



Research

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Sex differences in lizard escape decisions vary with latitude, but not sexual dimorphism

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Sexual selection is a powerful evolutionary mechanism that has shaped the physiology, behaviour and morphology of the sexes to the extent that it can reduce viability while promoting traits that enhance reproductive success. Predation is one of the underlying mechanisms accounting for viability costs of sexual displays. Therefore, we should expect that individuals of the two sexes adjust their anti-predator behaviour in response to changes in predation risk. We conducted a meta-analysis of 28 studies (42 species) of sex differences in risk-taking behaviour in lizards and tested whether these differences could be explained by sexual dichromatism, by sexual size dimorphism or by latitude. Latitude was the best predictor of the inter-specific heterogeneity in sex-specific behaviour. Males did not change their escape behaviour with latitude, whereas females had increasingly reduced wariness at higher latitudes. We hypothesize that this sex difference in risk-taking behaviour is linked to sex-specific environmental constraints that more strongly affect the reproductive effort of females than males. This novel latitudinal effect on sex-specific anti-predator behaviour has important implications for responses to climate change and for the relative roles of natural and sexual selection in different species.

1. Introduction

Sex differences may evolve via sexual selection, which may result in natural selection operating differently in males and females due to differences in mating success [1]. Sexual selection may arise from competition among individuals of the same sex for access to mates or from individuals of one sex showing a preference for certain individuals of the other sex [1,2]. Yet, sexually selected traits may result in or arise from differential selection pressures on the sexes [2]. For example, predation risk may differ among sexes owing to sexually selected differences in body size or brightness [3], implying differential optimal escape behaviour in males and females (i.e. that which optimizes the trade-offs between predation risk and the opportunity cost of lost foraging or mating opportunities [4,5]). Optimal escape behaviour will depend on environmental conditions that can affect the costs and benefits of fleeing. For example, ectothermic organisms will alter their escape behaviour relative to ambient temperature [6].

Optimal escape theory predicts that individuals that become conspicuous either as a consequence of their coloration, size or behaviour should take relatively fewer risks, unless the costs of an extravagant display are compensated by increased benefits in terms of fitness [7,8]. Thus, males that display at more exposed sites, which provide greater visibility to nearby females and

improved ability to detect sexual rivals, also take greater risks by tolerating closer approach by predators [9,10]. Specifically, they have shorter flight initiation distances (FIDs, the predator–prey distance when the escape begins) because their cost of leaving and losing access to their high-quality territory is much greater, especially when actively engaged in social behaviour [11,12]. Likewise, sex differences in body size or coloration linked to sexual selection may result in individuals of the conspicuous sex taking greater risks than individuals of the other because their potential reproductive rewards are greater, offsetting the predation risk [3,13].

An increasing body of evidence shows that many inter-specific interactions, such as predation, show consistent latitudinal clines [14,15]. Latitude could affect the two sexes differently because life history and hence mating effort in the two sexes changes differently with climatic conditions. In lizards, for example, a shorter reproductive season due to restriction of favourable climatic conditions for reproduction might constrain the reproductive behaviour of females at high latitudes more than that of males because females have higher ‘reproductive burden’ [16] and increased costs of reproduction should elicit changes in optimal anti-predator behaviour. Therefore, males and females may respond differently to predation risk as latitude increases. This is an unexplored question.

The objectives of this study were to test, using a systematic review and a meta-analysis of lizard studies, whether intersexual differences in risk-taking occur and are related to two sexually selected traits, sexual dichromatism and sexual dimorphism in body size, and to latitude as a proxy for environmental conditions. Lizards are an excellent taxon for investigating the relationship between risk-taking and sexually selected traits because sexual dimorphism in body size and coloration is widespread in lizards [17], and because data on intersexual difference in optimal escape behaviour are available for many lizard species [6].

We hypothesized that the intensity of sexual dichromatism or sexual dimorphism in body size could affect anti-predator responses in one of two ways. On the one hand, the more brightly coloured or larger sex (usually male) might compensate for its potentially higher risk of predation due to its conspicuousness by fleeing from predators at greater distances. On the other hand, the most brightly coloured or larger sex must engage in active mate searching, territorial aggression and patrolling, mate-guarding and/or conspicuous courtship. Because abandoning such activities makes fleeing more costly for the more conspicuous sex, the larger or more brightly coloured sex might accept greater risk and flee at shorter distances.

