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

Authors: Barbara Class[1*], Kasha Strickland[2], Dominique Potvin[3], Nicola Jackson[4], Shinichi Nakagawa[5], Celine Frere[4]

[1] Department of Biology, Ludwig-Maximilians-Universität München, Großhaderner Straße 2, 82152 Planegg-Martinsried, Germany

[2] Institute of Ecology and Evolution, School of Biological Science, University of Edinburgh, Edinburgh, EH9 3FL, UK

[3]School of Science, Technology and Engineering, University of the Sunshine Coast, Petrie, QLD, 4502, Australia

[4] School of the Environment, The University of Queensland, St Lucia, QLD 4067, Australia

[5] Evolution & Ecology Research Centre, Centre for Ecosystem Science, and School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, 2052, Australia

*Correspondance: class@biologie.uni-muenchen.de

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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 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 predictability of social behaviour 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. Females, which were more sociable than males, exhibited slightly higher levels of among-individual variation but similar social predictabilities as males. Females that were more sociable were also more predictable while no association was found between social behaviour and predictability in males. Finally, social behaviour and its predictability showed sex-specific associations with survival and reproductive success. These findings partly support predictions from the social niche hypothesis and highlight the importance of behavioural predictability in social evolution.

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 in order 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, in some species, 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 both in the wild and in the lab (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 traits' 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 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 gregarious and long-lived agamid lizard that exhibits long-term social associations and avoidances (Strickland et al., 2017). Females are polyandrous and males exhibit mating strategies varying from territorial to satellite behaviours (Baird et al., 2012; Ball et al., 2023; Frère et al., 2015). In this sexually dimorphic species, sexes differ in the repeatability and plasticity of their social behaviours (Strickland & Frère, 2018, 2019) and plastic responses in social behaviour consistently vary between individuals (Strickland et al., 2021).

In particular, we test predictions from the social niche 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, males show various mating strategies due to a strong intra-sexual competition, which may drive a higher among-individual variation and a higher predictability in their social behaviour compared to females. Alternatively, and because mating strategies may be unrelated to social tolerance, we could also find the opposite pattern as females occur at higher densities than males (Strickland & Frère, 2019) and may compete more for resources. The latter would be supported by a recent study suggesting that females are more repeatable than males in a range of social behaviours (Delmé et al., 2023). Predictions from the social niche 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).

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). This approach notably requires substantial sample sizes and amounts of repeated measures, which remain rare in behavioural ecology studies (Mitchell et al., 2021). Using DHGLMs and >30000 observations made over 4 years in >300 individuals, we provide rare estimates of predictability in social behaviour and its association with fitness in the wild.

Methods

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 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). Behavioural surveys were conducted by researchers, 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). Sex was determined 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, the minimum distance (in m) to other individuals present within the same survey was used as a proxy for social tolerance such that the higher the distance, the less socially tolerant an individual was. Importantly, observations during which individuals were engaged in agonistic or mating interactions were excluded 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, additional annual sampling was conducted to complement behavioural survey data. Annual sampling data used in this study were collected between 2010 and 2020. This involved catching all possible adult individuals using a lassoing technique and collecting 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 described facial scale method identification method. DNA was extracted from blood and tissue using DNeasy Blood and Tissue extraction kits (Qiagen) as per manufactures instructions and sequenced using DArTcap^{TM} technology through Diversity Arrays Technology, Canberra (Feutry et al., 2020). This resulted in a total of 6,425 SNPs prior to filtering, across 1285 individuals for which 775 were adults with behavioural survey data. As per Delmé et al., 2023, we filtered homozygote SNPs for a read depth of 5, and using the *dartR* package SNPs were further filtered for an individual call rate of 80% or greater, a SNP call rate of 99% or greater, removal of monomorphic loci, the proportion of technical replicates assay pairs of at least 99%, only one SNP per short read tag was retained. We used *plink* to filter for linkage disequilibrium with SNP 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 SNP 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 ≥0.43 producing a resultant data set of 179 high quality SNPs 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, survival, and reproductive rate. Lifetime reproductive success (LRS) was the total number of adult offspring of individuals that were assumed to be dead (not seen during the 2022-2023 field season). In this rather closed population (Littleford-Colquhoun et al., 2017), 95% of individuals known to be alive had consecutive sightings that were lower than 160 days and 99% were resighted within 327 days. LRS was corrected for the year of appearance (hereafter "cohort") 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 LRS. In particular, we expected that individuals last seen in field seasons 2020-2021 and 2021-2022 had lower LRS than individuals last seen earlier during this study because their offspring may not have been sampled yet. However, this did not seem to be the case as no negative association was found between year of disappearance and LRS. Lifetime reproductive success data was available for 125 females and 134 males.

