Male scent-marks predict fitness via socio-spatial dominance, but not female choice, in a lacertid lizard

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Abstract (195 words, max. 200)

Chemical communication via scent-marks is widely recognised as a key mediator of sexual selection in lizards, yet their role remains contentious because we mostly ignore how scent-mark composition ultimately impacts male fitness in nature. Male scent-marks are often proposed to function as condition-dependent honest sexual signals mediating female choice, but an arising alternative hypothesis is that they primarily function in male–male competition. We provide a comprehensive test of these competing hypotheses. We studied common wall lizards (*Podarcis muralis*) in outdoor enclosures and combined chemical analyses of scent-marks with detailed behavioural and spatial data, genetic parentage assignment, and path analysis to quantify how scent composition relates to mating behaviour, contest outcomes, sperm competition, and male reproductive success. We found no evidence that females assess mates based on candidate compounds proposed as signals of male quality, or that these predict hatchling mass (i.e. no evidence of potential indirect benefits of female choice). Instead, female settlement and fertilisation patterns were driven by resource distribution and spatial proximity. Furthermore, several compounds correlated with dominance and male–male competition emerged as the primary driver of reproductive success, strongly suggesting that scent-marks mediate territorial dynamics, rather than female choice.

Keywords: Sexual selection, animal communication, pheromones, chemical signals, reptiles

1. Introduction

Sexual selection is a major evolutionary force shaping phenotypic diversity, and chemical communication is one of the main avenues through which it operates [1,2]. Lizards exhibit sophisticated chemosensory abilities and a striking diversity in sexually selected traits, emerging in the last few decades as ideal vertebrate models to study the interplay between chemical communication and sexual selection [3–5]. Males of many species deposit scent-marks onto substrates, consisting of serous secretions produced by epidermal glands located in the precloacal or femoral region [6]. While scent-mark composition varies between individuals and species, lipids are present in the scent-marks of all lizard families studied [7–9]. Some of these lipids have been proposed to act as honest signals of male quality mediating sexual selection through both male-male competition and female mate choice [3,6,10]. However, there is a contentious debate about the relative role of scent-marks in mediating these two processes in lizards.

The prevailing hypothesis posits that females assess male scent-mark composition to obtain information about individual quality and choose mates that provide higher fitness benefits [11–14]. Several compounds have been identified as potential honest signals, including α-tocopherol (vitamin E), oleic acid, and two vitamin D precursors (i.e. ergosterol, or provitamin D_2; and cholesta-5,7-dien-3-ol, or provitamin D_3). Because these compounds play essential roles in physiology and development, allocating them to scent-marks may entail trade-offs [10], which could ensure honesty via condition-dependent signalling [15]. For example, some studies have reported female preferences to male scent-marks with high levels of vitamin E [16,17], and carboxylic acids (hexadecenoic and octadecanoic acid) and steroids (campesterol, sitosterol, and ergosta-5,8-dien-3-ol) have been linked to stress physiology [18]. Altogether, the interplay between physiological trade-offs and female responses has provided a rationale to consider scent-marks as key elements in female mate assessment (reviewed in [5,10]). However, most of the evidence supporting female attraction to compounds in male scent-marks is indirect, largely based on laboratory assays, and remains largely untested under natural, ecologically realistic conditions.

An alternative hypothesis challenges this interpretation [3,19–21]. First, most lacertid lizards show a resource-based territorial system, which provides little opportunity for female choice. Females typically occupy smaller home ranges than males [22,23], making mate search costly in time, energy, and predation risk [22,24]. Moreover, increased exposure to males results in male harassment, with significant costs to females [25,26]. Thus, high mating rates

and multiple paternity [27] seem largely driven by male mating pressure rather than female mate-sampling [28]. Second, females settling in conspecific high-quality territories should, even in the absence of information about male quality, indirectly mate with males of high resource-holding potential [29,30]. Consistent with this view, while ample evidence shows that lacertid lizards use scent-marks for species [19,31,32], and sex recognition (i.e. mate recognition; [33], whether females employ scent-marks for mate assessment remains contested [3,21]. Moreover, mate assessment can evolve only if it yields net direct or indirect fitness benefits to females [34]. In species lacking parental care, such as lacertid lizards, these benefits are expected to be predominantly indirect (i.e. good genes), yet experimental evidence to this respect is completely lacking.

