.38), which was lower than females' survival (mean =3.80, sd=2.47) but variability in survival was quite similar between the sexes (lnCVR = 0.08).

Individual variation in mean social distance

Neither body size nor time of the day influenced social distance, which increased within field seasons in females and decreased across years in both sexes (Table 1). Females were hence less socially tolerant towards the end of a field season but both sexes were increasingly tolerant across years. The model pooling both sexes confirmed that males and females statistically differed in their mean social distance, males having higher values (indicative of lower social tolerance) than females (0.16 [0.07; 0.25], Table 2, Figure 1). In both sexes, we detected long-term (across years) among-individual variation in mean social distance (sd = 0.28 [0.24; 0.33] for males and 0.34 [0.29; 0.40] for females). The point estimate of among-individual variance was larger in females than in males although evidence for this female bias was weak (lnCVR = -0.19 [-0.48; 0.09]). Long-term individual effects were greater contributors to variation in social distance than date (sd=0.12 [0.10; 0.14] for both) and within-season individual effects (sd = 0.17 [0.13; 0.20] for males and 0.20 [0.17; 0.24] for females). While social distance had a rather low long-term repeatability in both sexes, females tended to be slightly more repeatable than males (R = 0.18 [0.14; 0.24] for females and 0.13 [0.09; 0.17] for males, Table 1).

Individual variation in predictability of social distance

Similar to mean social distance, predictability in social distance was not associated with body size or age but individuals were increasingly predictable (decrease in IIV) within and between seasons (Table 1). The model pooling both sexes did not show any statistical difference between sexes in average predictability (difference=-0.01 [-0.04; 0.03], Table 2, Figure 1). Males and females both exhibited long-term among-individual variation in predictability (sd=0.08 [0.05; 0.11] in males and 0.07 [0.04; 0.09] in females). This long-term individual component was a slightly greater contributor to variation in predictability than date (sd=0.02 [0.00; 0.05] for males and 0.07 [0.05; 0.09] for females) and short-term individual effects (sd=0.06 [0.01; 0.09] for males and 0.04 [0.00; 0.07] for females). There was however no evidence that among-individual variation in predictability differed between sexes (Table 1, lnCVR = 0.23 [-0.34; 0.74]) and the repeatability of this intra-individual component (i.e., its relative importance compared to the total phenotypic variance for this trait) was very low (1%) in both sexes. This is because the dispersion model explained a very small proportion (3%) of the residual variance from the mean model (Table S6). As a result, most of the variance in social distance was left unassigned (76% for males, 68% for females). Finally, we found within females that individuals with higher social distances were less predictable (higher intra-individual variation, or IIV) as evidenced by a strong positive correlation between mean social distance and IIV (0.79 [0.49; 0.98]) while males did not exhibit any association between social distance and IIV (0.00 [-0.29; 0.31], Table 1, Figure 1).

Table 1. Estimates (median and 95% credible intervals) from double hierarchical mixed models fitting social distance in males and females separately. Raw-scale repeatability (R) and coefficient of variation (CV) were calculated for the individual component in both the mean and the dispersion parts of the model. The model directly estimated the correlation between mean and intra-individual variance in social distance (Cor mean-dispersion). In the random effects, the Individual_Season component estimates within-year among-individual variation. Fixed effects for which the 95% CI did not include zero are printed in bold.

