Article

Disentangling the causes of temporal variation in the opportunity for sexual selection

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In principle, temporal fluctuations in the potential for sexual selection can be estimated as changes in intrasexual variance in reproductive success (i.e. the opportunity for selection). However, we know little about how opportunity measures vary over time, and the extent to which such dynamics are affected by stochasticity. We use published mating data from multiple species to investigate temporal variation in the opportunity for sexual selection. First, we show that the opportunity for precopulatory sexual selection typically declines over successive days in both sexes and shorter sampling periods lead to substantial overestimates. Second, by utilising randomised null models, we also find that these dynamics are largely explained by an accumulation of random matings, but that intrasexual competition may slow temporal declines. Third, using data from a red junglefowl (*Gallus gallus*) population, we show that declines in precopulatory measures over a breeding period were mirrored by declines in the opportunity for both postcopulatory and total sexual selection. Collectively, we show that variance-based metrics of selection change rapidly, are highly sensitive to sampling durations, and likely lead to substantial misinterpretation if used as indicators of sexual selection. However, simulations can begin to disentangle stochastic variation from biological mechanisms.

Driven by intrasexual competition over reproductive opportunities, sexual selection is a powerful evolutionary mechanism, which varies widely over space and time[1–9]. Understanding the causes and consequences of such variation is an enduring challenge in evolutionary biology. Temporal fluctuations in sexual selection can affect processes that ultimately determine net selection across a reproductive period, with repercussions for rates of adaptation, the evolution of alternative reproductive tactics, the maintenance of variation in competitive traits, plasticity in sexual phenotypes and dynamism in evolutionary sex roles[10–13]. Temporal fluctuations may arise as a consequence of variation in the ecological[4,10,14–20] or social environment[8,11,21–26], drastically changing mating dynamics[8,27]. While some of these environmental changes may be long-term[28,29], others can be more rapid, e.g.

within a breeding season[9,11]. Sexual receptivity, courtship effort, mating propensity and mate choice preferences often change sharply in matters of few hours or days[30–35]. While studies have assessed changes in sexual selection across multiple breeding seasons or years[4,10,36–40], less is known about the potential for rapid fluctuations in sexual selection over these much shorter, but still biologically relevant, scales.

The strength of sexual selection is measured by regressing measures of reproductive success over given phenotypic measures among members of the same sex within a population (i.e. selection gradients[41]). However, identifying and measuring the traits (e.g. ornament expression, courtship behaviour or sperm quality) causally related to the outcome of intrasexual competition and variation in reproductive success is often very challenging[42–46]. Thus, a widely used

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alternative approach estimates the potential for – rather than the strength of – sexual selection in a population as standardised intra-sexual variance in reproductive success. This metric, known as the 'opportunity for selection', captures the maximum potential strength of sexual selection in a population even when little is known about the phenotypic traits that mediate intrasexual competition[47,48]. In addition, the opportunity for selection can be utilised to dissect the potential for sexual selection into components driven by variance in the number of sexual partners (precopulatory sexual selection) and in the proportion of gametes fertilised (postcopulatory sexual selection)[49]. The value of these variance-based metrics however, remains debated, largely due to their inability to distinguish between variation that arises due to intrasexual competition and variation in reproductive success due to stochastic processes[42,43,50,51]. For example, Klug et al.[42] showed that the number of unmated individuals tends to increase as the operational sex ratio becomes more biased, so the opportunity for sexual selection will also increase even if individuals mate at random. Moreover, variance-based metrics may be particularly sensitive to sampling effort (i.e. the period of time over which sampling occurs), and because they measure patterns of variance relative to mean reproductive success, these metrics may be strongly impacted by temporal increases in mean reproductive success[50]. For example, sampling for an insufficient period may overestimate opportunity measures by inflating the number of non-mating individuals[52–54]. Alternatively, temporal changes in the opportunity for sexual selection may be driven by competitive biological processes. In principle, behavioural shifts towards increased monogamy, promiscuity, mate monopolisation or increased sperm competition over time may all dynamically change the opportunity for sexual selection. However, because the opportunity for sexual selection only measures the max-imum potential for sexual selection and does not discriminate between competitive and stochastic processes[42,43,51], there is a risk that sys-tematic changes in this metric over time may be mistakenly inter-preted as changes in actual sexual selection. An important step toward understanding temporal dynamics of sexual selection is therefore to resolve how variance-based metrics change over a reproductive period and the extent to which these patterns are reflective of biological *versus* methodological and stochastic processes (e.g. variation in the sampling period; random mating). However, currently there is little information on how the opportunity for sexual selection behaves over time, and the methodological and biological processes that contribute to such dynamics. Understanding how variance-based metrics behave through time in relation to deterministic and stochastic processes is important because variance in reproductive success is a prerequisite for sexual selection.

Here, we address this knowledge gap by utilising fine-scale tem-poral data, at the resolution of a day, on sexual behaviour across dif-ferent vertebrate and invertebrate species. First, we characterise temporal changes in the opportunity for precopulatory sexual selection over cumulative days in males and females. Second, we assess the extent to which temporal changes in the opportunity for precopulatory sexual selection arise as a consequence of stochastic processes under the null expectation of random mating (as opposed to deterministic processes such as behavioural shifts in mating dynamics)[42]. Third, we establish the impact of sampling effort by comparing observed opportunity esti-mates based on cumulative patterns of mating (i.e. where mating suc-cess for each individual is summed across all preceding days and thus represents the maximum possible strength of selection over a sampling period up to and including a given day) with 'instantaneous' estimates calculated independently each day. Finally, using available parentage data from a population of red junglefowl (*Gallus gallus*) - a poly-gynandrous bird - we explore to what extent patterns identified for precopulatory sexual selection are also reflected in the opportunity for postcopulatory sexual selection (i.e. standardised variance in paternity share) and in the total opportunity for selection on reproductive success (i.e. standardised variance in reproductive success). We show that the opportunity for sexual selection varies sharply over time, is highly sensitive to sampling duration, and may lead to substantial mis-interpretation if used as an indicator of sexual selection. However, simulations should help to disentangle variation arising from stochastic and deterministic processes.

Results

Dynamics in the opportunity for precopulatory sexual selection across species

Our results demonstrate broadly consistent decreases over time (i.e. successive days within a breeding period) in the cumulative opportunity for precopulatory sexual selection on mating success (I_M) within both males and females across species (Fig. 1, Table 1) - with one exception. In the socially monogamous jackdaw (*Corvus monedula*) cumulative I_M did not significantly change over time in males but increased towards the end of the study period in females (Fig. 1, Table 1).

We evaluated whether temporal trends in cumulative I_M could be driven by the 1st day of an observation period. This is because in experimental studies, day 1 can correspond to the day when previously sex-segregated individuals are introduced to the opposite sex, which may influence mating behaviour (e.g.[55,56]). To test the effect of day 1, we used permutations to randomly shuffle the day order of mating events in our data (e.g. mating events on day 10 were assigned to day 1, and vice versa). Temporal trends in cumulative I_M were qualitatively similar across permutations (Supplementary Fig. 1) suggesting patterns are not solely caused by the specific sequence of events occurring over days, but rather by the accumulation of mating events over time. This accumulation is exemplified by the increase in mean mating success across males and females of each species, although full saturation of the mating matrix was not observed in any species (i.e. in no group did all possible pairs of males and females copulate) (Supplemen-tary Fig. 2).

Null expectations for cumulative I_M that assume random patterns of mating showed qualitatively similar tendencies to decline over time as compared to observed cumulative I_M for both males and females (Fig. 1), demonstrating that a general temporal decline in I_M is expected as a consequence of the random accumulation of mating events over time. However, if changes in variance across species are at least par-tially driven by competitive biological processes (e.g. mate mono-polisation), we should expect observed opportunity values to deviate from null expectations (i.e. the 95% range of the simulated values). Consistent with this, we found that observed cumulative I_M values in some species were quantitatively higher than null expectations as observation periods progressed for both males and females, with significant deviations often starting from relatively early in the obser-vation period (Fig. 1). Two species showed sex-specific patterns. In squirrel monkeys (*Saimiri oerstedi*), while the observed cumulative I_M for males was higher than null expectations, female observed cumu-lative I_M consistently failed to deviate from null expectations. Similarly, cumulative I_M for male strawberry poison-dart frogs (*Dendrobates pumilio*) was higher than null expectations towards the end of the observational period whereas female cumulative I_M did not differ from null expectations.