Our second fitness proxy, reproductive rate, 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. Reproductive rate 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 cohort and detectability (the median time between its successive measurements). 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 *N. barbatae* (Peterson et al., 2020) were euthanized between 2018 and 2021. These individuals were excluded from the LRS 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

Statistical analyses were performed in R (R Core Team, 2022) using the package 'brms' (Bürkner, 2017). We fitted all models in males and females separately. 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. 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, 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).

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). This was done using three generalized linear models fitting reproductive rate and LRS with zero-inflated Poisson distributions (using the pscl package, Jackman, 2010; Zeileis et al., 2008), and survival with a Poisson distribution. Coefficients from each model and each posterior were stored and we calculated their distribution (median and 95% credible intervals). Caution has been raised against the use of BLUPs in subsequent analyses because 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.

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 were on average less social than females. Indeed, social distance was on average 7.1 m (sd=6.8) in males and 5.9 m (sd=6.4) in females. Social distance was overall slightly more variable in females than in males (lnCV= -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, lnCV=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, lnCV=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 (lnCV=0.08).

Individual variation in mean social distance

Neither body size nor time of the day influenced social distance, which mainly varied temporally within and between field seasons (Table 1). The model pooling both sexes showed that males and females 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). 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). These 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 were 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). This was possibly due to a higher among-individual variance in females compared to males (lnCVR= -0.19 [-0.48; 0.09]) although this female bias did not statistically differ from zero.

Individual variation in predictability of social distance

Similar to mean social distance, predictability in social distance varied between and within seasons but was not associated with body size or age (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). 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). Furthermore, males seemed more variable in their predictability than females but such difference did not differ statistically from zero (Table 1, lnCVR=0.23 [-0.34; 0.74]). The repeatability of this intra-individual component (i.e. its relative importance compared to the total phenotypic variance for this trait) was however 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).

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. 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. Fixed effects for which the 95% CI did not include zero are printed in bold.

		Estimates
Fixed effects		
Mean model	Intercept	1.64 [1.55; 1.72]
	Body size	0.02 [-0.01; 0.05]
	Time of day (pm)	-0.02 [-0.03; 0.00]
	Sex (male)	**0.16 [0.07; 0.25]**
	Season day	**0.03 [0.01; 0.04]**
	Season day^2	**0.00 [-0.02; 0.02]**
	Season 2017-2018	**-0.10 [-0.18;-0.03]**
	Season 2018-2019	**-0.14 [-0.21;-0.07]**
	Season 2019-2020	**-0.22 [-0.31;-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)	-0.01 [-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	**-0.13 [-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	0.08 [0.06; 0.09]
	Individual_Season	0.05 [0.02; 0.07]
	Cor mean-dispersion	0.38 [0.15; 0.59]

Links with fitness

In both sexes, we found evidence for associations between social distance and our fitness proxies. First, LRS was negatively associated with mean social distance in males (Figure 1, 2). Indeed, males that were more socially distant 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]). In contrast, there was a tendency for unpredictable males to have more offspring in their lifetime (0.27 [-0.01; 0.55]) but no clear relationship between unpredictability and the probability of siring no offspring (0.20 [-0.22; 0.69]). As a result, the relationship between unpredictability and LRS appeared weakly positive in males (Figure 2) and similar in magnitude to relationships found between social behaviour and LRS in females, which did not differ from zero (Figure 1, 2).

Second, reproductive rate was negatively associated with mean social distance in males (Figure 1, 3). While there was no evidence that more socially distant males produced fewer offspring at a given age (-0.09 [-0.29; 0.07]), these males had higher probabilities of siring no offspring (0.34 [0.08; 0.60]). In contrast, we found no evidence that reproductive rate was associated with predictability in males, mean social tolerance in females and predictability in females (Figure 1, 3).