		Males	**Females**
Fixed effects			
Mean model	Intercept	1.78 [1.69; 1.86]	1.65 [1.56; 1.75]
	Body size	0.01 [-0.02; 0.05]	0.02 [-0.02; 0.06]
	Time of day (pm)	-0.01 [-0.04; 0.02]	-0.02 [-0.05; 0.01]
	Season day	0.00 [-0.02; 0.02]	**0.05 [0.03; 0.07]**
	Season day^2	0.02 [0.00; 0.04]	**-0.03 [-0.05;-0.01]**
	Season 2017-2018	**-0.10 [-0.19;-0.01]**	**-0.12 [-0.21;-0.02]**
	Season 2018-2019	**-0.14 [-0.23;-0.05]**	**-0.15 [-0.24;-0.05]**
	Season 2019-2020	**-0.21 [-0.32;-0.10]**	**-0.23 [-0.34;-0.11]**
Dispersion model	Intercept	-0.14 [-0.18;-0.10]	-0.17 [-0.21;-0.13]
	Body size	0.02 [0.00; 0.03]	0.01 [-0.01; 0.03]
	Time of day (pm)	-0.02 [-0.04; 0.01]	0.02 [-0.01; 0.04]
	Season day	**-0.03 [-0.04;-0.01]**	**-0.03 [-0.04;-0.01]**
	Season day^2	**0.04 [0.03; 0.06]**	**0.04 [0.02; 0.05]**
	Season 2017-2018	**-0.12 [-0.16;-0.08]**	**-0.11 [-0.15;-0.06]**
	Season 2018-2019	**-0.14 [-0.18;-0.09]**	**-0.12 [-0.16;-0.07]**
	Season 2019-2020	**-0.17 [-0.22;-0.12]**	**-0.18 [-0.23;-0.12]**
Random effects (sd)			
Mean model	Date	0.12 [0.10; 0.14]	0.12 [0.10; 0.14]
	Individual	0.28 [0.24; 0.33]	0.34 [0.29; 0.40]
	Individual_Season	0.17 [0.13; 0.20]	0.20 [0.17; 0.24]
	R	0.13 [0.09; 0.17]	0.18 [0.14; 0.24]
	CV	0.35 [0.28; 0.42]	0.42 [0.34; 0.51]
Dispersion model	Date	0.02 [0.00; 0.05]	0.07 [0.05; 0.09]
	Individual	0.08 [0.05; 0.11]	0.07 [0.04; 0.09]
	Individual_Season	0.06 [0.01; 0.09]	0.04 [0.00; 0.07]
	Cor mean-dispersion	0.00 [-0.29; 0.31]	0.79 [0.49; 0.98]
	R	0.01 [0.00;0.02]	0.01 [0.00;0.01]
	CV	0.51 [0.32; 0.68]	0.41 [0.27; 0.55]

Table 2. Estimates (median and 95% credible intervals) from double hierarchical mixed models fitting social distance in both sexes. Sex was fitted as a fixed effect in the mean and dispersion models to test for sex-differences in social distance and its predictability. The model directly estimated the correlation between mean and intra-individual variance in social distance (Cor mean-dispersion). In the random effects, the 'Individual_Season' component estimates within-year among-individual variation. Fixed effects for which the 95% CI did not include zero are printed in bold.

		Estimates
Fixed effects		
Mean model	Intercept	1.65 [1.57; 1.74]
	Body size	0.02 [-0.02; 0.05]
	Time of day (pm)	-0.02 [-0.03; 0.00]
	Sex (male)	**0.12 [0.03; 0.21]**
	Season day	**0.05 [0.03; 0.07]**
	Season day^2	-0.02 [-0.05; 0.00]
	Sex (male) : Season day	**-0.05 [-0.07;-0.03]**
	Sex (male) : Season day^2	**0.05 [0.02; 0.04]**
	Season 2017-2018	**-0.10 [-0.17;-0.03]**
	Season 2018-2019	**-0.14 [-0.21;-0.07]**
	Season 2019-2020	**-0.22 [-0.30;-0.13]**
Dispersion model	Intercept	-0.15 [-0.19;-0.11]
	Body size	0.02 [0.00; 0.04]
	Time of day (pm)	0.00 [-0.02; 0.02]
	Sex (male)	0.00 [-0.04; 0.03]
	Season day	**-0.03 [-0.04;-0.02]**
	Season day^2	**0.04 [0.03; 0.05]**
	Season 2017-2018	**-0.12 [-0.15;-0.08]**
	Season 2018-2019	**-0.12 [-0.16;-0.09]**
	Season 2019-2020	**-0.18 [-0.22;-0.14]**
Random effects (sd)		
Mean model	Date	0.13 [0.11; 0.14]
	Individual	0.31 [0.28; 0.35]
	Individual_Season	0.18 [0.16; 0.21]
Dispersion model	Date	0.07 [0.05; 0.08]
	Individual	0.07 [0.05; 0.09]
	Individual_Season	0.05 [0.02; 0.08]
	Cor mean-dispersion	0.38 [0.15; 0.61]

Links with fitness

We found evidence for sex-specific associations between social distance and our fitness proxies. First, lifetime reproductive success was negatively associated with mean social distance in males but not in females (Figure 2, 3). Males that were less socially tolerant produced fewer offspring in their lifetime (-0.13 [-0.29; 0.00]) and had a higher probability of siring no offspring (0.27 [0.00; 0.54], Figure 2). As a result, more social males were predicted to have 1.3 offspring and less social males to have 0.2 offspring on average in their lifetime (Figure 3). In contrast, there was weak evidence for unpredictable males to have more offspring in their lifetime (0.27 [-0.01; 0.55]) and no evidence for a relationship between predictability and the probability of siring no offspring (0.20 [-0.22; 0.69], Figure 2). As a result, the overall relationship between IIV and lifetime reproductive success in males (0.2 offspring for predictable and 0.9 offspring for unpredictable males) did not differ from zero (Figure 3). This relationship was of similar in magnitude in females (0.3 offspring for predictable and 1.1 offspring for unpredictable females, Figure 3).