Whereas the reproductive efforts of males often are spread across multiple females, lizard females should ensure their reproductive success during a reproductive season based on only a very few ovipositions, especially when colder climates (e.g. at higher latitudes) necessitate shorter seasons favourable for reproduction. Because the reproductive season shortens with increasing latitude, we expect that as latitude increases females must increasingly expose themselves to risk while foraging to gain sufficient energy to successfully reproduce (e.g. through provisioning and carrying of their clutches). We predicted that this would result in females being more prone to take risks than males, and this would be reflected in reduced FIDs relative to males (figure 1*a,b*). Another possibility is that a shorter reproductive season at high latitude

forces males to display at higher rates, which would increase their conspicuousness to predators and result in males having longer FID owing to greater predation risk (figure 1*c,d*). Finally, it is also possible that both predicted effects occur simultaneously (figure 1*e*).

2. Material and methods

(a) Literature survey

We first compiled all lizard studies cited by Stankowich & Blumstein [18] in their review of all prey taxa. Next, we used the Web of Science, Scopus and Google Scholar databases to search for papers published prior to 31 December 2013 that cited Ydenberg & Dill [4] and Stankowich & Blumstein [18]. We searched in the same databases using the terms ‘lizards’ plus one of the following terms: ‘flight initiation distance’, ‘FID’, ‘flight distance’, ‘escape distance’, ‘approach distance’, ‘flushing distance’ and ‘response distance’. We checked all references of the papers identified to locate other studies not covered by our survey. Among the papers evaluated, we included in our dataset studies testing for the effect of sex on FID of lizards. The full dataset consisted of 48 effect size estimates from 28 studies across 42 species. The PRISMA diagram describing our literature search (electronic supplementary material, figure S1) and the complete list of effect sizes is provided in the electronic supplementary material.

All studies included used a standard protocol to measure FID in which, after sighting an immobile lizard, an experimenter walked directly toward it at a constant speed until the lizard began to flee (e.g. [11]). Although there was some variation in the approach speed used by experimenters (mean \pm s.e.: 72.27 ± 6.66 m min⁻¹, $N = 32$), a meta-regression between effect size and approach speed was not significant ($b = -0.01$, $p = 0.451$, $r^2 < 1\%$), implying that variation in approach speed was not important for explaining sexual dimorphism in risk-taking of lizards.

(b) Effect size estimates

We used Pearson’s product-moment correlation coefficient, r , as our measure of effect size. Here, r represents the magnitude of the difference between FID of males and FID of females. Positive r values mean that males permitted closer approach by predators, whereas negative r values indicate that females permitted closer approach by predators. To calculate r , we preferentially used mean, variance and sample size of FID of males and females provided by source papers. We further calculated Hedge’s d (bias corrected standardized difference between means) and converted it into r according to Borenstein *et al.* [19]. Otherwise, we used formulae in Rosenthal [20] to calculate r from statistical results provided by source papers (t , F and z).

Although most studies that tested differential risk-taking by gravid and non-gravid females did not report significant differences [21,22], the power of these studies was low. In at least one species (*Plestiodon laticeps*), gravid females have greatly reduced sprint speed and become less active and therefore less conspicuous, which could in turn affect FID [23]. Here we avoided possible confounding effects of reproductive state by using only FID data for non-gravid females to calculate the effect sizes. However, a separate analysis using FID data for gravid females yielded the same conclusions (electronic supplementary material). For analysis, r values were transformed to Fisher’s z to improve normality of data.