Under this alternative hypothesis, scent-marks are thought to have evolved mainly in the context of male-male competition [3,35]. Mounting evidence indicates that males are the sex more reliant on chemosensory processing in social and reproductive contexts [20,21]. Male lacertid lizards show larger olfactory bulbs and higher rates of seasonal adult neurogenesis in chemosensory brain regions than females [3,36]. Behavioral studies show that males assess scent-marks based on both pheromones and individually variable signature mixtures [37,38], enabling them to evaluate the competitive ability of unfamiliar rivals [39,40] and to recognize familiar individuals based solely on scent-marks [20]. Variation in scent-mark composition arising from ontogeny, parasites, diet, or basking may provide information relevant to male–male assessment [35,41]. However, direct evidence that scent-marks impact male fitness during male-male competition is also lacking.

To address these gaps in knowledge, we examined how variation in male scent-mark composition relates to socio-sexual behaviour and reproductive success in the European common wall lizard (*Podarcis muralis*), a widely used species in studies of lizard chemical communication [3,42]. We focused on the main candidate compounds previously suggested to contribute as signals of individual quality in the context of female choice: cholesterol, α-tocopherol, ergosterol (provitamin D_2), oleic acid, hexadecanoic acid, octadecanoic acid, campesterol, cholesta-5,7-dien-3-ol (provitamin D_3), sitosterol, and ergosta-5,8-dien-3-ol [5,10]. We conducted the study in outdoor mesocosms replicating natural vegetation, prey availability, light cycles, and habitat heterogeneity, allowing spontaneous social interactions and precise estimates of male reproductive success.

Materials and methods

1.1. Study species, sampling, and morphological measurements

To assess the link between scent-mark composition and sexual selection, we studied the European common wall lizard (*Podarcis muralis*), which produces scent-marks from femoral pores on the ventral thighs (**Fig. 1A**). We captured 190 lizards (100 females and 90 males) by noosing from 12 localities spread across the Cerdanya Valley (Eastern Pyrenees). In each of these localities, we captured 2–8 lizards (SVL ≥ 56 mm). Males were captured immediately before the onset of the experiment (May 2018). Females were captured at the end of the previous breeding season (September 2017) to avoid gravidity and housed under semi-natural outdoor conditions until the experiment [23].

Two days before the onset of the experiment, we measured the SVL (± 0.1 mm) and mass (± 0.01 g) of each lizard with a ruler and a spring balance (Pesola), as well as inter limb length (ILL) in females and head length (HL) in males using a digital caliper (± 0.01 mm; Mitutoyo, Telford, UK). We estimated body condition (BCI) for each sex as residuals from a log–log regression of body mass on SVL. The relationship was linear and residuals were homoscedastic [43,44]. Likewise, in males we estimated an index of relative head size (HL res) by obtaining the residual from a least squares linear regression of log(HL) against log(SVL). We also removed ~5 mm from the tail tip of each individual and preserved the tissue in 90% ethanol for genetic analyses.

1.2. Scent-mark composition analyses

Male femoral gland secretions (i.e. considered the main contributors to scent-marks; [21,45]) were collected from the left hindlimb of each male and analysed using gas chromatography–mass spectrometry (GC–MS). We first obtained a semi-quantitative overview of scent-mark composition using scan-mode analyses. For a general characterisation and semiquantitative analysis of its composition, each sample was treated with 100 µl of hexane containing 1 µg ml^{-1} of n-docosane D46 as an internal standard (IS). This internal standard allowed compound responses to be compared independently of each other [46], which is crucial when examining inter-individual variation in compound abundance. Compound identification followed standard procedures widely used in chemical studies of lacertid lizards [4,17], using: (1) retention time comparisons with available authentic standards analysed under similar conditions, and (2) mass spectral matches against the NIST 2017 library using the Mass Spectral Search Program. While this methodology provides a tentative broad overview of scent-mark composition, it is not optimal for the fine-scale identification and quantification