Second, the relationship between age-corrected reproductive success and mean social distance was also negative in males, although the magnitude and level of evidence of this relationship were both weaker (Figure 2, 3). Indeed, there was no evidence that less socially tolerant males produced fewer offspring at a given age (-0.09 [-0.29; 0.07]), but these males had higher probabilities of siring no offspring (0.34 [0.08; 0.60], Figure 2). As a result, more social males were predicted to have 1.1 offspring and less social males to have 0.7 offspring on average at age 6 (Figure 3). In contrast, we found no evidence that reproductive success was associated with mean social tolerance in females and social predictability in both sexes (Figure 2, 3).

Third, we found that less socially tolerant individuals of both sexes had shorter lifespans (Figure 2, 4). Indeed, the effect of social distance on the risk of death was positive and similar in magnitude in both sexes (0.33 [0.01; 0.65] in males, 0.29 [0.07; 0.52] in females, Figure 2). As a result, more socially tolerant individuals lived on average longer (Q1, Figure 4; 3.93 [3.84; 4.02] for males, 4.53 [4.45; 4.61] for females) than less socially tolerant individuals (Q3, Figure 4; 3.75 [3.65; 3.84] for males, 4.34 [4.26; 4.40] for females). In contrast, we found the association between predictability and survival to be positive in females (1.76 [0.38; 3.39]) and null in males (-0.80 [-2.44; 0.81], Figure 2). As a result, more predictable females lived longer on average (Q1, Figure 4; 4.55 [4.45; 4.66]) than less predictable females (Q3, Figure 4; 4.32 [4.22; 4.40]) while the mean survival of males did not differ between predictable (3.77 [3.63; 3.91]) and unpredictable males (3.91 [3.75; 4.07]).