(c) Analyses

We used both random and mixed effects (meta-regression) models to test for an overall effect size and the importance of our moderator variables, controlling for phylogeny and study

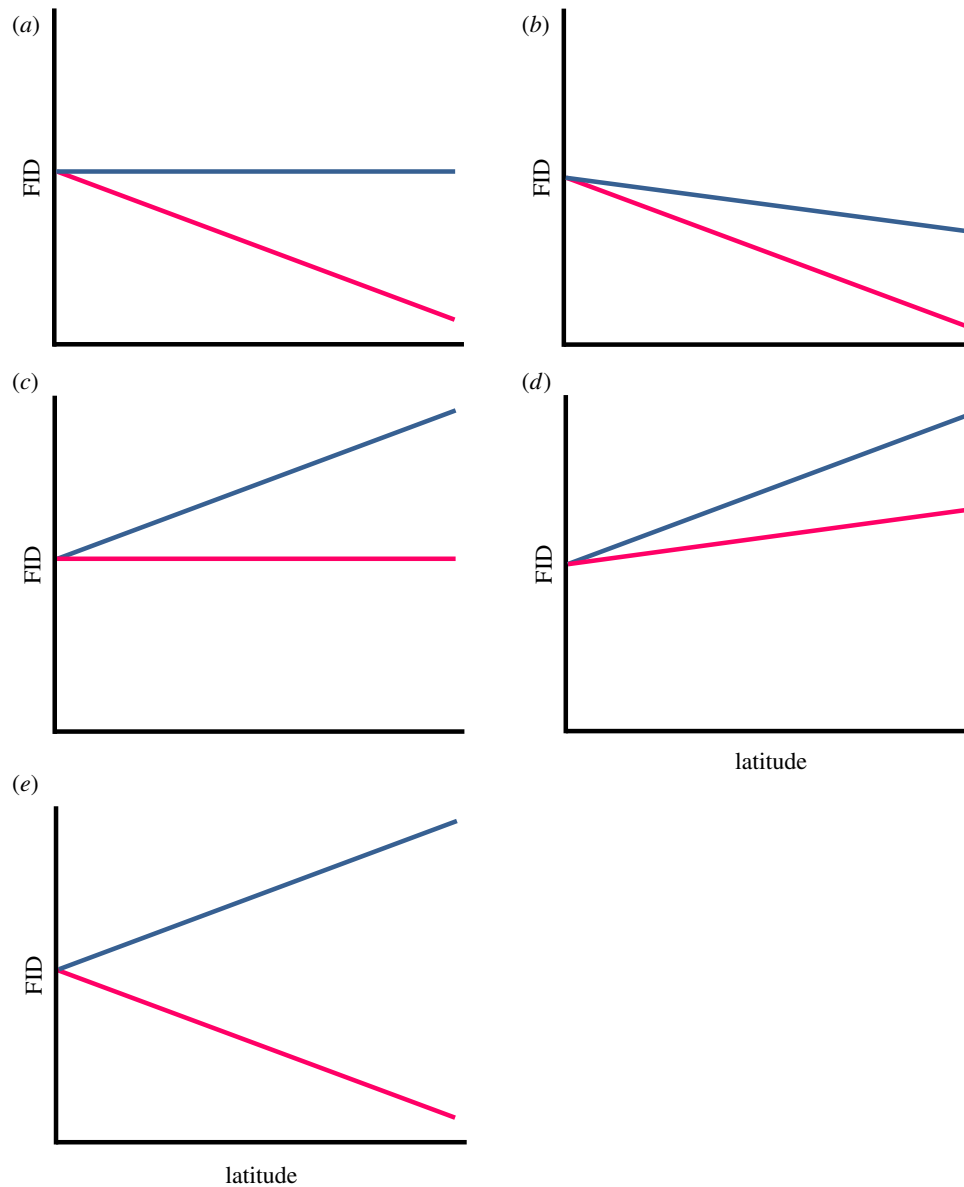


Figure 1. The five possible scenarios predicted for sex difference in risk-taking behaviour and latitude in lizards. Blue lines illustrate possible male trends; pink lines female trends. Risk-taking behaviour measured as flight initiation distance (FID). (Online version in colour.)

[24,25]. Although we have multiple estimates in a few species of our dataset, we did not include ‘species’ as an additional random effect because it did not significantly improve our models (see electronic supplementary material). To test for significant effects of our covariates, we used the between-groups heterogeneity statistic (Q_b) for categorical variables, and the slope estimates of the meta-regressions for the continuous variables [24]. The phylogeny was extracted from Pyron & Burbrink [26] (electronic supplementary material, figure S2).