of target compounds (see **Appendix S1**, **Table S1**, and **Fig S1** for comparison between scan and targeted analyses). Therefore, we implemented a second analysis focused on specific compounds of interest: cholesterol, α-tocopherol (vitamin E), ergosterol (provitamin D2), oleic acid, hexadecanoic acid, octadecanoic acid, campesterol, cholesta-5,7-dien-3-ol, sitosterol, and ergosta-5,8-dien-3-ol. These compounds were selected on the basis of their alleged role in sexual selection according to the literature [5,10]. Relative abundances were extracted from diagnostic ions and retention times. The analysis obtained information on the femoral secretions of 78 of the 90 sampled males. To be conservative, 22 samples were excluded because their chromatograms did not provide reliable signals (e.g. elevated baseline bleeding in the GC–MS trace and near-zero intensities for most compounds), despite two repeated injections. This limitation likely reflects an insufficient amount of secretion collected. However, given that the time required for full replenishment of chemical secretions is unknown, we opted not to extract from both hindlegs to avoid depleting males of their entire scent-mark reservoir. Detailed analytical procedures, compound identification criteria, and comparisons between scan and targeted analyses are described in **Appendix S1**.

1.3. Preprocessing of scent-mark composition data

Compound abundances were positively skewed and often contained extreme values (**Fig. S2**). To reduce the influence of outliers, values were Winsorized at the 95th percentile, zeros were handled using adaptive pseudo-count addition (10% of the smallest non-zero value across individuals), and data were log-transformed. All variables were then z-standardised to ensure comparability across compounds. Because compound abundances showed substantial covariation (**Fig. S3**), we reduced multicollinearity by retaining only variables with pairwise correlations $\leq |0.6|$ [47], resulting in a subset of seven representative compounds: cholesta-5,7-dien-3-ol, ergosterol, octadecanoic acid, campesterol, oleic acid, α-tocopherol, and sitosterol (**Appendix S1, Fig. S3, Table S2**).

1.4. Mesocosm experiment

We studied social behaviour in *Podarcis muralis* using ten semi-natural outdoor enclosures (47 m^2 each) located at the Metatron facility, an annex to the CNRS Station d'Écologie Théorique et Expérimentale (SETE) in Moulis (Caumont, France). Within each of these enclosures, we created two types of sites that varied in structural complexity [48,49]. Each site consisted of a wooden pallet (~1.2 m^2) with differing number of bricks, cinderblocks, rocks, and logs piled above, which acted both as shelter and perching/basking sites. We arranged three high-

and three low-quality sites in two rows along the N-S axis, separated by a line of six rocks, which we also considered low-quality sites (**Fig. 1B**).

On May 23rd 2018, nine males were released into each enclosure and monitored for seven days before nine females were added. To allow for individual identification lizards were both permanently marked in their ventral scales using a disposable cautery unit [50], and painted in their dorsum with a white Edding©751 marker [51]. To minimise prior experience effects, individuals were size-matched within sex (≤2 mm SVL difference) and originated from locations ≥300 m apart. Males were removed after one month and released at their capture sites, while females were housed individually until oviposition [52]. We lost 22 clutches due to failure to lay or unrecovered eggs within enclosures. For the remaining 68 females, we counted the number of fertile (N = 385) and infertile eggs (N = 155) within each clutch. The resulting 230 fertile eggs were incubated, and upon hatching (**Fig. 1D**), each of the 208 born juveniles was measured (SVL; ± 0.1 mm), weighed (± 0.001 g), sampled for DNA, permanently marked, and released at the outdoor tanks in SETE Moulis [23,49].

1.5. Behavioural observations

Spatial and social behaviour was recorded daily between 09:00 and 19:30 from May 23 to June 22. Positional data were collected using scan sampling at 2.5 h intervals, while social interactions were recorded using behaviour sampling during standardized observation sessions (**Table S3**). Consecutive encounters between the same individuals were treated as independent events whenever the participants remained further than 30 cm apart for longer than 2 min. Full observational procedures are detailed in **Appendix S1**.

1.6. Behavioural analyses

1.6.1. Spatial behaviour

Habitat use was quantified using fixed-kernel density estimates [53]. Each lizard was assigned residency at a specific site based on the location of peak density within the 50% kernel estimate (see **Appendix S1** for more details). Across the experiment, we recorded 7,189 re-sightings from 614 scans. Females had a significantly higher probability of being found in high-quality sites (probability = 0.75 [CI95: 0.64–0.83]) than males (0.22 [CI95: 0.14–0.32]), with an odds ratio of 10.7 (Tukey-adjusted $P < 0.001$) (**Table S4**; [23,49]).