Daily instantaneous estimates of I_M did not show a temporal decline and consistently overestimated I_M when compared to cumu-lative estimates, particularly later in an observational period (Fig.1, Table 1). These results indicate that the opportunity for sexual selec-tion can be substantially overestimated when measured over a restricted period.

Dynamics in the opportunity for total and postcopulatory sexual selection in red junglefowl

The cumulative opportunity for total sexual selection (I_T) in both male and female red junglefowl consistently declined over time at a
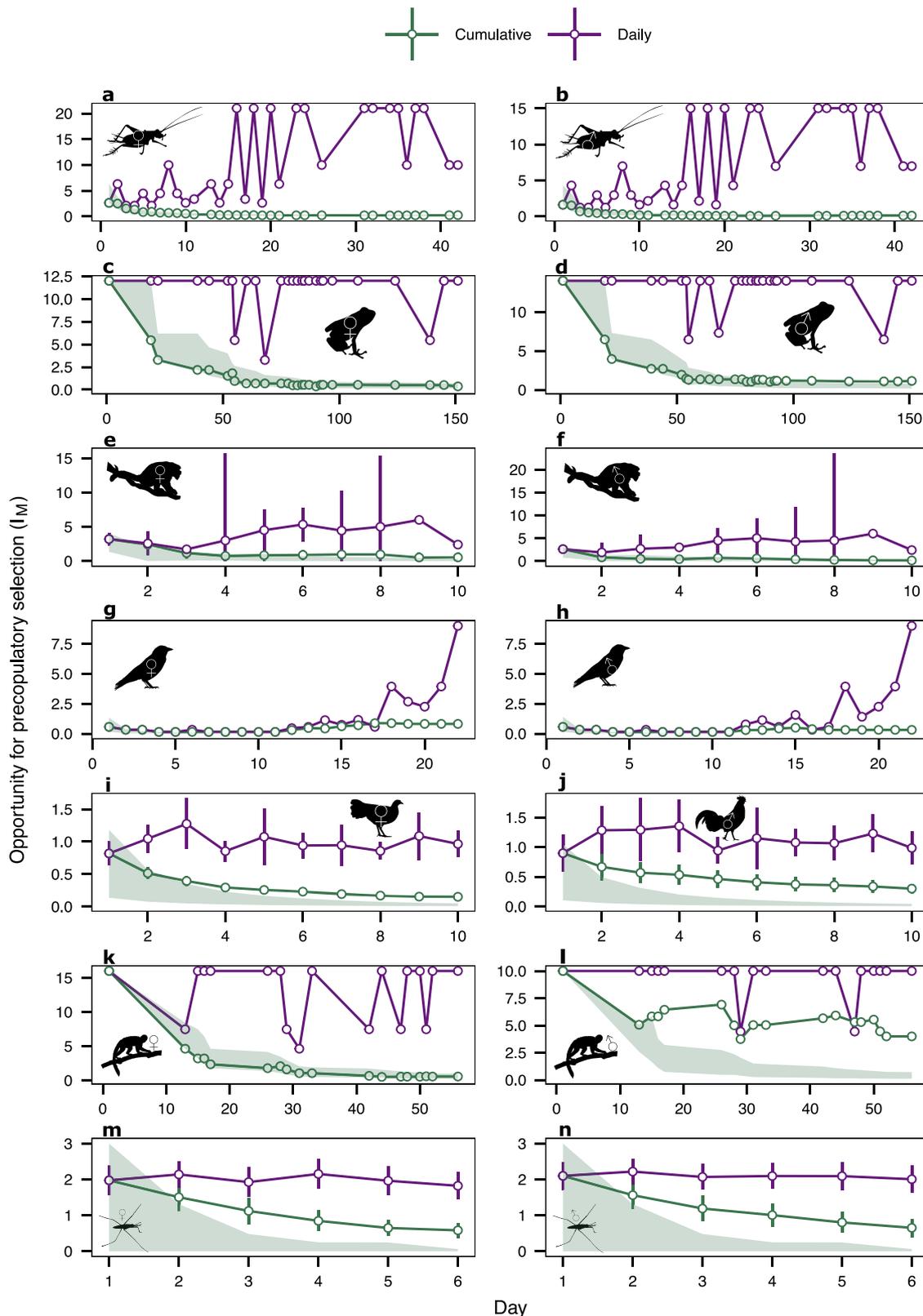
decelerating rate (Fig. 2a, b, Table 2). A similar pattern was observed when considering variance in the fecundity of males' sexual partners (I_N), which also decreased over time at a decelerating rate (Fig. 2c, Table 2). Finally, the opportunity for postcopulatory sexual selection (I_P) on male paternity share (P) also decreased over successive days, but this time linearly (Fig. 2d).

Similar to the opportunity for precopulatory sexual selection on mating success (I_M), simulations assuming random mating and fertilisations showed that measures of the total opportunity for sexual selection (I_T) and its constituent components (I_N and I_P) decreased over time (Fig. 2). In comparison, observed estimates were often higher than null expectations, particularly later in a trial (Fig. 2). However, in

Fig. 1 | Short-term temporal dynamics in the opportunity for precopulatory sexual selection across species. Mean (95% c.i) values for the opportunity for precopulatory sexual selection (I_M) across vertebrate and invertebrates species over time (days) during a breeding period. Females (♀) and males (♂) are represented on the left and right panels, respectively. Species from top to bottom represent: **a**, **b** Hawaiian swordtail crickets[79] (*Laupala cerasina*) n groups = 1. **c**, **d** Strawberry poison-dart frogs[78] (*Dendrobates pumilio*) n groups = 1; **e**, **f** howler monkeys[77] (*Alouatta caraya*) n groups = 6. **g**, **h** Jackdaws[80] (*Corvus monedula*) n groups = 1. **i**, **j** Red junglefowl[56,66,67,81] (*Gallus gallus*) n groups = 20. **k**, **l** Squirrel monkeys[66] (*Saimiri oerstedi*) n groups = 1. **m**, **n** Water striders[8] (*Aquarius remegis*) n groups = 40. Green points show I_M values calculated cumulatively and represent the maximum potential strength of precopulatory sexual selection on a given day taking into account patterns of mating over all preceding time units, and purple points show instantaneous values where opportunity for precopulatory sexual selection is assessed independently for each time unit (day). Bars represent the 95% confidence intervals (95% c.i) for studies with replicate groups. The lower range of c.i were capped at 0 to exclude negative values. Green shaded areas represent expectations for cumulative measures of I_M based on 10,000 random mating simulations (i.e. the 95% range of simulated estimates). Observed cumulative values with c.i lying within shaded areas were considered not to differ from null expectations. Source data are provided as a Source Data file.

females, observed I_T did not deviate from null expectations at any point in the trial (Fig. 2a). In males, observed I_T was higher than null expectations from the 8th day of sampling onwards (Fig. 2b). Similarly, observed male I_N and I_P were higher than null expectations from the 8th day (Fig. 2c, d).

Daily instantaneous measures led to a significant overestimation of most opportunity estimates in both sexes. Daily estimates of I_T were significantly higher than cumulative estimates (Fig. 2a, b, Table 2). Similarly, standardised variation in the fecundity of females mated by a male (I_N) was consistently higher when estimated using daily *versus* cumulative measures (Fig. 2c, Table 2). In contrast, we found no significant overall difference between daily and cumulative estimates of the potential for postcopulatory sexual selection (I_P) on males (Fig. 2d, Table 2).

Discussion

Determining the causes and consequences of temporal variation in mating and reproductive success is an important step in understanding the evolutionary diversity of reproductive strategies. However, temporal variation within reproductive events is often overlooked in sexual selection studies, and the value of variance-based metrics being used as a proxy to assess temporal patterns of sexual selection has not been considered. Here, we utilise the standardised variance in mating success (i.e. the opportunity for precopulatory sexual selection, I_M) – commonly used as a proxy for the strength of sexual selection – to evaluate temporal changes in the potential for precopulatory sexual selection over a reproductive period across different animal species. We show that (i) the opportunity for sexual selection may decline rapidly over the course of just a few days of sampling for both females and males, (ii) observed temporal decreases are broadly similar to those expected under random mating, although some studies show patterns of non-random mating which slow the decrease in opportunity over time, and (iii) estimates are consistently overestimated if calculated over restricted snapshots of time (i.e. daily instantaneous measures). Finally, using detailed parentage data in a polygynandrous bird, we show that consistent declines in precopulatory measures were mirrored by temporal patterns in the opportunity for postcopulatory and total sexual selection. These results reinforce previous suggestions that the opportunity for sexual selection should not be used as a proxy of actual sexual selection, but that the use of null models can provide insight into how random versus deterministic processes are expected to influence mating dynamics.