The overall effects of the models (i.e. the mean of the effect sizes weighted by the inverse of their variance) were considered significant if their 95% confidence intervals (CI) did not include zero [24]. We used I^2 as a measure of heterogeneity in the effect sizes [27]. I^2 represents the proportion of observed variation in data that is not random error (0%, all error; 100%, no error) [27]. To indirectly estimate publication bias, we used Egger’s regression on the effect sizes, in which intercepts significantly different from zero suggest potential publication bias [28]. Additionally, aiming to overcome the non-independent nature of our data (due to phylogeny and multiple estimates per study), we followed Roberts & Stanley [29] and also applied Egger’s regression on meta-analytic residuals of the best model (see [30] for similar approach).

We tested the effects on intersexual difference in risk-taking of potentially important covariates: absolute latitude (i.e. distance from the Equator) where species were studied, sexual dimorphism in body size (ratio between maximum snout–vent length of males and females; values > 1 means that males are larger than females), sexual dichromatism (equally conspicuous sexes or male brighter than female), and ‘social’ sexual dichromatism, to account for males of some species having bright coloration only on surfaces that are normally concealed from view except during social or defensive displays (similarly coloured sexes, or males always being more brightly coloured than females, or males being brighter than females only during social displays). Additional details about the species-level covariates are provided in the electronic supplementary material. Importantly, the factors tested showed low multicollinearity among the covariates (all $r < 0.2$).

We used Akaike’s information criterion corrected for small sample size (AICc) to evaluate the set of candidate models. Models with $\Delta AICc < 2$ are considered equally parsimonious [31]. Because only one of the four factors accounted for significant variation in sex effects on risk-taking during single factor tests, we did not test the different factors simultaneously. All analyses were conducted using the R package *metafor* v. 1.9–2 [32].