1.6.2. Social behaviour

We categorized interactions as intrasexual (competitive and non-competitive) or intersexual (reproductive and non-reproductive). Intrasexual interactions were considered competitive when one lizard (the loser) employed fast-paced locomotion to flee from another lizard (the winner) showing raised-body display behaviour and/or physical aggression (i.e. bite, or chase). (**Table S3**). Male–male contests were analysed using Bradley–Terry models fitted to the observed matrix of male-male contest outcomes within each enclosure [54]. Baseline models without predictors were used to derive dominance ranks (range: 1–9), and extended models incorporating individual and contest-level predictors were used to examine determinants of contest outcomes (see below).

1.7. Parentage analysis

Parentage was assigned using multilocus microsatellite genotypes and likelihood-based methods [23]. We could reliably assign paternity to every offspring examined (strict: 208 juveniles, relaxed: 230 juveniles). Detailed methods for parentage analysis are provided in **Appendix S1**. We quantified individual fitness as: mating success (i.e. the overall number of different mates with whom a lizard conceived offspring) and reproductive success (i.e. the total number of viable hatchlings sired). Since selection depends on relative rather than absolute fitness, we then divided the fitness measures of each lizard by the mean for all same-sex conspecific within its enclosure. In addition, to evaluate male differences in sperm competition intensity, for each male we determined the average number of competitors with which he shared paternity by dividing the number of co-sires by the number of mates (SCI = sperm competition intensity).

1.8. Statistical analyses

1.8.1. Structural equation modelling

To test relationships among chemical compounds, socio-spatial behaviour, and fitness-related variables, we applied piecewise structural equation modelling (pSEM) implemented in the R package *piecewiseSEM* [55], combining generalized linear mixed models (GLMMs) fitted with *glmmTMB* [56] and *lme4* [57]. Piecewise SEM allows modelling systems in which variables act as both predictors and responses while accommodating mixed-effects structures and non-Gaussian error distributions [58,59].

We first examined associations among key socio-spatial and fitness variables using Spearman rank correlations to guide construction of an initial biologically informed pSEM (**Fig. S4**). The initial pSEM (**Fig. S5**) included direct effects of dominance, HQ residency,

co-perchings per female, and mating success on reproductive success, as well as effects of dominance, HQ residency, and co-perchings on mating success and sperm competition intensity. Mass and HL residuals were selected because males were size-matched within enclosures and body condition index was highly correlated with mass (**Fig. S3**). Model fit was assessed using Shipley's test of directed separation [58,60]. Based on d-separation tests, a direct effect of ergosterol on mating success was added. Because males without offspring lacked estimates of sperm competition intensity, we repeated the analysis excluding these individuals (N = 25) to confirm robustness of inferred pathways. Further details in **Appendix S1**.

1.8.2. Models on male-male competition

Building on the pSEM results, we focused the role of chemical compounds in mediating dominance and high-quality site residency. We first tested whether scent-mark composition differed among males occupying high-quality, low-quality, and rock sites using robust multivariate analysis of variance (MANOVA) [61], followed by compound-specific robust ANOVAs when covariance assumptions were violated. Although rock sites are classified as low quality, we treated them separately as a conservative approach; pooling them with low-quality sites yielded identical results.

To investigate the relative importance of scent-mark composition and contest-related traits in predicting contest outcomes, we fitted Bradley–Terry models (R package BradleyTerry2; [54]. Male predictors included body mass, HL residuals, and the relative abundance of seven compounds. Contest-level predictors included display behaviours (raised-body, Type II foot shakes; **Table S3**), prior outcome, and residency (whether the contest occurred within the male's site). Models were simplified using backward deletion and likelihood ratio tests ($\alpha = 0.05$) [62]. To explore temporal dynamics, we fitted three models: a global model (N = 544), and early-phase model (days 1-9; N = 137), and a late-phase model (day 10 onward; N = 407). Further details in **Appendix S1**.

1.8.3. Models on fertilisation success

To test whether females bias fertilisation towards high-quality males, we modelled per-egg fertilisation success using mixed-effects beta-binomial models. For each reproducing female, the response was the number of eggs fertilised by a male relative to other potential sires. Predictors included male dominance, chemical relative abundances, and spatial proximity, measured either as same-site residency (binary) or parental site-quality combination (four

female-male levels: high–high, low–low, high–low, low–high). We fitted two models differing only in the proximity metric. Mother and male identities were included as random effects to account for repeated measures. For males lacking chemical data, compound values were set to the population mean (z-score = 0) to retain the full choice set; complete-case models confirmed robustness.