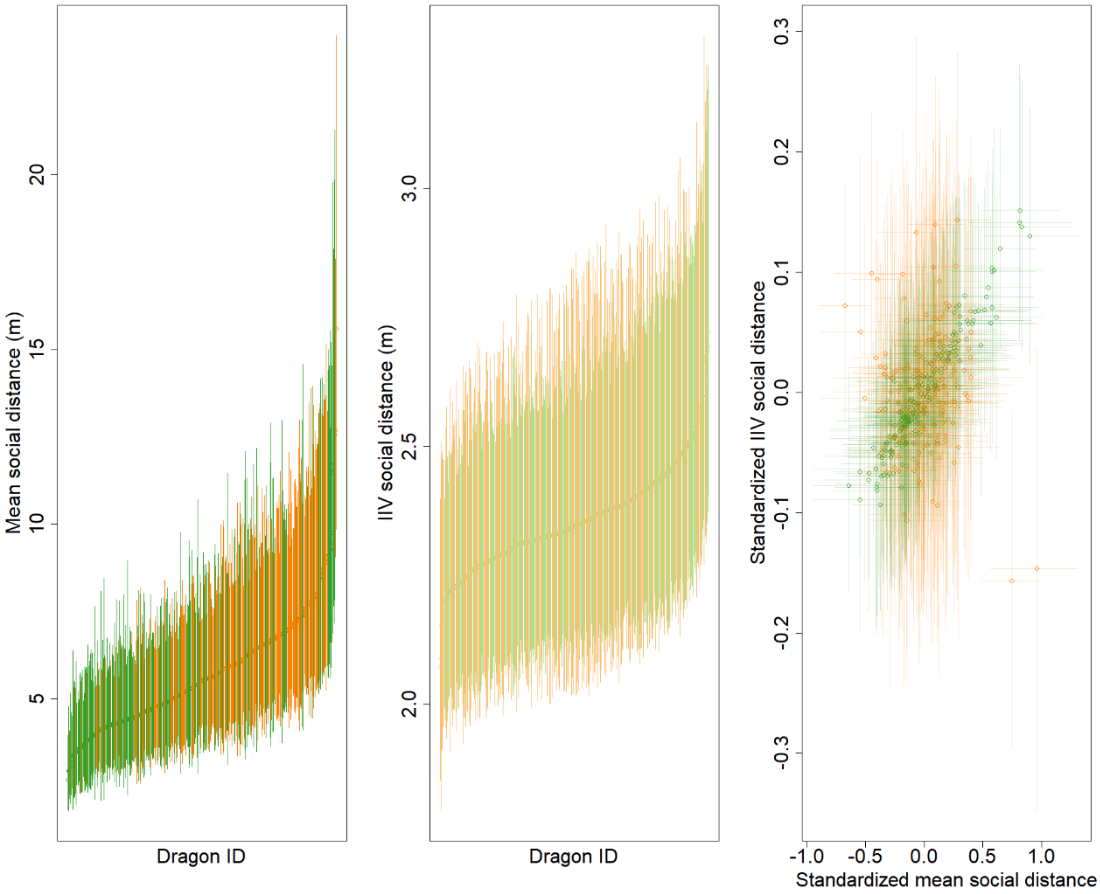

Figure 1: Posteriors of mean social distance, intra-individual variation (IIV) in social distance, and their relationship in 386 eastern water dragons (197 females in green, 189 males in orange). Each point corresponds to a posterior median and each vertical or horizontal segment denotes 95% credible intervals. In the left and middle panels, estimates were scaled back to the raw data scale (distance measured in meters units).

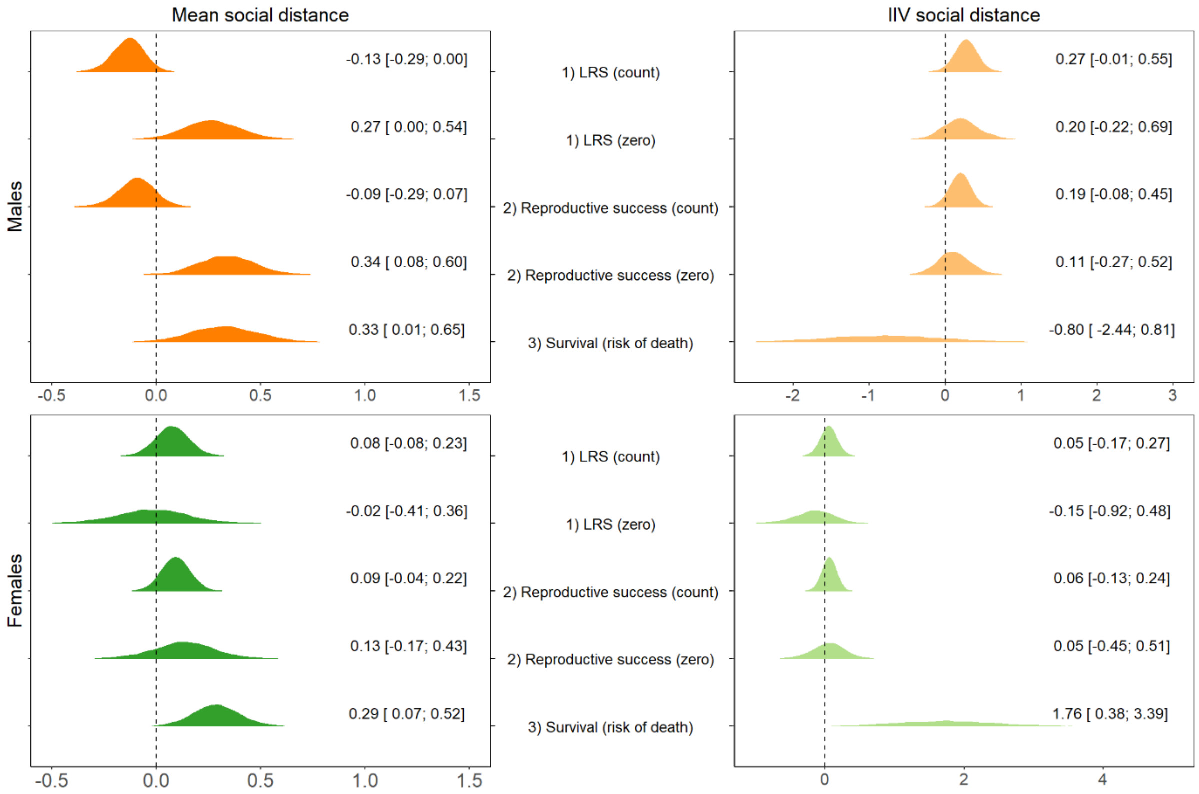

Figure 2: Full posterior distributions of the effects of individual social distance (mean: left, dark shades, intra-individual variation (IIV): right, light shades) on fitness measures in males (top, orange) and females (bottom, green). Coefficients were obtained by fitting each fitness proxy as a function of individual posteriors. For each fitness component (1: lifetime reproductive success (here LRS), 2: age-corrected reproductive success (here reproductive success), 3: Survival), we detail whether positive coefficients increase offspring number (count), the probability of having no offspring (zero) or decrease survival (increased risk of death). Posterior medians and 95% credible intervals are printed next to each distribution.