We observed a reduction in the opportunity for precopulatory sexual selection (I_M) over time, as males and females accumulate more mating partners. Previous studies have suggested that increases in polyandry in already moderately polygynandrous populations may reduce I_M in males by saturating the mating matrix and eroding intrasexual variation in mating success[55,57]. For example, in a rare study of short-term temporal variation in sexual selection over eight weeks in the hermaphroditic pond snail (*Lymnaea stagnalis*), variation in mating success in groups of five individuals was completely eroded in the first weeks of mating as all individuals had mated with all possible partners[7]. While mating matrices did not fully saturate in any of the

species in our present study, we demonstrate that I_M can erode over time even in species with strong social hierarchies, where social dominance is presumed to confer male control over access to mating opportunities and maintain reproductive skew (e.g. red junglefowl). This erosion could, in principle, occur if subordinate males engaging in alternative mating strategies[58,59] are able to progressively attain mating partners over extended periods. This conclusion holds true for red junglefowl since it has been repeatedly shown that subordinate males achieve some mating success through sexual coercion[60]. Alternatively, females may increasingly express preferences to mate with novel males, or otherwise phenotypically different males over time, resulting in temporal reduction in mating skew[61,62]. Similar mechanisms could explain our observed temporal declines in I_M in females, although this pattern has - to our knowledge - not been considered previously. In contrast, studies in socially monogamous populations indicate that some polyandry may increase variance in male mating success by allowing some males to attain more than one mate (i.e. via extra-pair copulations)[63]. In accordance with this, we showed that in the socially monogamous jackdaws, I_M in females increased towards the end of the sampling period, which could be caused by female extra-pair mating or sequential polyandry at later stages of the reproductive season[64,65]. Future studies should explicitly compare the erosion of I_M across an expanded range of socially monogamous species with systems characterised by strongly skewed mating patterns (e.g. lek and polygynous harem forming species) to understand the generality of such different temporal trajectories in opportunities for sexual selection. More importantly, such comparisons across different mating systems should include longitudinal measures of actual selection gradients[42] to explore how net patterns of phenotypic sexual selection are shaped by cumulative patterns of mating over time, such as via changes in female selectivity or alternative mating tactics.

Previous studies have criticised the use of opportunity estimates as reliable indicators of the strength of sexual selection, since variance in reproductive success may be partially driven by random mating or sampling issues alone (e.g.[42,43,50,51]). Our results strongly support this criticism, since temporal trends in opportunity estimates derived from simulations assuming random mating (all studies) and fertilisations (red junglefowl) were, to a large degree, qualitatively similar to observed values. Moreover, empirical estimates of opportunity often did not differ from simulated estimates, particularly early in a study period. One caveat is that our simulations had many simplifying assumptions and did not include detailed aspects of mating behaviour specific to each species. Moreover, in some field studies not all individuals were screened simultaneously, whereas in our simulations all individuals were assumed to be present on each sampling day. Despite these important limitations, we show that comparing null expectations with observed measures should help disentangling temporal trends driven by random mating from possible biological causes. For example, observed I_M in male squirrel monkeys was higher than the simulated range as early as the third day of the sampled period, which can be explained by the largest male obtaining 70% of observed copulations in the original study[66]. This scenario, in which mate monopolisation is substantial, has been previously identified as one of the

Table 1 | Temporal patterns in the opportunity for precopulatory sexual selection (I_M) across successive days (Day) calculated using two different methods (i.e. cumulative or daily instantaneous mating success) for multiple animal species

Predictor	Estimate±s.e	Statistic	p	Estimate±s.e	Statistic	p
Strawberry poison dart frog (Dendrobates pumilio)[A]						
		Males			Females	
Intercept [Cumulative]	0.2 ± 0.05	-	-	−0.46 ± 0.07	-	-
Method [Daily]	2.37 ± 0.05	$F_{1,48} = 1144.0$	**< 0.001**	2.83 ± 0.09	$F_{1,48} = 895.3$	**< 0.001**
Day	−0.01 ± 0.00	$F_{1,48} = 156.9$	**< 0.001**	−0.02 ± 0.00	$F_{1,48} = 191.5$	**< 0.001**
Day^2	0 ± 0.00	$F_{1,48} = 79.3$	**< 0.001**	0 ± 0.00	$F_{1,48} = 61.9$	**< 0.001**
Method [Daily] *Day	0.01 ± 0.00	$F_{1,48} = 71.0$	**< 0.001**	0.02 ± 0.00	$F_{1,48} = 90.9$	**< 0.001**
Method [Daily] *Day^2	0 ± 0.00	$F_{1,48} = 41.6$	**< 0.001**	0 ± 0.00	$F_{1,48} = 29.9$	**< 0.001**
Jackdaw (Corvus monedula)[A]						
		Males			Females	
Intercept [Cumulative]	−1.59 ± 0.17	-	-	−1.59 ± 0.14	-	-
Method [Daily]	0.33 ± 0.24	$F_{1,38} = 1.8$	0.191	0.47 ± 0.15	$F_{1,39} = 9.8$	**0.003**
Day	0.02 ± 0.02	$F_{1,38} = 1.9$	0.180	0.08 ± 0.02	$F_{1,39} = 24.0$	**< 0.001**
Day^2	0.01 ± 0.00	$F_{1,38} = 2.5$	0.125	0.01 ± 0.00	$F_{1,39} = 10.0$	**< 0.001**
Method [Daily] *Day	0.12 ± 0.03	$F_{1,38} = 23.1$	**< 0.001**	0.08 ± 0.02	$F_{1,39} = 39.1$	**0.003**
Method [Daily] *Day^2	0.01 ± 0.00	$F_{1,38} = 5.9$	**0.020**	-	-	-
Hawaiian sword tail cricket (Laupala cerasina)[A]						
		Males			Females	
Intercept [Cumulative]	−2.48 ± 0.13	-	-	−1.53 ± 0.12	-	-
Method [Daily]	4.36 ± 0.19	$F_{1,58} = 349.7$	**< 0.001**	3.80 ± 0.17	$F_{1,58} = 501.1$	**< 0.001**
Day	−0.07 ± 0.01	$F_{1,58} = 82.7$	**< 0.001**	−0.06 ± 0.01	$F_{1,58} = 90.0$	**< 0.001**
Day^2	0.00 ± 0.00	$F_{1,58} = 39.0$	**< 0.001**	0.00 ± 0.00	$F_{1,58} = 33.6$	**< 0.001**
Method [Daily] *Day	0.13 ± 0.01	$F_{1,58} = 144.2$	**< 0.001**	0.12 ± 0.01	$F_{1,58} = 153.4$	**< 0.001**
Method [Daily] *Day^2	−0.01 ± 0.00	$F_{1,58} = 37.4$	**< 0.001**	−0.00 ± 0.00	$F_{1,58} = 33.9$	**< 0.001**
Squirrel monkey (Saimiri oerstedi)[A]						
		Males			Females	
Intercept [Cumulative]	1.85 ± 0.10	$F_{1,33} = 365.2$	**< 0.001**	0.08 ± 0.10	$F_{1,31} = 0.7$	0.410
Method [Daily]	0.53 ± 0.08	$F_{1,33} = 46.7$	**< 0.001**	2.24 ± 0.11	$F_{1,31} = 416.7$	**< 0.001**
Day	−0.01 ± 0.00	$F_{1,33} = 4.3$	**0.046**	−0.05 ± 0.00	$F_{1,31} = 116.0$	**< 0.001**
Day^2	-	-	-	0.00 ± 0.00	$F_{1,31} = 8.7$	**0.006**
Method [Daily] *Day	-	-	-	0.06 ± 0.01	$F_{1,31} = 64.4$	**< 0.001**
Howler monkey (Alouatta caraya)[B]						
		Males			Females	
Intercept [Cumulative]	0.70 ± 0.08	-	-	0.91 ± 0.08	-	-
Method [Daily]	0.68 ± 0.10	$F_{1,52} = 48.3$	**< 0.001**	0.60 ± 0.08	$F_{1,58} = 51.0$	**< 0.001**
Day	−0.08 ± 0.03	$F_{1,55} = 0.1$	0.742	−0.09 ± 0.02	$F_{1,60} = 0.8$	0.376
Method [Daily] *Day	0.15 ± 0.04	$F_{1,52} = 17.6$	**< 0.001**	0.16 ± 0.03	$F_{1,58} = 25.9$	**< 0.001**
Water strider (Aquarius remegis)[B]						
		Males			Females	
Intercept [Cumulative]	0.67 ± 0.05	-	-	0.64 ± 0.05	-	-
Method [Daily]	0.40 ± 0.04	$F_{1,357} = 112.0$	**< 0.001**	0.41 ± 0.04	$F_{1,357} = 131.5$	**< 0.001**
Day	−0.12 ± 0.02	$F_{1,358} = 31.8$	**< 0.001**	−0.12 ± 0.01	$F_{1,358} = 40.0$	**< 0.001**
Method [Daily] *Day	0.11 ± 0.02	$F_{1,355} = 24.0$	**< 0.001**	0.11 ± 0.02	$F_{1,356} = 28.1$	**< 0.001**
Red junglefowl (Gallus gallus)[B]						
		Males			Females	
Intercept [Cumulative]	−1.04 ± 0.12	-	-	−1.75 ± 0.12	-	-
Method [Daily]	1.00 ± 0.06	$F_{1,375} = 309.5$	**< 0.001**	1.87 ± 0.07	$F_{1,374} = 813.9$	**< 0.001**
Day	−0.11 ± 0.01	$F_{1,375} = 64.2$	**< 0.001**	−0.19 ± 0.01	$F_{1,374} = 80.6$	**< 0.001**
Day^2	0.01 ± 0.00	$F_{1,375} = 1.5$	0.219	0.02 ± 0.00	$F_{1,374} = 4.8$	**0.029**
Method [Daily] *Day	0.11 ± 0.01	$F_{1,375} = 72.6$	**< 0.001**	0.24 ± 0.02	$F_{1,374} = 248.6$	**< 0.001**
Method [Daily] *Day^2	−0.01 ± 0.01	$F_{1,375} = 7.1$	**0.008**	−0.03 ± 0.01	$F_{1,374} = 23.7$	**< 0.001**