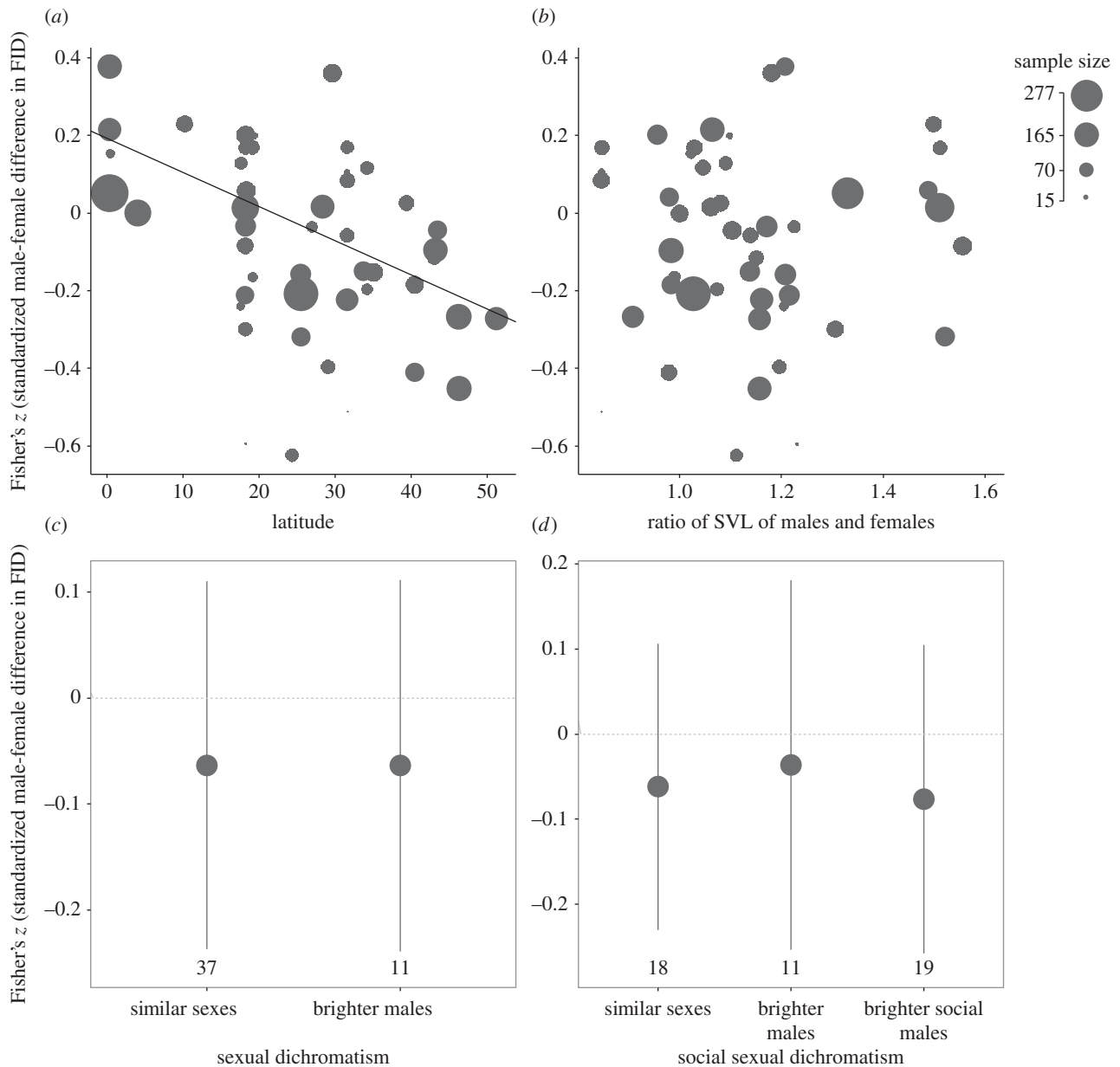


Figure 2. Relationship between effect sizes (Fisher's z) for sex difference in risk-taking behaviour in lizards and (a) latitude, (b) ratio of maximum snout-vent length (SVL) of males and females (values > 1 means that males are larger than females), (c) sexual dichromatism (mean \pm 95% CIs) and (d) social sexual dichromatism (i.e. species in which males have bright coloration on surfaces that are normally concealed from view except during social or defensive displays; mean \pm 95% CIs are shown). Fisher's z scores greater than zero indicate male flight initiation distance (FID) $<$ female FID; z scores less than zero indicate female FID $<$ male FID. Different sizes of symbols in plots a and b reflect differences in sample size. Sample size of each level of the factor is shown in the bottom of c and d.

Table 1. Results of the meta-regression models performed to explain variation of effect sizes for sex difference in risk-taking behaviour. Q_b , between-groups heterogeneity statistic; b , slope of meta-regression; p , p -values of the models; AICc, corrected Akaike's information criterion values; Δ AICc, AICc difference in relation to the best model.

model	statistics	p	AICc	Δ AICc
latitude	$b = -0.009$	< 0.001	-9.34	0
sexual size dimorphism	$b = -0.046$	0.799	0.17	9.51
sexual dichromatism	$Q_b < 0.001$	0.996	0.23	9.57
social sexual dichromatism	$Q_b = 0.142$	0.932	2.73	12.07

3. Results

The overall effect size did not suggest an average difference in risk-taking behaviour between the sexes ($r = -0.06$, CI: -0.23 , 0.10 , AICc = -2.27). However, the substantial heterogeneity in the effect sizes ($I^2 = 71.06\%$) indicates that the presence and direction of intersexual differences varies among species. This variation motivated our exploration of the effects of covariates on sexual difference in risk-taking.