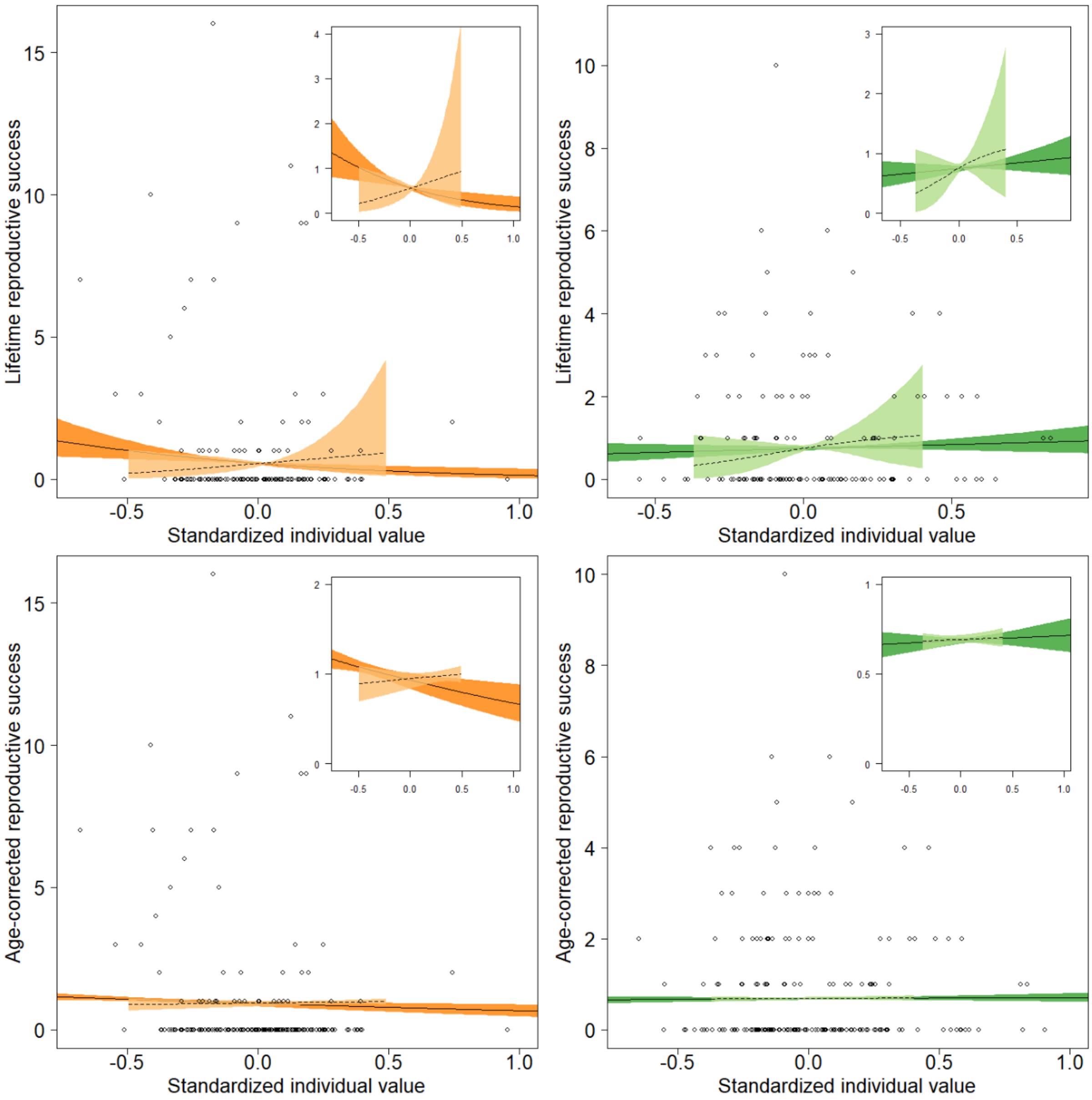

Figure 3: Predicted lifetime reproductive success (top) and age-corrected reproductive success at a given age (here, 6 years, bottom) as a function of individual values for mean (dark shades) and intra-individual variation (light shades) in social distance in males (orange, left) and females (green, right). The black lines and shaded areas depict the median estimates and 95% credible intervals of the distribution of coefficients derived from zero-inflated Poisson models fitting each individual posterior. A close-up view of each of these relationships is printed in the top right corner of each plot. Raw fitness measures as a function of standardized mean social distance are depicted by open circles.