Third, we found a tendency for more socially distant individuals to have shorter lifespans in males (-0.12 [-0.26; 0.01]) and females (-0.09 [-0.19; 0.01], Figure 1, 4). In contrast, the association between unpredictability and survival showed different signs between the sexes, being positive in males (0.34 [-0.35; 1.01]), and negative in females (-0.52 [-1.22; 0.10]). These estimates, however, did not statistically differ from zero in either sex.

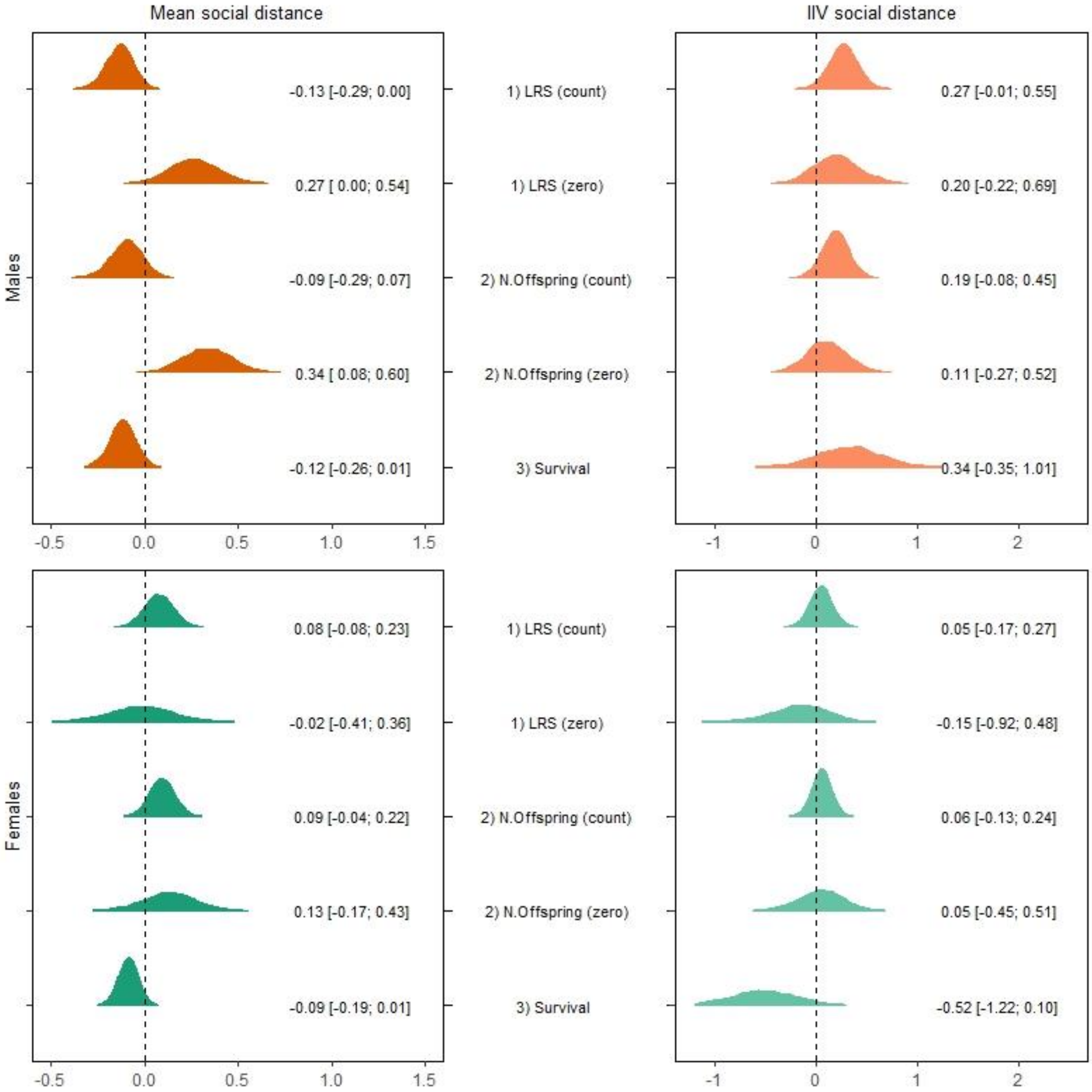

Figure 1: Posterior distributions of the effects of individual social distance (mean on the left, IIV on the right) on fitness in each sex (males in top row, females in bottom row). These estimates were obtained by fitting each fitness proxy as a function of posterior distributions of individual values derived from a DHGLM. Posterior median and 95% credible intervals are printed next to each distribution.