The results for males and females are shown on the left and right, respectively. Models were run separately per each species and sex. We used linear regression (LR) analyses for studies with a single observation per day (A), and linear mixed models (LMMs) including a random effect of group identity for studies with more than one replicate (B). Response variables (I_M) were log-transformed to meet model assumptions, and continuous predictors (i.e. Day, Day^2) were centred to facilitate interpretation of fixed effects coefficients. Statistically significant results ($p < 0.05$) are in bold. F-statistics, p-values and degrees of freedom for LMMs were calculated using the Satterthwaite approximation.
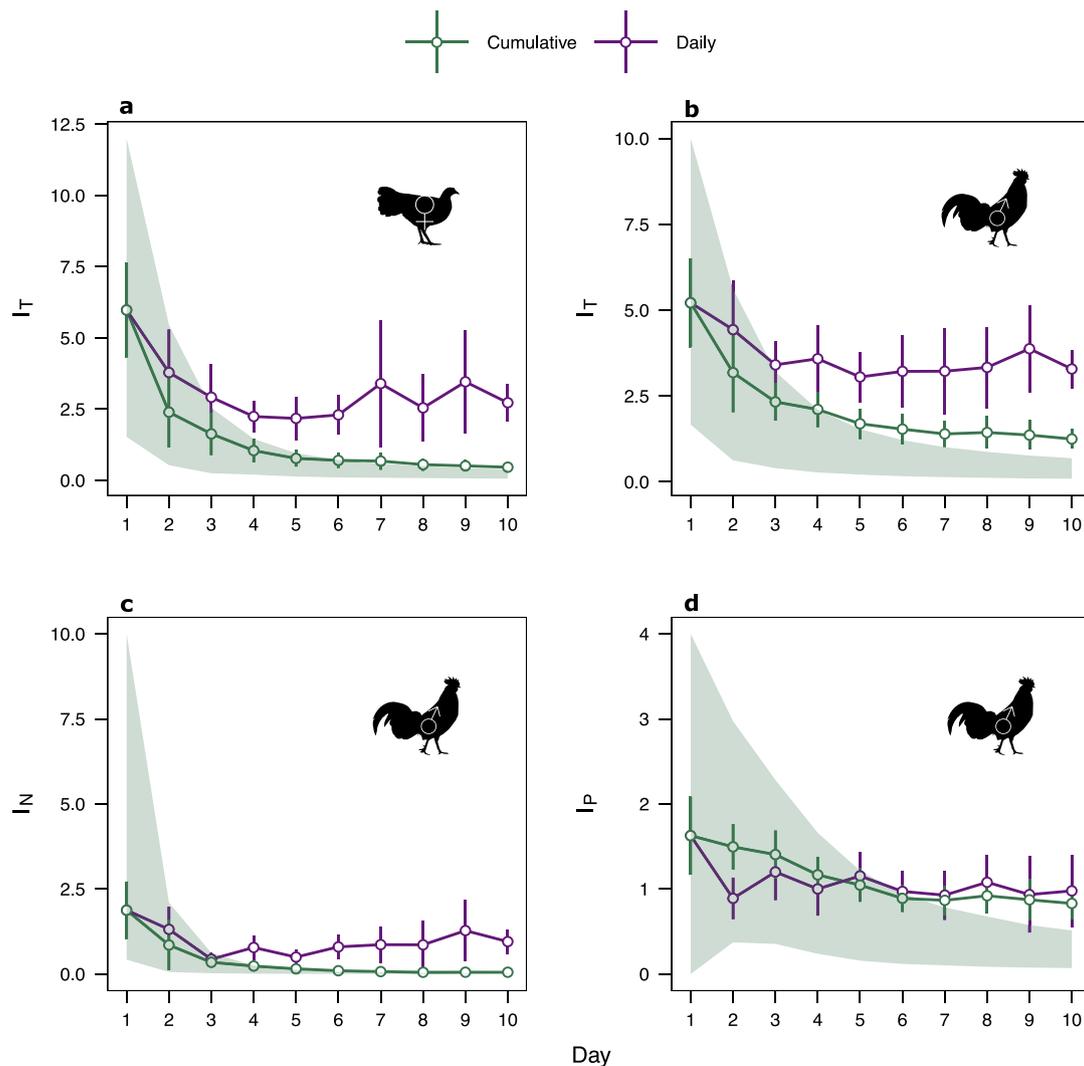
Fig. 2 | Short-term temporal dynamics in multiple opportunity for selection episodes in a polygynandrous bird. Patterns of opportunity estimates across different components of reproductive success in male and female red junglefowl (*Gallus gallus*) *n* groups = 20. Points represent observed mean opportunity estimates, bars represent 95% confidence intervals (95% c.i.) and point colour reflects the sampling method (green: cumulative; purple: daily). Green shaded areas represent expectations for cumulative measures of opportunity for selection based on 10,000 random mating simulations (i.e. the 95% range of simulated estimates). Observed cumulative values with c.i. lying within shaded areas were considered not to differ from null expectations. Females (♀): **a** Standardised variance in reproductive success (opportunity for total selection, I_T). Males (♂): **b** Opportunity for total selection (I_T), **c** Standardised variance in partner's fecundity (opportunity for sexual selection on partner fecundity, I_N), **d** Standardised variance in paternity share (opportunity for postcopulatory sexual selection, I_P). Source data are provided as a Source Data file.

few cases where opportunity estimates may correlate with actual sexual selection[42]. Similarly, the higher I_M than expected by chance in male red junglefowl is likely driven by a combination of male-male competition and female choice. Previous research with this red junglefowl dataset has shown that younger and more aggressive individuals tend to secure more mating partners and copulate more frequently[56,67]. Moreover, observed values of the opportunity for postcopulatory sexual selection (I_P) and total selection (I_T) deviated from null expectations much later in the trial than I_M. This suggests that consistent skew in mating success may take time to translate into biases in paternity share and reproductive success. This is because sperm from more successful males still must compete with rival sperm from earlier inseminations, which must be used up, or leaked, from the female reproductive tract before any consistent advantage is observed[68,69]. Together, these results reinforce previous suggestions indicating that null models should be included in sexual selection studies to adequately disentangle variance arising from competitive

versus stochastic causes[42,43]. For simulations to be biologically relevant, assumptions should be carefully defined in order to reflect particularities of the study system e.g. mating frequencies and sperm storage duration.