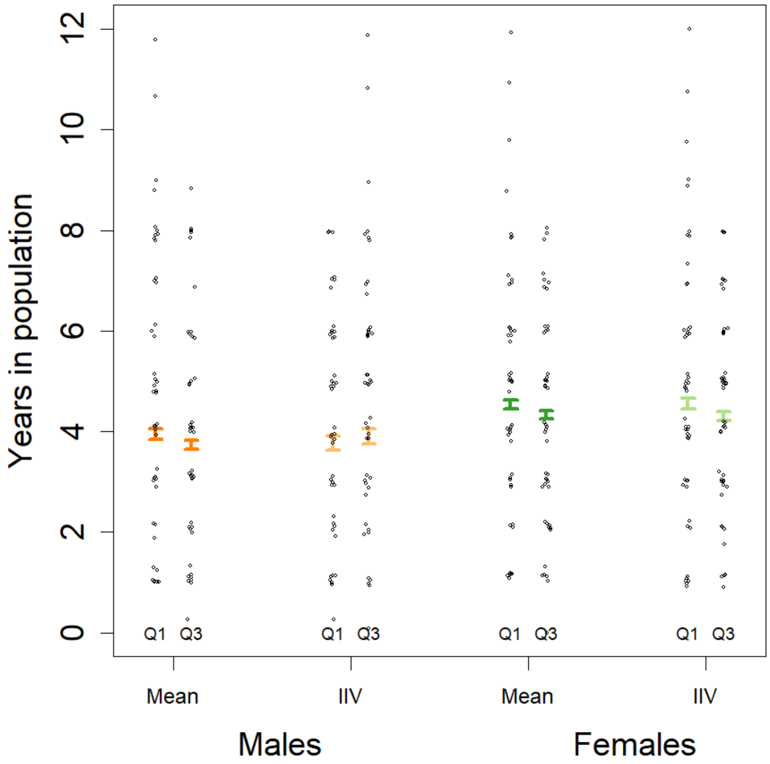

Figure 4: Predicted mean survival (95% credible interval, CI) in males (orange) and females (green) for the first and third quartiles (Q1 and Q3, respectively) of mean social distance (dark shades) and intra-individual variation (IIV) in social distance (light shades). These estimates were obtained by fitting the number of years individuals were seen in the population as a function of individual posteriors in a Cox proportional-hazards model. Observed survival when individuals' values are ≤ Q1 and ≥ Q3 are depicted by open circles.

Discussion

This study investigated for the first time the links between social behaviour, its predictability and fitness. We demonstrated, in eastern water dragons, that i) females were more social than males but both sexes exhibited similar among-individual variation and predictability in their social behaviour; ii) individuals varied in their average social behaviour and predictability; iii) more social females were also more predictable in their social behaviour; iv) more social males had a higher fitness (survival and reproductive success) while more social and predictable females lived longer lives. These findings provide partial support for the social niche specialization hypothesis, which posits that higher density environments should favour niche partitioning and behavioural predictability. We detail below how our results align or differ from predictions of the social niche specialization hypothesis and discuss their broader implications.

Sex differences in means, variance and predictability

Sexual dimorphism arises because sexes are subject to different selective pressures and can manifest not only in the average value of a trait, but also in the variability of the trait among and within individuals (Poissant et al., 2010; Zajitschek et al., 2020). In this study, we found that female dragons are on average more social than males, which is in line with previous research (Strickland & Frère, 2019). However, evidence for a female bias in among-individual variation was weak and there was no evidence for sex-differences in predictability. These findings therefore did not clearly support the social niche specialization hypothesis, which predicted that the more social sex, here females, would be more variable and more predictable.

Various mechanisms have been proposed to explain sex-differences in trait variance (Zajitschek et al., 2020). For instance, the ‘greater male variability hypothesis’, predicts condition-dependent sexual traits to vary more among males than among females (Cuervo & Møller, 1999, 2001; Pomiankowski & Møller, 1997) as a result of sexual selection, and was mainly supported for morphological traits. In this population, males indeed appeared to be more variable in their reproductive success than females, which likely results from intra-sexual competition for mating opportunities (Bateman, 1948; Wade, 1979). In contrast, there was no evidence for social behaviour to be more variable in males, probably because our studied trait was not associated with body size, an important contributor to reproductive success in males (Piza-Roca et al., 2020).