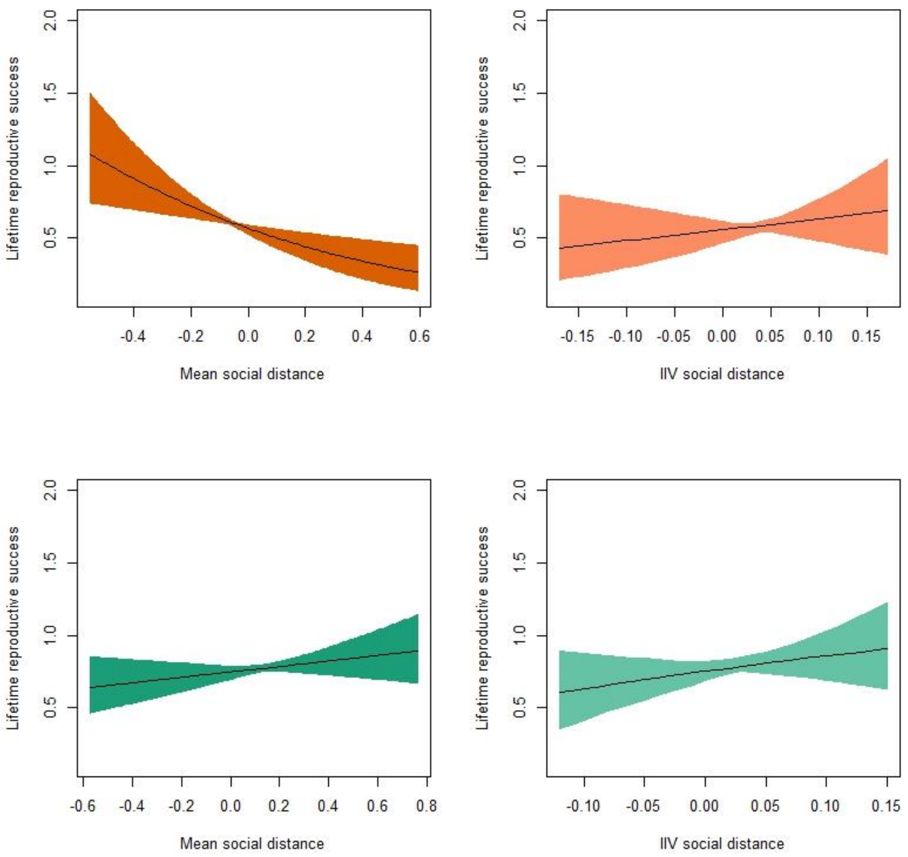

Figure 2: Predicted lifetime reproductive success as a function of individual mean social distance (left, dark colours) and IIV (right, light colours) in males (top row, orange) and females (bottom row, green). The black lines and the shaded areas depict the median estimates and 95% credible intervals of the distribution of coefficients derived from zero-inflated Poisson models fitting each individual posterior.