Among the candidate models, the latitude model best explained differential risk-taking between sexes (table 1). The negative relationship between effect size and latitude indicated that females accept greater risk than males as latitude increases ($r^2 = 52.9\%$; figure 2), i.e. female FID decreased relative to that of males as latitude increased (figure 3). There was no evidence of publication bias according to Egger's regression (on effect sizes: intercept = -0.62 , $p = 0.334$; on meta-analytic residuals: intercept = -0.42 , $p = 0.424$; electronic

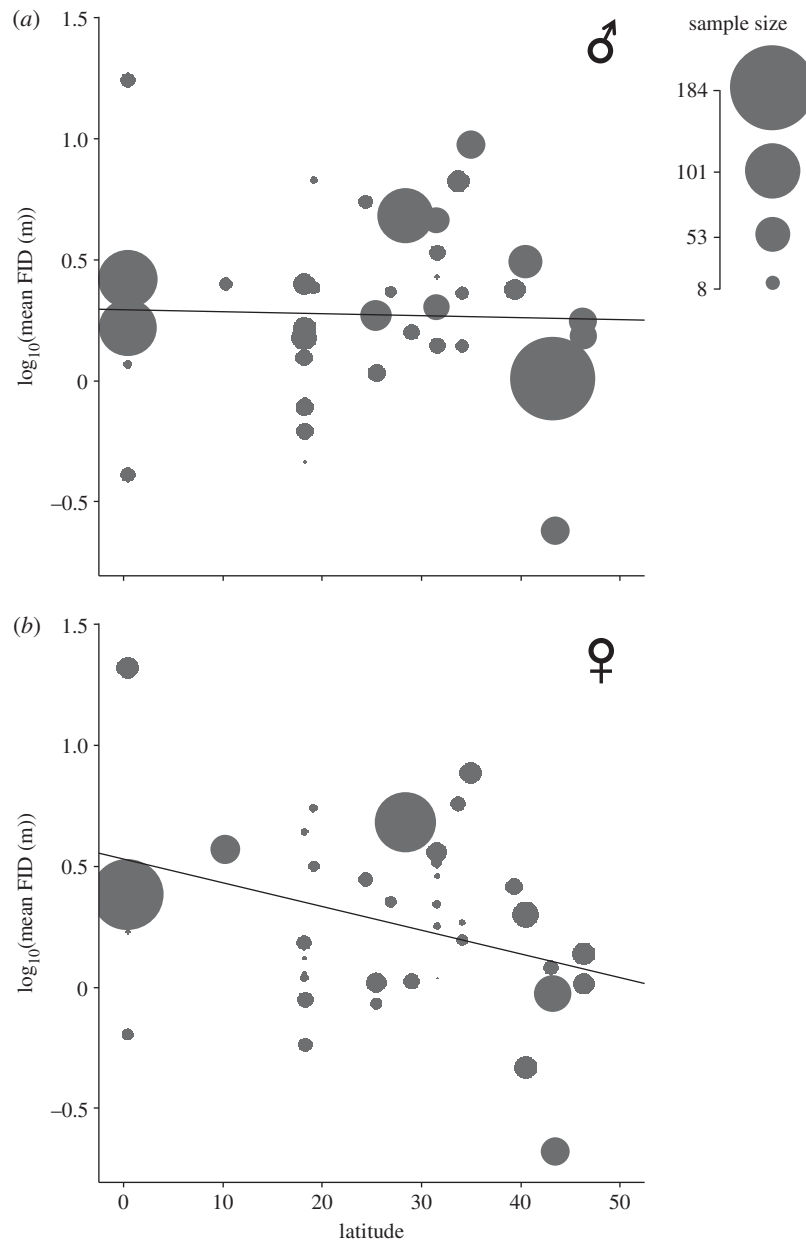


Figure 3. (a,b) Relationship between mean flight initiation distance (FID) of male and female lizards and latitude. The line is the linear regression line and different sizes of symbols reflect differences in sample size.

supplementary material, figure S3). Sexual difference in risk-taking was not significantly related to sexual dimorphism in body size or coloration (table 1 and figure 2).

4. Discussion

We have conducted the first meta-analysis evaluating differential risk-taking behaviour between sexes. Overall, the mean effect size did not differ from zero. However, we found substantial and significant heterogeneity in the effect size among species, implying that differences in risk-taking behaviour exist among species and that residual variance remained to be explained. We investigated whether four variables could account for this variation. Although there were no obvious effects of sexual dichromatism or sexual size dimorphism on sex difference in risk-taking, we found a strong latitudinal effect: FID became increasingly more dimorphic as latitude increased. Specifically, FID decreased in females as latitude increased, but did not vary with latitude in males.