Alternatively, the ‘estrus-mediated variability hypothesis’ predicts that females are more variable than males due to experiencing different stages of their reproductive cycle, and is predominantly supported by evidence using physiological traits (Zajitschek et al., 2020). In eastern water dragons, reproduction is seasonal and mainly occurs during the first half of the field season (i.e., between September and December, Thompson, 1993). Whether female dragons vary in their seasonal hormonal changes and which hormones influence dragons’ social behaviour remain unknown. Females likely experience higher levels of sexual harassment and higher competition over resources during the reproductive period, which may explain their seasonal change in social distance. However, previous research did not find females to vary in their seasonal social plasticity (Strickland & Frère, 2019).

Finally, sex-differences in predictability opposite to predictions of the social niche specialization hypothesis could have been the result of sexual selection. For instance, females could have preferred males that were more behaviourally predictable, while unpredictability in females could have helped them avoid sexual coercion from males. However, we did not find evidence for sex-differences in predictability and our estimates of sex-specific associations between predictability and fitness were in opposite direction to this prediction.

Mean-predictability relationships

Previous studies have reported associations between mean behaviour (e.g., boldness, aggression, sociability, movement) and its predictability in other vertebrates (Hertel et al., 2020, 2021; Jolles et al., 2019; Mitchell et al., 2016; O’Dea et al., 2022). Our findings align with one of these studies (O’Dea et al., 2022) in that more social females were also more predictable, although one should keep in mind that relationships between mean behaviours and their predictability likely vary between populations and traits (Mitchell et al., 2021). Here, we showed that this correlation could also differ between sexes and we propose an explanation below.

First of all, the magnitude of the mean-predictability correlation found in females was higher than all other mean-predictability correlations ever reported. One may argue that such a mean-variance relationship can mathematically arise with distance data as its distribution is likely non-normal (bound to zero and right-skewed). However, simulations showed that our model accurately estimated the mean-predictability correlation for a trait that had a similar distribution as the studied trait (Text S2, Figure S1). More importantly, this bias would not explain the strikingly different mean-predictability correlations between sexes. Therefore, these results are probably better explained by the eastern water dragon's social structure.

While the positive mean-predictability correlation found in females aligns with predictions from the social niche specialization hypothesis, the absence of correlation in males does not necessarily rule it out and may provide interesting nuance. An intuitive mechanism underlying the social niche specialization hypothesis is the social enforcement of predictability via density. Previous research in this population indeed showed that density not only increases interaction opportunities but also the number of non-random associations in both sexes (Strickland et al., 2018). By definition, non-random associations imply a certain level of social predictability, and because females experience higher densities than males (Text S4), predictability would thus be more enforced in females than in males. Whether this explains the magnitude of the sex-difference in mean-predictability correlations is however unclear. One may speculate that female-female interactions, which are the most frequent in this species may be the main driver of social niches. In contrast, the benefits of predictability in female-male or male-male interactions may vary (but see below). Recent work in this population (Delmé et al., 2023) showed a higher degree and social tendency towards the opposite sex to be positively associated with reproductive success in males. Future research investigating the sex-specific links between social predictability and fitness would provide interesting new insights on when the social niche specialization hypothesis may apply.

Despite the strong mean-predictability relationship found in females, individual variation in mean and predictability represented small to very small proportions of the total variance in social behaviour. This means that most of the phenotypic variation, which consisted of intra-individual variation, was due to factors that other than intrinsic properties of individuals. Such variance partitioning reflects the high lability of our studied trait. Indeed, social distance depends on the respective locations of an individual and its social environment, which are influenced by variation in resources and risks. Such environmental variation may be particularly unpredictable in this highly frequented urban park and may have hence been the main contributor of intra-individual variation in social distance. This explanation contrasts with behaviours being generally more repeatable in the field than in the lab (Bell et al., 2009), although the influence of habitat on the repeatability of intra-individual variation has not been studied yet.

Association with fitness

While, the fitness benefits of social behaviours have been investigated and reported in several species (Brent et al., 2013; Frère et al., 2010; Kohn, 2017; Silk, 2007) including this study system (Delmé et al., 2023), our study goes one step further by investigating the relationships between different fitness components and social predictability. This study is also one of the rare studies connecting behavioural predictability and fitness in the wild (Cain et al., 2023; Patrick et al., 2021).