We also identified other concerns associated with using I_M as a surrogate for the strength of sexual selection. Our comparisons between cumulative and daily instantaneous measures of opportunity for selection indicate that even small differences in sampling periods of a few days can lead to very different conclusions regarding the potential for sexual selection. Daily instantaneous measures consistently overestimated variance in components of reproductive success, suggesting that studies using relatively short periods of sampling relative to the overall length of the breeding event must be careful when interpreting results, particularly those pointing to a strong opportunity for sexual selection. Future studies aimed at quantifying the opportunity for sexual selection should devise the sampling duration carefully and be aware of the strong potential to overestimate

Table 2 | Temporal patterns in the opportunity for total selection (I_T) and its components (I_N, I_P), across successive days (Day) calculated using two different methods (i.e. cumulative or daily instantaneous reproductive success) across multiple replicate groups of red junglefowl (*Gallus gallus*)

Response	Predictors	Estimate±s.e	Statistic	p
Females				
I_T	Intercept [Cumulative]	−0.5 ± 0.12	-	-
	Method [Daily]	1.06 ± 0.05	$F_{1,369} = 477.2$	**< 0.001**
	Day	−0.24 ± 0.01	$F_{1,369} = 313.2$	**< 0.001**
	Day²	0.04 ± 0.00	$F_{1,369} = 109.5$	**< 0.001**
	Method [Daily] *Day	0.18 ± 0.02	$F_{1,369} = 112.2$	**< 0.001**
Males				
I_T	Intercept [Cumulative]	0.35 ± 0.09	-	-
	Method [Daily]	0.61 ± 0.04	$F_{1,369} = 210.5$	**< 0.001**
	Day	−0.14 ± 0.01	$F_{1,369} = 141.6$	**< 0.001**
	Day²	0.02 ± 0.00	$F_{1,369} = 54.5$	**< 0.001**
	Method [Daily] *Day	0.1 ± 0.01	$F_{1,369} = 45.0$	**< 0.001**
I_N	Intercept [Cumulative]	0.09 ± 0.05	-	-
	Method [Daily]	0.33 ± 0.03	$F_{1,369} = 110.1$	**< 0.001**
	Day	−0.07 ± 0.01	$F_{1,369} = 62.1$	**< 0.001**
	Day²	0.02 ± 0.00	$F_{1,369} = 59.5$	**< 0.001**
	Method [Daily] *Day	0.06 ± 0.01	$F_{1,369} = 27.9$	**< 0.001**
I_P	Intercept [Cumulative]	0.71 ± 0.03	-	-
	Method [Daily]	−0.04 ± 0.03	$F_{1,359} = 2.1$	0.144
	Day	−0.03 ± 0.01	$F_{1,359} = 33.4$	**< 0.001**

Notes: Linear mixed models including the identity of the mating group as a random effect were run separately for each sex. Response variables (I_T, I_N, I_P) were log-transformed to meet model assumptions, and predictors (Day, Day²) were centred to facilitate interpretation of fixed effects coefficients. Statistically significant results ($p < 0.05$) are in bold. F-statistics, p-values and degrees of freedom were calculated using the Satterthwaite approximation.

variance-based metrics due to insufficiently long sampling of mating and parentage data. Our approach suggests that sampling durations substantially shorter than the length of a selective window (e.g. mating season or breeding event) will result in overestimations. Practically, prolonged sampling for entire reproductive periods, particularly in species without clearly demarcated reproductive events (e.g. defined breeding seasons), will be challenging. In such cases appropriate sampling durations could be determined empirically by estimating the length of time required for opportunity estimates to reach an asymptote, or statistically controlling for the duration of sampling. Our results also suggest future cross-study comparisons of measures of the opportunity for sexual selection should seek to control for variation in the sampling duration and frequency of sampling.

Despite the limitations associated with measuring opportunity instantaneously, we identify a potential utility in combining cumulative and shorter-term instantaneous approaches to gather insights over how changes in mating behaviour may contribute to dynamic changes in the opportunity for sexual selection. While cumulative opportunity estimates provide the most accurate representation of the maximum potential strength of sexual selection over a breeding event, daily instantaneous estimates (or otherwise highly temporally restricted instantaneous estimates) may help identify the periods or conditions under which mating patterns change. For example, while intrasexual competition and non-random mating may slow the erosion of I_M over

time, instantaneous measures over shorter time-windows may allow researchers to identify the conditions or seasonal periods that correlate with increases in non-random trends in cumulative opportunity measures. For example, shorter-term instantaneous measures may indicate an increase in variance in reproductive success over time, suggesting sustained decreases in the cumulative opportunity for selection may be accelerated by shifts in patterns of competition over time (e.g. via alternative tactics[9,70], environmental conditions[18,71], and mating preferences[72,73]) versus simply due to the accumulation of repeated iterations of broadly similar mating patterns. When accompanied with appropriate null models of random mating, such instantaneous and cumulative comparisons may give insights over how changes in mating behaviour may contribute to dynamic changes in opportunities for sexual selection.

In summary, our results reveal that estimates of opportunity for pre- and postcopulatory sexual selection can drastically decrease over short time scales and that this decrease can be at least partially explained by cumulative patterns of random mating alone, but also indicate that intrasexual competition contributes to slow the decrease over time. We show that mating data collected over short snapshots of time will overestimate the opportunity for sexual selection, particularly if sampling is conducted towards the end of a reproductive period. Collecting longitudinal data should mitigate this issue provided the sampling period is sufficiently long to detect the cumulative effect of intrasexual competition. Finally, our work highlights the pitfalls of using variance-based metrics as surrogate measures of sexual selection, particularly over highly restricted time periods, and indicate that simulations are required to disentangle temporal variation in the opportunity for sexual selection driven by stochastic and biological processes.

Methods
All analyses were conducted using R v.3.6.2[74]. Linear models were run using base R, and linear mixed models (LMMs) were run using the package 'lme4' v1.1-30[75]. F-statistics, p-values and degrees of freedom for LMMs were calculated using the Satterthwaite approximation implemented in the package 'lmerTest' v3.1-3[76].

Calculating opportunities for sexual selection
We collected data from the literature encompassing seven studies totalling 60 mating datasets across seven species in both natural and artificial settings. Datasets included water striders[8] (*Aquarius remegis*), howler monkeys[77] (*Alouatta caraya*), squirrel monkeys[66] (*Saimiri oerstedi*), strawberry poison-dart frogs[78] (*Dendrobates pumilio*), Hawaiian swordtail crickets[79] (*Laupala cerasina*), jackdaws[80] (*Corvus monedula*) and red junglefowl, (*Gallus gallus*)[56,67,68,81]. We used datasets from a set of studies that had been compiled by a previously published review, which conducted a literature search to examine the mating patterns of multiple species[82]. Briefly, this previous review conducted multiple searches on Web of Science aimed at locating published behavioural data of mating groups that provided information on which males copulated with which females, required to calculate temporal patterns in opportunity for precopulatory selection. A subset of studies was not included because they only provided temporal mating data for a minority of the observed males and females. We further supplemented and updated this initial set of studies, by conducting updated versions of the searches on Web of Science spanning from the time of the original search (14th February 2017) until the 19th March 2021 (i.e. searches were limited to 2017–2021). Search terms were tailored to locate studies with behavioural mating data or that reported sexual selection metrics that required the appropriate raw mating data.

The first search used the TOPIC field and contained the following search terms ("Bateman* gradient*") OR ("Bateman* slope*") OR ("Bateman* principle*") OR ("opportunity* for selection") OR ("opportunity* for sexual selection") AND ("Sexual selection").

This resulted in 35 records. The second search included the TOPIC terms (sexual network* OR social network*) AND (sexual selection OR mating system). This search returned 234 records. The third search contained the TOPIC terms (mating* or copulat*) AND (behavio*) AND (observ*), and was restricted to the journals Animal Behaviour, Behavioral Ecology, and Behavioral Ecology and Sociobiology. This returned 100 records. Searches spanned the following Web of Science indexes: SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC. Studies were selected on the basis that they provided clear information on which males copulated with which females over successive days, which is required to calculate temporal patterns in opportunity for precopulatory selection. Studies with group sizes of only two males or females, or where individuals were not allowed to freely interact and mate with each other (e.g. repeated experimental pairs) were not included. Similarly, studies relying solely on molecular parentage to infer mating data with no behavioural mating observations were not included (for full details of each study, see Supplementary Table 1). Time spans over which data was collected within the studies varied between 6 and 150 days, where the first day of the available dataset was treated as day 1. For each dataset mating was inferred either behaviourally – or in the case of red junglefowl – through a combination of behaviour and genetic parentage analysis where pairs that were not observed mating, but produced offspring together, were assumed to have copulated. Individuals that did not copulate were allocated an M of zero[52–54].