1.8.4. Models on hatching mass at birth

To test whether male scent-mark composition confers indirect fitness benefits, we modelled hatchling mass at birth using a linear mixed-effects model, with clutch size and the relative abundances of seven compounds as fixed effects. Clutch size accounted for the trade-off between offspring number and size [63]. Maternal and paternal identities were initially included as random effects, but maternal identity was removed following AICc comparison.

1.8.5. Model fitting and selection

All models were fitted in R using mixed-effects frameworks [56,57], with predictors centred and scaled and experimental cell included as a random effect [64]. Model assumptions and fit were evaluated using simulated residuals [65], and model selection was based on AICc [66]. Piecewise structural equation models were simplified by backwards selection from a saturated model [67], and uncertainty in standardized effects was quantified using bootstrapped confidence intervals [68]. Exhaustive model selection and model averaging were used to refine inference on individual pathways [69], with significance assessed using confidence intervals and relative variable importance [62]. All analyses were conducted in R v.4.2.2. [70]. Full details of model fitting, diagnostics, selection criteria, and robustness checks are provided in **Appendix S1**.

2. Results

2.1. Scent-marks and male fitness

The structure, strength, and direction of the pathways in the pSEM supported an indirect effect of scent-mark composition on male relative reproductive success (**Fig. 2**). Importantly, the non-significant Fisher's C statistic (Fisher's C = 27.12, df = 44, p = 0.979) indicates that the model adequately fits the data and that no major causal pathways appear to have been omitted (**Table S5-S6**).

Three of the seven examined compounds (i.e. ergosterol, campesterol, and oleic acid) were retained in the final model (**Table 1**), suggesting that they may influence key mediating traits—such as dominance and a high-quality territory—that ultimately affect male fitness. Reproductive success was found to result from the combined effect of mating success (bootstrapped standardised β [CI_{95}] = 0.07 [0.04, 0.13]), sperm competition intensity (β [CI_{95}] = -0.05 [-0.13, -0.00]), and a high-quality site (β [CI_{95}] = 0.04 [0.00, 0.09]), confirming that exclusive access to multiple females is the key determinant of male fitness. Ergosterol emerged as a particularly interesting compound, as it showed a negative effect on both dominance (β [CI_{95}] = -0.32 [-0.43, -0.17]) and mating success (β [CI_{95}] = -0.05 [-0.07, -0.03])). Dominance had a strong effect increasing the odds that a male occupied a high-quality site (β [CI_{95}] = 0.09 [0.06, 0.14]), but these odds were also positively affected by campesterol levels (β [CI_{95}] = 0.07 [0.04, 0.15]). High-quality site residency had both a direct impact on reproductive success, but also an indirect one through its negative effect on sperm competition intensity (β [CI_{95}] = -0.08 [-0.21, -0.03]). Due to the high density of females in high-quality sites (see below), resident males were found to guard a higher number of different females (**Fig. S4**), while also engaging in a higher number of co-perching interactions per female (β [CI_{95}] = 0.03 [0.02, 0.05]). Co-perching interactions increased also with dominance (β [CI_{95}] = 0.04 [0.02, 0.06]) and levels of oleic acid (β [CI_{95}] = 0.03 [0.02, 0.04]).

We found no evidence that dominance or residency at a high-quality site predicted overall mating success, indicating that while some males may achieve copulations through territory ownership and mate guarding, others likely rely on alternative strategies such as opportunistic mating as sneakers. The direct effect of high-quality sites on male reproductive success, independent of mating success and sperm competition intensity, suggests that males in high-quality sites gained greater fitness from each mating (**Table 1; Fig. 2**). Consistent with this, males in high-quality sites tended to mate with females that were, on average, slightly larger (LLM on average mate SVL: mean ± SEM = high-quality: 66.9 ± 1.0; low-quality: 65.6 ± 0.6; t = 1.1, P = 0.285) and more fecund (LLM on average number of fertile eggs laid by sired females: high-quality: 6.1 ± 0.4; low-quality: 5.5 ± 0.2; t = 1.3, P = 0.211) than those of males in low-quality sites.