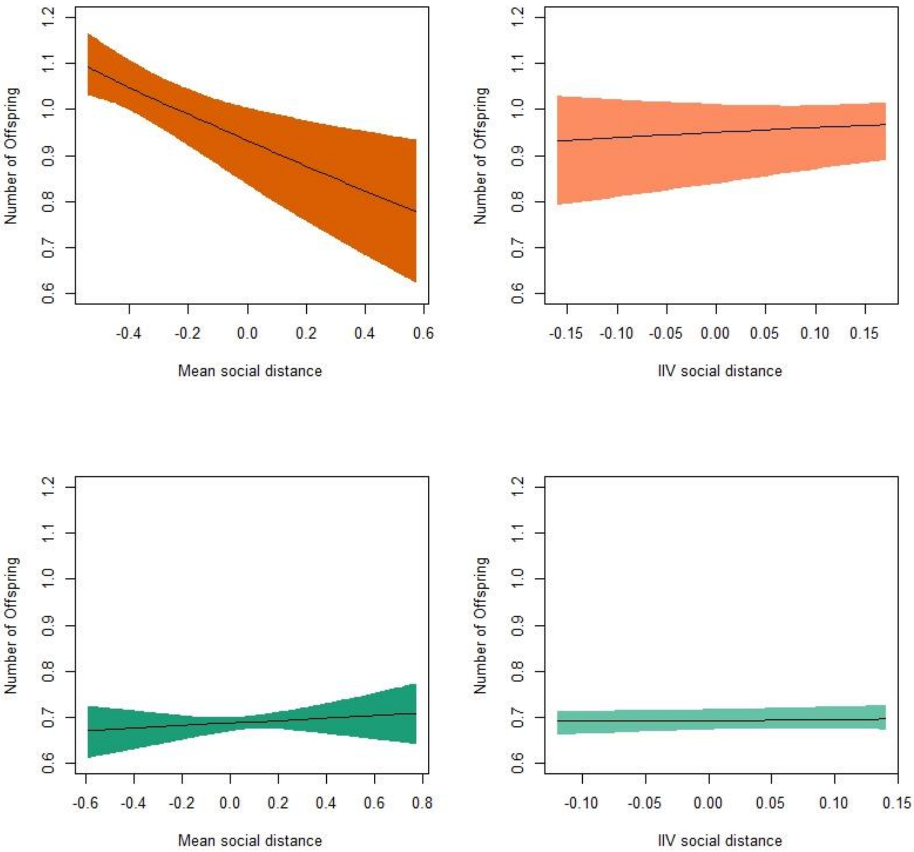

Figure 3: Predicted reproductive rate as a function of individual mean social distance (left, dark colours) and IIV (right, light colours) in males (top row, orange) and females (bottom row, green). The black lines and the shaded areas depict the median estimates and 95% credible intervals of the distribution of coefficients derived from zero-inflated Poisson models fitting each individual posterior.