For each dataset we calculated the opportunity for precopulatory selection (I_M) over successive days for males and females across all species. I_M is the standardised variance in mating success ($I_M = \sigma_M^2/\bar{M}^2$, where M = the number of mating partners) - a widely used index estimating the maximum potential strength of precopulatory sexual selection[3,25,47,83]. For the red junglefowl dataset we utilised parentage data containing the order, lay day and parentage of each fertilised egg, to assess temporal patterns in additional opportunity estimates namely: the standardised variance in average partners' fecundity (I_N), the opportunity for postcopulatory sexual selection (I_P), and the opportunity for total sexual selection (I_T). Opportunity estimates are calculated as $I_x = \sigma_x^2/\bar{x}^2$ where x is the given measure of reproductive success or its components i.e. number of offspring (T), the mean fecundity of male mating partners (N) and male paternity share (P).

We calculated opportunities over successive days in two ways, (1) cumulatively, where estimates considered reproductive patterns from all preceding days; and (2) instantaneously, where estimates were considered independently on each day. In all species cumulative M was calculated as the number of unique mating partners up to and including that day, and therefore cumulative I_M represents the maximum possible strength of selection over a sampling period up to and including a given day. Daily (i.e. instantaneous) calculations of I_M on the other hand, only included unique mating partners (M) on each separate day. Therefore, consistent changes in daily instantaneous I_M would suggest that patterns of mating on individual days themselves shift over-time (e.g. towards more or less egalitarian share of mating success) rather than changes in I_M resulting from the daily accumulation of consistent mating patterns.

In red junglefowl cumulative reproductive success (T) was calculated as the total number of embryos assigned to males and females up to a given day, while daily T was calculated as the number of embryos assigned to an individual on each individual day. Cumulative male paternity share (P) was calculated as the percentage of embryos sired by a male across all the eggs laid by females he successfully mated with on the previous days, while daily P was calculated as the percentage of embryos sired by a male on a single day. Cumulative N was calculated as the average number of embryos produced by all the females a male successfully mated with during previous days[49,84], while daily N refers to the average number of embryos generated by these females on a given day. Given that in red junglefowl the sperm from an insemination is stored within female sperm storage tubules for up to 14 days, copulations on the first day of a trial can be assumed to compete for fertilisation of ova across all subsequent days[68,85]. Males that failed to copulate successfully were excluded from calculations of P, whereas males that successfully copulated but sired no offspring received zero P. Additionally, if a male mated successfully with a female for the first time on the day she laid an egg, this egg did not enter the calculation of his P or N since his sperm were unlikely to fertilise that egg[85].

Comparing temporal patterns in cumulative and instantaneous opportunities for sexual selection

We evaluated temporal trends in I_M and the impact of cumulative versus daily instantaneous approaches for each species and sex separately. We used linear regression analyses for studies without replicate groups, and linear mixed-effects models (LMMs) including a random effect of group identity for studies with more than one replicate group. We included I_M as the response variable with day of the mating trial (continuous), the sampling method (2-level factor, cumulative vs. daily), and their interaction as predictors. For the red junglefowl dataset we ran additional LMMs including the different opportunity indices (i.e. I_T, I_N, and I_P) as response variables, and mating groups ($n = 20$) as random effects. When models violated the assumption of homoscedasticity, responses (i.e. I_M, I_N, I_P, I_T) were log-transformed. Moreover, in many models relationships were curvilineal despite transformations, so for these models we included a quadratic effect of day order (Day^2) and its interaction with the sampling method ($Day^2 \times$ Method). Predictors were centred around their means to facilitate interpretation of model coefficients[86].

Because in experimental studies day 1 corresponds to when sexually isolated individuals are first introduced to the opposite sex, several sexual behaviours may change drastically over the first days as initial sexual novelty and mating propensity are replaced by familiarity and resistance/choosiness[87,88]. To investigate this potentially confounding effect and assess the robustness of temporal patterns in cumulative I_M, we ran 1000 simulations swapping the day sequence arbitrarily (code available in figshare[89]). If mating behaviour on day 1 is the main factor driving temporal patterns in I_M, we expect results across simulations to vary drastically in slope.

Testing for deviations from null expectations based on random matings and fertilisations

We assessed whether observed temporal trends in the opportunity for precopulatory sexual selection (I_M) across males and females deviated from trends calculated from simulations assuming random mating for all species. For red junglefowl we additionally compared temporal trends in male cumulative opportunity for selection on partner fecundity (I_N) and paternity share (I_P), and male and female total opportunity for sexual selection on reproductive success (I_T) against trends generated from simulations assuming random fertilisations.

For each species we ran 10,000 random mating simulations using custom scripts (code available in figshare[89]) with the following assumptions: (i) individuals mate randomly over a reproductive period, with the sex ratio and group size being equal to those reported by a study or extrapolated from its dataset, (ii) the total number of mating events on each day and for each individual is an integer value[51] and equal to the number of mating events in the dataset, and (iii) all individuals are assumed to be present – and available to mate – on each day of the trial. For the red junglefowl datasets we additionally simulated random fertilisations which included two extra assumptions: (iv) the probability each female will lay an egg is equal to the average laying probability across females in the empirical data, which was calculated independently for each day of the trial and only included fertilised eggs, and (v) all males that copulated with a female at least one day before her laying an egg had an equal probability of fertilising that egg. For simplicity, the number of copulations of a male with the same

female did not affect his probability of fertilising an egg. Calculations of simulated cumulative opportunity indices (i.e. I_M, I_N, I_P, I_T) were performed as described above. We compared predicted means and 95% confidence intervals of observed I_T, I_M I_N, and I_P with the 95% range of the simulated values. Days in which mean observed values and confidence intervals fell outside the 95% range of simulated values were considered to be significantly different from randomised values[90,91].

Comparing observed data against null expectations is particularly important because opportunity indices have been criticised for being unable to distinguish variance arising from competitive and stochastic processes[42,43,50]. Therefore, simulations seek to identify possible temporal trends that are caused by factors other than sexual selection. For example, I_M should decrease over time as individuals tend to progressively mate with a larger proportion of the available members of the opposite sex, thus achieving a similarly high M (i.e. given enough time, all individuals of a population can mate with all available partners exhausting intrasexual variation in M). Similarly, I_P may also decrease over time due to variation in P decreasing as a function of sample size (i.e. given enough eggs, all males mating with a female ought to sire some embryos). Therefore, assessing whether observed cumulative opportunity indices exceed null expectations elucidates whether variance in some components of reproductive success is higher than expected by chance, consistent with the signature of sexually selected traits or strategies.

Reporting summary
Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability
The data generated in this study have been deposited in the figshare database under accession code https://doi.org/10.6084/m9.figshare.21902133.v1[89]. Raw mating data used to generate the opportunity estimates can be found at: Hawaiian swordtail crickets[79] (*Laupala cerasina*): https://doi.org/10.5061/dryad.9jd86, jackdaws[80] (*Corvus monedula*): https://doi.org/10.5061/dryad.j0zpc868z, red junglefowl[56,66,67,81] (*Gallus gallus*): https://doi.org/10.6084/m9.figshare.21902133.v1, water striders[8] (*Aquarius remegis*): https://doi.org/10.5061/dryad.rq56t, squirrel monkeys[66] (*Saimiri oerstedi*): Table 2 in the original paper, howler monkeys[77] (*Alouatta caraya*): Table 2 in the original paper, strawberry poison-dart frogs[78] (*Dendrobates pumilio*): Appendix 1 in the original paper. Source data are provided with this paper.

Code availability
Custom R scripts for random mating simulations and shuffling of the day order have been deposited in the figshare database under accession code https://doi.org/10.6084/m9.figshare.21902133.v1[89].