The best-fitting pSEM excluding males without offspring exhibited a similar pathway structure to the model described above, with chemical compounds exerting indirect effects on key mediators of reproductive success (Fisher's C = 34.52, df = 50, P = 0.953; **Fig. 2**). A

notable distinction from the previous model was the lack of support for a direct effect of ergosterol on mating success in the best supported pSEM model. In addition, we found evidence of a positive effect of mass on dominance (β [CI_{95}] = 0.03 [0.00, 0.05]), and a strong positive effect of high-quality sites on coperchings (β [CI_{95}] = 0.07 [0.05, 0.09]) (**Table S7-S9**).

2.2. Scent-marks and male-male contests

The Bradley–Terry model successfully predicted the contest outcome in 84% of 544 cases. Behaviours, residence, and previous wins were more strongly associated with contest outcome than scent-mark composition (**Table S10**). Raised-body displays markedly increased the odds of winning by a factor of 18, while type II foot shakes were linked to a three-fold increase in the odds of losing. Resident males (i.e. males settled at the site where the contest took place) were three times more likely to prevail, and individuals that had won their previous contest were twice as likely to win the next one. Among targeted compounds, a one standard deviation advantage in either cholesta-5,7-dien-3β-ol or α-tocopherol was associated with nearly a twofold increase in the odds of winning. In contrast, higher levels of ergosterol were linked to a halving of those odds. A positive effect of cholesta-5,7-dien-3β-ol and α-tocopherol was also supported by results from the dominance component model of the pSEM (**Table S6**). The early-contest model (interactions from days 1–9; N = 137) predicted outcomes with 72% accuracy, while the late-contest model (day 10 onwards; N = 407) achieved 85% accuracy. Coefficients for compounds and raised-body displays were higher in early contests, whereas the effects of type II foot shakes, residency status, and prior contest history became more pronounced in later stages of the experiment (**Table S9**; **Figure 3**).

2.3. Scent-marks and residency in high-quality sites

The robust MANOVA detected no evidence of a multivariate difference in the scent-mark composition of males settled in high-quality vs. low-quality quality sites, or the rocks in between (WTS = 28.00, df = 20, P = 0.109), and this result was supported by parametric bootstrap resampling (P = 0.482 for WTS; P = 0.569 for MATS). Accordingly, none of the examined chemical compounds showed significant differences among site quality categories in the robust one-way ANOVAs (**Table S11**). Pooling rock and low-quality sites yielded qualitatively identical results. Although the asymptotic WTS was significant (WTS = 21.35, df = 10, P = 0.019), this effect was not supported by parametric bootstrap resampling (P = 0.130 for WTS; P = 0.311 for MATS).

2.4. *Scent-marks and fertilisation success*

Across analyses, fertilisation success was primarily driven by male–female spatial proximity, whether modelled as exact co-residency or as the parental site-quality combination (**Fig. 4a**). In contrast, scent-mark composition and dominance rank contributed little explanatory power. Ergosterol was the only compound associated with fertilisation success, showing a negative effect, whereas all other compounds and dominance rank had weak support (RIV < 0.50) (**Table 2**; **Fig. 4b**).

Tukey-adjusted pairwise contrasts revealed that mixed-quality pairs (f-m: high-quality-low-quality or low-quality-high-quality) had markedly lower fertilisation success compared to high-quality–high-quality (odds ratios 0.38 and 0.18, respectively; both $p <$ 0.04). In contrast, low-quality–low-quality pairs achieved fertilisation probabilities statistically indistinguishable from high-quality–high-quality (OR = 0.90, p = 0.99), and substantially higher than mixed-quality combinations (e.g. low-quality–low-quality vs high-quality–low-quality: OR = 2.36, p = 0.0048). Predicted fertilisation probabilities reflected the same pattern: high-quality–high-quality (0.18) and low-quality–low-quality (0.15) pairs showed similarly high success, while high-quality–low-quality (0.07) and low-quality–high-quality (0.04) were consistently lower (**Fig. 4c**). The complete-case analyses (excluding males lacking chemical data) produced nearly identical qualitative results (**Table S12**): same-site residency (Std. β = 1.59) and ergosterol (Std. β = –0.66) remained the only strong predictors, and the site-quality combinations showed the same hierarchy (high-quality–high-quality ≈ low-quality–low-quality > mixed-quality).