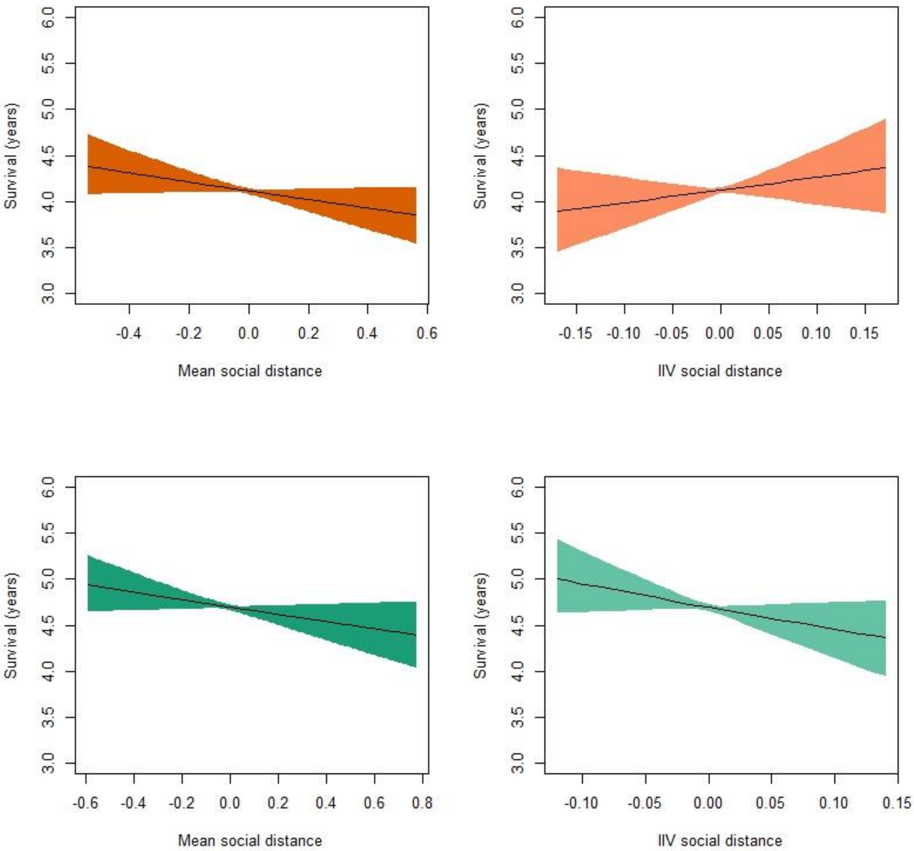

Figure 4: Predicted survival as a function of individual mean social distance (left, dark colours) and IIV (right, light colours) in males (top row, orange) and females (bottom row, green). The black lines and the shaded areas depict the median estimates and 95% credible intervals of the distribution of coefficients derived from Poisson models fitting each individual posterior.

Discussion

This study not only provided the first estimates of predictability of social behaviour, but also investigated for the first time its link with social behaviour and fitness in a wild animal. We demonstrated, in eastern water dragons, that i) females were more social and slightly more variable in their social behaviour than males, but both sexes were similarly predictable in their social behaviour; ii) in both sexes, individuals varied both in their average and in the predictability of their social behaviour; 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 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 hypothesis and discuss their broader implications.

Sex differences in means, variance and predictability

Sexual dimorphism arises because sexes are subject to different selective pressures. Thus, especially for behavioural traits, sexual dimorphism can manifest not only in the strength or average level of a trait, but also in the variability of the trait among individuals (Zajitschek et al., 2020). While our finding that male dragons are less social than females is in line with earlier studies in this system (Strickland & Frère, 2019), our results do not align with the ‘greater male variability hypothesis’, which predicts condition-dependent sexual traits to vary more among males than among females (Cuervo & Møller, 1999, 2001; Pomiankowski & Møller, 1997). In this population, males indeed appeared to be more variable in their reproductive success than females, which likely results from competition for mating opportunities. In contrast, evidence that males are more variable than females for behavioural traits to date remains equivocal (Wyman & Rowe, 2014; Zajitschek et al., 2020), which may be because behaviours are not necessarily body condition-dependent. This is seen in our study, whereby social behaviour was not associated with body size, an important contributor to fitness in males. In contrast to the greater male variability hypothesis, the social niche hypothesis would predict the more social sex, here females, to be more variable and more predictable. Here, we found weak support for this prediction, as females were slightly more variable than males in their social behaviour but we did not find evidence for sex-differences in predictability. Similar sex-differences in among-individual variance and repeatability of social behaviour, were previously found in this population (Delmé et al., 2023), in bighorn sheep (*Ovis canadensis*, Vander Wal et al., 2015) and in chimpanzees (*Pan troglodytes*, Tkaczynski et al., 2020), and could be caused by sex-differences in selection rather than a greater social niche partitioning in females (see below).

Mean-predictability relationships

Previous laboratory studies of behavioural predictability under experimental conditions have found associations between mean behaviours and their predictabilities. For example, Mitchell et al. (2016) found that more active individual guppies (*Poecilia reticulata*) were also more predictable, and Jolles et al. (2019) found that bolder three-spined sticklebacks (*Gasterosteus aculeatus*) were also more predictable. An extensive study by O'Dea et al. (2022) in zebrafish (*Danio rerio*) also found that more active and more social individuals were more predictable, that neophobic and aggressive individuals were less predictable, and that boldness and its predictability did not correlate. Our social tolerance results align with this latter study 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 the sexes in a sexually dimorphic species, potentially because of sex-specific social constraints (see below).

A few studies have also quantified mean-predictability relationships in wild animals (Hertel et al., 2020, 2021; Martin et al., 2017). For example, previous studies in bears (*Ursus arctos*) and elephants (*Loxodonta africanus*) found that individuals that moved large daily distances were less predictable than individuals that moved shorter distances (Hertel et al., 2020, 2021). Correlations between distances moved and predictability in these distances were also relatively strong, although not as strong as the correlation we found for social behaviour in female dragons. 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, this would then have also driven a positive mean-predictability correlation in males, which we did not find. Furthermore, simulations showed that our model accurately estimated the mean-predictability correlation for a trait that had a similar distribution as social distance (Text S2, Figure S1). We also note that contrary to experimental studies performed in controlled conditions, predictability in the wild may also include plasticity to unknown environmental factors (Stamps et al., 2012; Westneat et al., 2015) and thus reflects how generally plastic vs. constrained an individual's behaviour is. Our results therefore suggest that the strong positive correlations between mean behaviour and its predictability are caused by female-specific constraints on social behaviour. This individual-level association between social behaviour and predictability would align with the social niche predictions even though we expected to find this pattern in both sexes. The fact that this association only occurred in females however does not contradict our prediction that individuals in the more social sex may exhibit stronger constraints on their social behaviour. While our analyses of fitness could not detect such constraints on adult females' social behaviour (see below), we cannot rule out selection on social behaviour at earlier life stages (Nuñez et al., 2015).