References
1. Darwin, C. *The Descent of Man and Selection in Relation to Sex*. (John Murray, 1871).
2. Andersson, M. *Sexual Selection*. (Princeton University Press, 1994).
3. Shuster, S. & Wade, M. J. *Mating Systems and Strategies*. (Princeton University Press, 2003).
4. Gosden, T. P. & Svensson, E. I. Spatial and temporal dynamics in a sexual selection mosaic. *Evolution* **62**, 845–856 (2008).
5. Kasumovic, M. M., Bruce, M. J., Andrade, M. C. B. & Herberstein, M. E. Spatial and temporal demographic variation drives within-season fluctuations in sexual selection. *Evolution* **62**, 2316–2325 (2008).
6. Mobley, K. B. & Jones, A. G. Environmental, demographic, and genetic mating system variation among five geographically distinct dusky pipefish (*Syngnathus floridae*) populations. *Mol. Ecol.* **18**, 1476–1490 (2009).
7. Hoffer, J. N., Mariën, J., Ellers, J. & Koene, J. M. Sexual selection gradients change over time in a simultaneous hermaphrodite. *eLife* **6**, e25139 (2017).
8. Sih, A., Montiglio, P.-O., Wey, T. W. & Fogarty, S. Altered physical and social conditions produce rapidly reversible mating systems in water striders. *Behav. Ecol.* **28**, 632–639 (2017).
9. Preston, B. T., Stevenson, I. R., Pemberton, J. M. & Wilson, K. Dominant rams lose out by sperm depletion. *Nature* **409**, 681–682 (2001).
10. Cornwallis, C. K. & Uller, T. Towards an evolutionary ecology of sexual traits. *Trends Ecol. Evol.* **25**, 145–152 (2010).
11. Forsgren, E., Amundsen, T., Borg, A. A. & Bjelvenmark, J. Unusually dynamic sex roles in a fish. *Nature* **429**, 551–554 (2004).
12. Hare, R. M. & Simmons, L. W. Sexual selection maintains a female-specific character in a species with dynamic sex roles. *Behav. Ecol.* **32**, 609–616 (2021).
13. Fox, R. J., Donelson, J. M., Schunter, C., Ravasi, T. & Gaitán-Espitia, J. D. Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Philos. Trans. R. Soc. B* **374**, 20180174 (2019).
14. Ingleby, F. C., Hunt, J. & Hosken, D. J. The role of genotype-by-environment interactions in sexual selection. *J. Evol. Biol.* **23**, 2031–2045 (2010).
15. Lindström, J., Pike, T. W., Blount, J. D. & Metcalfe, N. B. Optimization of resource allocation can explain the temporal dynamics and honesty of sexual signals. *Am. Nat.* **174**, 515–525 (2009).
16. Janicke, T., David, P. & Chapuis, E. Environment-dependent sexual selection: Bateman's parameters under varying levels of food availability. *Am. Nat.* **185**, 756–768 (2015).
17. Morimoto, J., Pizzari, T. & Wigby, S. Developmental environment effects on sexual selection in male and female *Drosophila melanogaster*. *PLoS ONE* **11**, e0154468 (2016).
18. Cattelan, S., Evans, J. P., Garcia-Gonzalez, F., Morbiato, E. & Pilastro, A. Dietary stress increases the total opportunity for sexual selection and modifies selection on condition-dependent traits. *Ecol. Lett.* **23**, 447–456 (2020).
19. Glavaschi, A., Cattelan, S., Grapputo, A. & Pilastro, A. Imminent risk of predation reduces the relative strength of postcopulatory sexual selection in the guppy. *Philos. Trans. R. Soc. B* **375**, 20200076 (2020).
20. Clark, D. C., DeBano, S. J. & Moore, A. J. The influence of environmental quality on sexual selection in *Nauphoeta cinerea* (Dictyoptera: Blaberidae). *Behav. Ecol.* **8**, 46–53 (1997).
21. Emlen, S. & Oring, L. Ecology, sexual selection and the evolution of mating systems. *Science* **197**, 215–223 (1977).
22. Liker, A., Freckleton, R. P. & Székely, T. The evolution of sex roles in birds is related to adult sex ratio. *Nat. Commun.* **4**, 1–6 (2013).
23. Wacker, S. et al. Operational sex ratio but not density affects sexual selection in a fish. *Evolution* **67**, 1937–1949 (2013).
24. Wacker, S., Ness, M. H., Östlund-Nilsson, S. & Amundsen, T. Social structure affects mating competition in a damselfish. *Coral Reefs* **36**, 1279–1289 (2017).
25. Janicke, T. & Morrow, E. H. Operational sex ratio predicts the opportunity and direction of sexual selection across animals. *Ecol. Lett.* **21**, 384–391 (2018).
26. Procter, D. S., Moore, A. J. & Miller, C. W. The form of sexual selection arising from male-male competition depends on the presence of females in the social environment. *J. Evol. Biol.* **25**, 803–812 (2012).
27. Eldakar, O. T., Dlugos, M. J., Pepper, J. W. & Wilson, D. S. Population structure mediates sexual conflict in Water striders. *Science* **326**, 816–816 (2009).
28. Martin, A. M., Festa-Bianchet, M., Coltman, D. W. & Pelletier, F. Demographic drivers of age-dependent sexual selection. *J. Evol. Biol.* **29**, 1437–1446 (2016).

29. Pilakouta, N. & Ålund, M. Sexual selection and environmental change: what do we know and what comes next? *Curr. Zool.* **67**, 293–298 (2021).

30. Kahn, A. T., Dolstra, T., Jennions, M. D. & Backwell, P. R. Y. Strategic male courtship effort varies in concert with adaptive shifts in female mating preferences. *Behav. Ecol.* **24**, 906–913 (2013).

31. Jordan, L. A. & Brooks, R. C. Recent social history alters male courtship preferences. *Evolution* **66**, 280–287 (2012).

32. Wilson, D. R., Nelson, X. J. & Evans, C. S. Seizing the opportunity: Subordinate male fowl respond rapidly to variation in social context. *Ethology* **115**, 996–1004 (2009).

33. Gwynne, D. T., Bailey, W. J. & Annells, A. The sex in short supply for matings varies over small Spatial scales in a Katydid (*Kawanaphila nartee*, Orthoptera: Tettigoniidae). *Behav. Ecol. Sociobiol.* **42**, 157–162 (1998).

34. Fedina, T. Y. & Lewis, S. M. Female mate choice across mating stages and between sequential mates in flour beetles. *J. Evol. Biol.* **20**, 2138–2143 (2007).

35. Clark, H. L. & Backwell, P. R. Y. Temporal and spatial variation in female mating preferences in a fiddler crab. *Behav. Ecol. Sociobiol.* **69**, 1779–1784 (2015).

36. Serbezov, D., Bernatchez, L., Olsen, E. M. & Vøllestad, L. A. Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. *Mol. Ecol.* **19**, 3193–3205 (2010).

37. Gerlach, N. M., McGlothlin, J. W., Parker, P. G. & Ketterson, E. D. Reinterpreting Bateman gradients: multiple mating and selection in both sexes of a songbird species. *Behav. Ecol.* **23**, 1078–1088 (2012).

38. Dubuc, C., Ruiz-Lambides, A. & Widdig, A. Variance in male lifetime reproductive success and estimation of the degree of polygyny in a primate. *Behav. Ecol.* **25**, 878–889 (2014).

39. Breuer, T. et al. Variance in the male reproductive success of western gorillas: acquiring females is just the beginning. *Behav. Ecol. Sociobiol.* **64**, 515–528 (2010).

40. Germain, R. R., Hallworth, M. T., Kaiser, S. A., Sillett, T. S. & Webster, M. S. Variance in within-pair reproductive success influences the opportunity for selection annually and over the lifetimes of males in a multi-brooded songbird. *Evolution* **75**, 915–930 (2021).

41. Lande, R. & Arnold, S. J. The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226 (1983).

42. Klug, H., Heuschele, J., Jennions, M. D. & Kokko, H. The mismeasurement of sexual selection. *J. Evol. Biol.* **23**, 447–462 (2010).

43. Jennions, M. D., Kokko, H. & Klug, H. The opportunity to be misled in studies of sexual selection. *J. Evol. Biol.* **25**, 591–598 (2012).

44. Krakauer, A. H., Webster, M. S., Duval, E. H., Jones, A. G. & Shuster, S. M. The opportunity for sexual selection: not mismeasured, just misunderstood. *J. Evol. Biol.* **24**, 2064–2071 (2011).

45. Hebets, E. A., Stafstrom, J. A., Rodriguez, R. L. & Wilgers, D. J. Enigmatic ornamentation eases male reliance on courtship performance for mating success. *Anim. Behav.* **81**, 963–972 (2011).

46. Fitzpatrick, J. L. & Lüpold, S. Sexual selection and the evolution of sperm quality. *Mol. Hum. Reprod.* **20**, 1180–1189 (2014).

47. Jones, A. G. On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* **63**, 1673–1684 (2009).

48. Henshaw, J. M., Kahn, A. T. & Fritzsche, K. A rigorous comparison of sexual selection indexes via simulations of diverse mating systems. *Proc. Natl Acad. Sci. USA* **113**, E300–E308 (2016).