2.5. *Scent-marks and hatchling mass at birth*

We found little association between father scent-mark composition and hatchling mass at birth. Across candidate models, only clutch size showed moderate support (RIV = 0.68), with a weak negative association with hatchling mass (β [CI_{95}] = -0.004 [-0.009, 0.001]). None of the seven focal compounds showed meaningful associations with hatchling mass (**Table S13**).

3. Discussion

This study provides a comprehensive empirical test of the links between male scent-mark composition and sexual selection in a lacertid lizard, integrating reproductive success and

socio-spatial behaviour in semi-natural conditions. We show that scent-mark composition predicts male reproductive success indirectly through associations with socio-spatial dominance. By contrast, we found no evidence that females use male scent-mark composition for mate assessment. Reproductive success was unrelated to chemical compounds previously suggested to mediate female choice, aside from a negative association with ergosterol, and we detected no signature of cryptic female choice. Fertilisation patterns were instead overwhelmingly shaped by spatial proximity, whereby females preferentially established themselves in high quality territories and dominant resident males predominantly reproduced with them. Additionally, none of the examined compounds predicted hatchling mass at birth, providing no evidence for indirect fitness benefits. Overall, our findings indicate that scent-marks function primarily in male-male competition and territorial dynamics rather than female choice.

3.1. The role of scent-marks in male intrasexual competition

Residency in high-quality sites was the strongest predictor of male reproductive success (**Figure 2**), and dominance determined which males acquired and retained these territories. High-quality territories offer improved basking conditions, refuge structure, and proximity to females, resulting in reduced sperm competition and higher reproductive returns. Males in high-quality sites also mated with larger, more fecund females, resulting in higher reproductive returns per mating. These findings support the idea that competition for spatial resources, rather than chemically mediated female choice, defines the landscape of sexual selection for male *P. muralis* [3,71].

Consistent with prior work, our experiment supports a central role of chemical communication in male territorial behaviour [6,72]. We detected several links between scent-mark composition and socio-spatial dominance. Campesterol levels (tightly correlated with ergosta-5,8-dien-3-ol) were positively associated with residency in high-quality sites, and ergosterol showed a consistent negative association with dominance. After controlling for key determinants of contest outcome such as behavioural displays, prior contest history, and residency status [49], our analyses revealed that males with high levels of cholesta-5,7-dien-3-ol and α-tocopherol, and low levels of ergosterol, were more likely to prevail in agonistic confrontations (**Figure 3**). These associations were generally stronger in early contests than in later ones, whereas behavioural displays, residency, and accumulated winning record grew in importance as territorial relationships crystallised. This dynamic is consistent with the idea that relatively static, condition-dependent compounds may function as quality signals early

428 in territory establishment, whereas dynamic signals and limited-war mechanisms—conveying
429 information on motivation, identity, and experience—become increasingly influential once
430 dominance relationships and territories are established [73].

431 *3.2. The role of scent-marks in female choice*

432 Across multiple modelling approaches, we found no evidence that females favoured males
433 with higher levels of α-tocopherol, oleic acid, cholesta-5,7-dien-3-ol, or other compounds
434 previously proposed as honest signals of male quality [10]. Moreover, most females settled
435 in high-quality sites even though scent-mark composition did not differ between males
436 occupying high-quality and low-quality sites. These results suggest that females prioritise
437 high-quality habitat patches over male traits when choosing where to settle. Because females
438 arrived in enclosures where males were already established, their settlement patterns provide
439 a stringent test: if females were attracted to males' chemical compounds, they should have
440 preferentially settled near males with preferred scent-mark composition or biased fertilisation
441 toward such males. Instead, females aggregated in high-quality sites, and their eggs were
442 primarily fertilised by males that co-settled with them—typically a minority of dominant
443 males occupying these sites. Crucially, females settled in low-quality sites did not bias
444 fertilisations towards males in high-quality sites or those with higher levels of examined
445 compounds, reinforcing that spatial proximity, rather than chemical assessment, determines
446 fertilisation outcomes (**Fig. 4**). Our results provide an additional line of evidence against a
447 major role for female choice. Hatchling mass is positively associated with viability (i.e.
448 foraging and antipredator performance) and annual survival in lizards, and thus represents a
449 reliable proxy of offspring quality [52,74]. The absence of any relationship between paternal
450 scent-mark composition and offspring mass therefore offers no support for the hypothesis
451 that females obtain indirect fitness benefits by chemically selecting mates. Together, these
452 findings weaken the case for strong scent-based female choice in wall lizards and support
453 growing evidence for a limited scope of active female choice under resource-based
454 territoriality, where ecological costs of mate sampling may be high and indirect benefits
455 limited [3,20,42].