The strong negative relationship between effect size and latitude could be generated by five scenarios (figure 1). By plotting the mean FIDs of species, we found support for scenario 1 (figure 1a), suggesting that the latitudinal pattern was caused by males having a constant anti-predator behaviour across latitudes, whereas females strongly reduced their anti-predator behaviour with increasing latitude (figure 3).

The latitudinal effect cannot be attributed to female reproductive status because meta-analyses including and excluding gravid females yielded similar results (electronic supplementary material). Likewise, other potentially important covariates did not vary, such as reproductive mode (all but one species was oviparous) and diet (all but four species are insectivorous). Although latitude was strongly correlated with 6 of 11 temperature variables of WorldClim (<http://www.worldclim.org/>), latitude produced a superior model to those including temperature variables, both in terms of AICc and r^2 (electronic supplementary material, table S1). Latitude explained almost twice the variance of the best models fitted with climatic

variables (temperature seasonality), indicating the latitudinal pattern of differential risk-taking between sexes is not due to the climatic factors *per se*.

The negative latitudinal cline in the risk-taking behaviour of females is consistent with our expectation of differential effects of climatic conditions on the two sexes. We hypothesize that this novel effect arises from females experiencing ectothermic constraints on the time needed to gain sufficient energy for reproduction and overwintering. This environmental constraint exceeds the effects of 'traditional' indices of sexual selection such as sexual dichromatism and sexual size dimorphism because the effects of latitude differ in male and female lizards in several ways.

First, females at higher latitudes may have less time to provision their eggs and restore their body condition between oviposition and hibernation because they can only function optimally when conditions of temperature and insolation permit them to maintain a sufficiently high body temperature. The annual duration of such conditions decreases as latitude increases.

Second, male lizards must search for mates, defend territories and forage at all latitudes, and the activities needed for mate searching, patrolling, visually scanning and defending territories are compatible with foraging at all latitudes. Female lizards must trade-off increased foraging activity against increased risk via conspicuousness while moving with the potential for only modest gains in the number of offspring by finding and copulating with multiple mates.

For both of these reasons, the opportunity cost of fleeing [4,5] should be greater for females, but not males at higher latitudes. Therefore, we propose that latitude affects differential risk-taking between sexes via very limited variation in its effects on sexual selection in males, and via clinal effects limiting reproductive and post-reproductive provisioning in females.

Studies of birds have shown strong relationships between the extent of sexual display and predation risk, and also relationships between sexual display and anti-predator behaviour [9,10]. In addition, male birds often differ in FID from females [33]. Superficially, we might expect similar findings for lizards. Surprisingly, we found only negligible effects of sexual dichromatism and sexual size dimorphism on the sex difference in anti-predator behaviour in lizards, even when controlling statistically for a number of the most likely potentially confounding variables. Hence, it seems unlikely that accumulation of additional studies will change

this pattern for sexual dichromatism and sexual size dimorphism. One possibility is that effects of increased risk and increased cost of fleeing for the larger or more brightly coloured sex counteract each other, producing equal FIDs in males and females.

Our findings have important implications for future research. First, because current climate change will alter the environment, and that these effects are enhanced at high latitudes [34], we expect that it will also have an effect on sex differences in risk-taking as a function of latitude [33]. Second, we predict that the relative importance of sexual selection (sexual size dimorphism and sexual dichromatism) and latitude (the environment) as determinants of the sex difference in risk-taking should change over time as the climate becomes warmer. These predictions can be reliably checked in the future by using within-species design studies comparing intersexual difference in risk-taking along the latitudinal distribution of species.

In conclusion, although several studies of homeothermic organisms have shown important relationships between sexual display and sex differences in anti-predator behaviour, we found no evidence of such effects in lizards, which are ectothermic. We did, however, show that latitude was the single most important predictor of the sex difference in anti-predator behaviour, most likely due to the constraining effects of increasingly limited time for provisioning by females due to harshening environmental conditions at higher latitudes. Would a meta-analysis with endotherms yield different results? This novel finding opens a window for research to test predictions of our hypothesis about the cause of the cline in sexual dimorphism of escape behaviour and to ascertain whether similar clines occur in other taxa.

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