49. Evans, J. P. & Garcia-Gonzalez, F. The total opportunity for sexual selection and the integration of pre- and post-mating episodes of sexual selection in a complex world. *J. Evol. Biol.* **29**, 2338–2361 (2016).

50. Downhower, J. F., Blumer, L. S. & Brown, L. Opportunity for selection: an appropriate measure for evaluating variation in the potential for selection? *Evolution* **41**, 1395–1400 (1987).

51. Klug, H. & Stone, L. More than just noise: Chance, mating success, and sexual selection. *Ecol. Evol.* **11**, 6326–6340 (2021).

52. Anthes, N., Häderer, I. K., Michiels, N. K. & Janicke, T. Measuring and interpreting sexual selection metrics: evaluation and guidelines. *Methods Ecol. Evol.* **8**, 918–931 (2016).

53. Klug, H., Lindström, K. & Kokko, H. Who to include in measures of sexual selection is no trivial matter. *Ecol. Lett.* **13**, 1094–1102 (2010).

54. Collet, J. M., Dean, R. F., Worley, K., Richardson, D. S. & Pizzari, T. The measure and significance of Bateman's principles. *Proc. R. Soc. B* **281**, 20132973 (2014).

55. Collet, J., Richardson, D. S., Worley, K. & Pizzari, T. Sexual selection and the differential effect of polyandry. *Proc. Natl Acad. Sci. USA* **109**, 8641–8645 (2012).

56. McDonald, G. C., Spurgin, L. G., Fairfield, E. A., Richardson, D. S. & Pizzari, T. Pre- and postcopulatory sexual selection favor aggressive, young males in polyandrous groups of red junglefowl. *Evolution* **71**, 1653–1669 (2017).

57. Morimoto, J. et al. Sex peptide receptor-regulated polyandry modulates the balance of pre- and post-copulatory sexual selection in *Drosophila*. *Nat. Commun.* **10**, 283 (2019).

58. Shuster, S. M., Willen, R. M., Keane, B. & Solomon, N. G. Alternative mating tactics in socially monogamous prairie voles, *Microtus ochrogaster*. *Front. Ecol. Evol.* **7**, 7 (2019).

59. Dowling, J. & Webster, M. S. Working with what you've got: unattractive males show greater mate-guarding effort in a duetting songbird. *Biol. Lett.* **13**, 20160682 (2017).

60. Pizzari, T. & McDonald, G. C. Sexual selection in socially structured, polyandrous populations: Some insights from the fowl. *Adv. Study Behav.* **51**, 77–141 (2019).

61. Archer, M. S. & Elgar, M. A. Female preference for multiple partners: sperm competition in the hide beetle, *Dermestes maculatus* (DeGeer). *Anim. Behav.* **58**, 669–675 (1999).

62. Qvarnström, A. & Forsgren, E. Should females prefer dominant males? *Trends Ecol. Evol.* **13**, 498–501 (1998).

63. Webster, M. S., Tarvin, K. A., Tuttle, E. M. & Pruett-Jones, S. Promiscuity drives sexual selection in a socially monogamous bird. *Evolution* **61**, 2205–2211 (2007).

64. Brunton, D. H. Energy expenditure in reproductive effort of male and female Killdeer (*Charadrius vociferus*). *Auk* **105**, 553–564 (1988).

65. Johnson, L. S., Hicks, B. G. & Masters, B. S. Increased cuckoldry as a cost of breeding late for male house wrens (*Troglodytes aedon*). *Behav. Ecol.* **13**, 670–675 (2002).

66. Boinski, S. Mating patterns in squirrel monkeys (*Saimiri oerstedi*): implications for seasonal sexual dimorphism. *Behav. Ecol. Sociobiol.* **21**, 13–21 (1987).

67. McDonald, G. C., Spurgin, L. G., Fairfield, E. A., Richardson, D. S. & Pizzari, T. Differential female sociality is linked with the fine-scale structure of sexual interactions in replicate groups of red junglefowl, *Gallus gallus*. *Proc. R. Soc. B* **286**, 20191734 (2019).

68. Carleial, R. et al. Temporal dynamics of competitive fertilization in social groups of red junglefowl (*Gallus gallus*) shed new light on avian sperm competition. *Philos. Trans. R. Soc. B* **375**, 20200081 (2020).

69. Lessells, C. M. & Birkhead, T. R. Mechanisms of sperm competition in birds: mathematical models. *Behav. Ecol. Sociobiol.* **27**, 325–337 (1990).

70. Taborsky, T., Oliveira, R. F. & Brockmann, H. J. The Evolution of Alternative Reproductive Tactics: Concepts and Questions. in *Alternative Reproductive Tactics: An Integrative Approach* (Cambridge University Press, 2008).

71. Ghislandi, P. G. et al. Resource availability, mating opportunity and sexual selection intensity influence the expression of male alternative reproductive tactics. *J. Evol. Biol.* **31**, 1035–1046 (2018).

72. Lehtonen, T. K., Wong, B. B. M. & Lindström, K. Fluctuating mate preferences in a marine fish. *Biol. Lett.* **6**, 21–23 (2010).

73. Chaine, A. S. & Lyon, B. E. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science* **319**, 459–462 (2008).

74. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, 2019).

75. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw*. **67**, 1–48 (2015).

76. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw*. **82**, 1–26 (2017).

77. Oklander, L. I., Kowalewski, M. & Corach, D. Male reproductive strategies in black and gold howler monkeys (*Alouatta caraya*). *Am. J. Primatol*. **76**, 43–55 (2014).

78. Pröhl, H. & Hödl, W. Parental investment, potential reproductive rates, and mating system in the strawberry dart-poison frog, *Dendrobates pumilio*. *Behav. Ecol. Sociobiol*. **46**, 215–220 (1999).

79. Turnell, B. R. & Shaw, K. L. High opportunity for postcopulatory sexual selection under field conditions. *Evolution* **69**, 2094–2104 (2015).

80. Gill, L. F., van Schaik, J., von Bayern, A. M. P. & Gahr, M. L. Genetic monogamy despite frequent extrapair copulations in "strictly monogamous" wild jackdaws. *Behav. Ecol*. **31**, 247–260 (2020).

81. Carleial, R., McDonald, G. C. & Pizzari, T. Dynamic phenotypic correlates of social status and mating effort in male and female red junglefowl, *Gallus gallus*. *J. Evol. Biol*. **33**, 22–40 (2020).

82. McDonald, G. C. & Pizzari, T. Structure of sexual networks determines the operation of sexual selection. *Proc. Natl Acad. Sci. USA* **115**, E53–E61 (2018).

83. Janicke, T., Häderer, I. K., Lajeunesse, M. J. & Anthes, N. Darwinian sex roles confirmed across the animal kingdom. *Sci. Adv*. **2**, e1500983 (2016).

84. Webster, M. S., Pruett-Jones, S., Westneat, D. F. & Arnold, S. J. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution* **49**, 1147–1157 (1995).

85. Etches, R. J. *Reproduction in Poultry*. (CABI, 1996).

86. Schielzeth, H. Simple means to improve the interpretability of regression coefficients: *Interpretation of regression coefficients*. *Methods Ecol. Evol*. **1**, 103–113 (2010).

87. Løvlie, H., Cornwallis, C. K. & Pizzari, T. Male mounting alone reduces female promiscuity in the fowl. *Curr. Biol*. **15**, 1222–1227 (2005).

88. Berglund, A. Many mates make male pipefish choosy. *Behaviour* **132**, 213–218 (1995).

89. Carleial, R., Pizzari, T., Richardson, D. S. & McDonald, G. C. Data for: Disentangling the causes of temporal variation in the opportunity for sexual selection. figshare Dataset (2023) https://doi.org/10.6084/m9.figshare.21902133.v1.

90. McLain, D. K., Burnette, L. B. & Deeds, D. A. Within season variation in the intensity of sexual selection on body size in the bug *Margus obscurator* (Hemiptera Coreidae). *Ethol. Ecol. Evol*. **5**, 75–86 (1993).

91. Schlicht, E. & Kempenaers, B. Effects of social and extra-pair mating on sexual selection in Blue tits (*Cyanistes caeruleus*). *Evolution* **67**, 1420–1434 (2013).

Author contributions

R.C., G.C.M., and T.P. conceived the study. G.C.M. conducted the fieldwork and led the literature search. R.C. analysed the data, developed the simulations, and produced the figures. D.S.R. performed the molecular work and analyses for parentage assignment. R.C., T.P., and G.C.M. wrote the manuscript, with input from D.S.R. All authors gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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