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) and a previous study reported sex-specific selection on social behaviours in this study system (Delmé et al., 2023), our study goes one step further by simultaneously investigating different components of fitness and incorporating predictability. Importantly, 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 slightly 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 social associations with females, which increased mating opportunities for more social males. As directional selection is expected to deplete additive genetic variation of traits, the finding that males had slightly lower among-individual variation than females could therefore be a consequence of such sex-specific selective regime. Interestingly, unpredictability seemed to be associated with a higher lifetime reproductive success in that unpredictable males that had offspring had more of them than predictable males. The magnitude of the relationship between predictability and reproductive rate was similar in magnitude to that with LRS, while predictability was clearly not associated with survival in males. These results would suggest reproductive benefits of unpredictability for males, although power to detect such effects was likely limited in our dataset. Because unpredictability includes unmeasured plasticity, its positive association with reproduction could be caused by males adjusting their behaviour more appropriately to social contexts, which may provide them with increased mating opportunities. These benefits of unpredictability were however masked when considering total reproductive outputs (including failures to reproduce). The reason why predictability did not associate with the probability to produce offspring in males remains unclear.

For females, we found no evidence that social behaviour and its predictability were associated with reproductive rate 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. As for males, we found that more social (and predictable) females had a slightly higher survival. We note that the very high correlation between mean and predictability was probably causing both aspects of females' social behaviour to be similarly associated with survival (Figure 3). This possible survival advantage of being more social however did not seem to translate into a higher lifetime reproductive success in females. This could be because social behaviour was only (and weakly) 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 small positive association between social behaviour and survival in both sexes, 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). In contrast to mean social behaviour, we did not find behavioural predictability to clearly associate with survival in either sex. In dragons, we expected that more predictable individuals would survive longer due to experiencing lower levels of conflict or, alternatively, that unpredictable individuals would be favoured in contest situations due to being more plastic (Briffa & Lane, 2017). These negative results contrasted with a recent study in barn owls (*Tyto alba*) finding that individuals that were less predictable in their movement behaviour had a higher survival (Cain et al., 2023), and therefore (unsurprisingly) suggest that benefits of behavioural predictability are context-dependent. Additionally, although sex-specific associations between survival and predictability were very uncertain should be interpreted with caution, their difference in signs raises the idea that selection on predictability could also be sex-specific.

An important finding of this study is that sexes differed in how their mean social behaviour and, to some extent, its predictability, associated with reproductive success. Sex-differences in reproductive selection and similar survival selection in both sexes was previously found in a bighorn sheep population where social behaviour increased reproductive success in females only and increased survival in both sexes (Vander Wal et al., 2015). 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 reproductive 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. Females, which were more social than males exhibited a slightly higher among-individual variation and a strong positive association between social behaviour and predictability. Although sexes did not differ in the predictability of their social behaviour, this mean-predictability association was absent in males. Mean social behaviour was associated with a higher reproductive success in males and a slightly higher survival in both sexes. Altogether, these findings partly supported predictions from the social niche hypothesis at the sex and individual levels. 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 will hopefully promote further research on the links between social behaviour, animal personality and predictability.

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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Ethics statement

This research was conducted with the approval of the University of the Sunshine Coast's animal ethics committee (approval numbers: ANA1487, ANA20161, ANS1858).

Data accessibility

Data and R code used for this study are available on OSF: https://osf.io/3y6s7/?view_only=512a97f97623411781eacdd81bf2b6cd

Conflict of interest disclosure

Authors declare no conflict of interest

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