For males, we found that more social individuals lived longer lives and produced more offspring, which resulted in a higher lifetime reproductive success and suggested that mean social tolerance may be under directional selection. This positive relationship between males' social behaviour and reproductive success was consistent with Delmé et al. (2023) and was likely driven by increased mating opportunities. In dragons, males mainly interact with females (Baird et al., 2012; Strickland et al., 2014) and shorter social distances may hence signal stronger social bonds with potential mates. As directional selection is expected to deplete additive genetic variance (Fisher, 1930), which contributes to among-individual variance, we would have expected this sex-specific selective regime to drive a lower among-individual variance in males than females. Evidence for this was, however, weak. In contrast, the association between predictability and fitness in males was rather mixed, which may explain its zero correlation with mean social behaviour. Indeed, predictability was not associated with survival or the probability to have offspring but unpredictable individuals that had offspring had more of them. Given the species' biology, we can speculate that reproductive success and survival in males mainly result from interactions with females and males, respectively. While being unpredictable did not seem to provide benefits in male-male contests (contrary to predictions by Briffa & Lane, 2017), which is known to be particularly costly (Baxter-Gilbert & Whiting, 2019), it may increase mating success (e.g., via sexual coercion) in males that have a greater access to females, namely territorial males (Baird et al., 2012). On the other hand, the null correlation between predictability and survival could signal that social predictability and male mating strategies are independent.

For females, we found no evidence that social behaviour and its predictability were associated with reproductive success which was also consistent with Delmé et al. (2023) but contrasted with numerous studies in mammals (Silk, 2007). Because breeding systems may affect the adaptive value of females' social behaviour (Silk, 2007), our findings might be explained by the absence of parental care in dragons, which precludes any form of cooperation over offspring rearing. While the positive association between mean social behaviour and survival was similar to that in males, we also found such positive association for social predictability in females. These results aligned with predictions from the social niche specialization hypothesis and may have been driven by correlational selection on mean and predictability of social behaviour. Alternatively, the very high mean-predictability correlation may have driven their positive association with survival. Interestingly, the survival advantage of being more social did not translate into a higher lifetime reproductive success in females. This could be because social behaviour was only associated with one fitness component in females (as opposed to both fitness components in males) and because females exhibited less variance in lifetime reproductive success than males.

In both sexes, we found a positive association between social behaviour and survival which could be due to social tolerance decreasing the costs of competition (e.g., fights for resources or territories, Haunhorst et al., 2017), sexual harassment of females by males (Fox, 2002), or increasing social information about the location of food sources (Aplin et al., 2012) or predators (Beauchamp, 2010). Individuals that are more socially tolerant (and females that are more predictable) may also occupy a different position in the social network, which has repeatedly been found to correlate with longevity (Barocas et al., 2011; Holt-Lunstad et al., 2010; Silk et al., 2010; Vander Wal et al., 2015). Alternatively, a higher social tolerance could be found in dominant individuals, which pay low costs of social proximity to other subordinate individuals. However, here, social behaviour was not associated with individual size, a predictor of dominance in this species (Piza-Roca et al., 2020).

Altogether, our findings that social behaviour, its predictability and survival were all positively correlated in females provided partial support for the social niche specialization hypothesis in eastern water dragons. This study also provided new insights into sex-specific functions of social behaviour and suggested that in dragons, not only mean social behaviour but also its predictability have different fitness consequences between sexes. Assuming that mean and predictability in social behaviour are heritable and genetically correlated across sexes (Connallon & Clark, 2014; Kaufmann et al., 2023), one could speculate sex-specific selection to be a mechanism maintaining among-individual variation in these traits (Schuett et al., 2010). We are hence yet to determine whether social behaviour and its predictability are heritable and genetically correlated between sexes in eastern water dragons.

Conclusion

Our study demonstrated that social behaviour and its predictability covary with each other and with fitness in a sex-specific way in a wild lizard. While sexes did not clearly differ in their among-individual variation or predictability, females exhibited a strong positive association between social behaviour, its predictability, and survival. In males, we found mean social behaviour to be positively associated with fitness but not with predictability, which did not have clear fitness benefits. These findings hence partly supported predictions from the social niche specialization hypothesis in that social enforcement of behavioural predictability may only have occurred in the more social sex. We also provided rare empirical estimates of behavioural predictability and of its association with fitness in a wild animal. This study therefore highlights the evolutionary relevance of behavioural predictability and aims to promote further research on the links between social behaviour, animal personality and predictability.

Data and Code accessibility

Data and R code used for this study are available on OSF (https://osf.io/3y6s7/)

Authors Contributions

BC,CF, SN conceived the original idea of the study. BC performed the statistical analyses and wrote the manuscript, with input from all other authors. NJ performed the parentage analyses. BC,CF,NJ,KS contributed to data collection. All authors provided comments on the manuscript and agreed on the final version to be submitted for publication.

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Conflict of interest disclosure

Authors declare no conflict of interest

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