456 Among the examined compounds, only ergosterol (vitamin D_2) showed a detectable
457 direct association with relative mating success, with higher levels linked to fewer mates (**Fig.**
458 **2a**). However, this effect disappeared once the analysis was restricted to males with
459 confirmed offspring (**Fig. 2b**), suggesting that the initial association originated from
460 differential ergosterol levels between successful and unsuccessful reproducing males, rather

than a quantitative relationship with relative mating success. In both analyses, ergosterol remained negatively related to male dominance, suggesting that any influence of this compound on fitness is indirect and mediated through territorial dynamics. Another intriguing result was the relationship between oleic acid and male–female co-perching interactions, coupled with a negative relationship with fertilisation success. Elevated oleic acid levels have been reported in *P. muralis* males with lower parasite loads, stronger immune responses, or greater basking opportunities [35,41]. In the Algerian sand-racer (*Psammodromus algirus*), however, lower oleic acid levels characterise older males, which typically secure more matings [75]. If a similar pattern occurs in *P. muralis*, males with high oleic acid levels may represent younger, low-threat competitors tolerated by dominant males in high-quality sites [76], explaining their frequent proximity to females but limited reproductive success.

Some authors argue that females might rely on scent-mark composition to indirectly assess territory quality [10,12], but our results offer little support for this hypothesis. Females preferentially settled in high-quality sites despite dominant males there producing lower ergosterol and showing no elevated levels of other examined compounds. A much more parsimonious explanation is that females assess habitat features directly [22], rather than relying on an indirect (and in our study inexistent) relationship with male scent-marks. Similarly, the idea that females use scent-mark composition for mate assessment is based on laboratory trials relying on preference proxies such as tongue-flick rates or time spent near odours. Our results, together with a critical reading of past work, suggest that these behavioural proxies may instead reflect species or sex recognition, rather than mate assessment [3,77]. For example, females of *Iberolacerta cyreni* show elevated tongue-flick responses to ergosterol, but responses barely exceed those elicited by natural male secretions [12], suggesting that ergosterol may act as a species-typical male cue rather than a quality signal. Similarly, female aggregation in ergosterol-enriched areas may reflect detection of male-occupied territories rather than preference for higher ergosterol levels [78]. In fact, lacertid females tend to prefer areas scented by adult males [79], and even areas scented by multiple males [80]. Such patterns are consistent with females being attracted to areas with conspecific scent-marks—often corresponding to high-quality sites—without necessarily discriminating among individual males [3,19,79].

3.3. Conclusions

Research on chemical communication in lizards, and lacertids in particular, has expanded substantially over the past two decades, providing key insights into how scent-marks mediate

behaviour, social interactions, and evolutionary processes [4,81,82]. However, debate on the role of scent marks in mediating male-male competition and female choice has dragged in the literature for decades—mostly due to a lack of studies integrating scent mark composition with behaviour and its ultimate consequences in terms of fitness outcomes in natural settings. Here we show that a subset of scent-mark compounds correlated with male reproductive fitness via their association with socio-spatial dominance, whereas female settlement and fertilisation patterns were driven by resource distribution and spatial proximity to males, pointing to a role of scent marks in territorial dynamics rather than female choice. Further progress will likely require reassessing some long-standing assumptions in the field. For instance, the prevailing focus on lipophilic compounds in femoral gland secretions partly reflects assumptions about the species-specificity and information content of proteins relative to lipids that have since been questioned [7,21]. Experimental approaches will also need to move beyond indirect laboratory preference assays. Such tests may reflect exploratory behaviour rather than attraction, and tongue-flick rates are notoriously difficult to interpret [83,84], as lizards can discriminate between scent-marked areas without showing differential tongue-flick responses [35,39]. In addition, many studies do not clearly distinguish between pheromonal signals and individually variable signature mixtures, despite their different functional roles, which may complicate the interpretation of reported behavioural effects [37]. More generally, the role of scent-mark composition should be evaluated not only in terms of informational content but also signal efficacy—that is, how chemical properties influence the persistence and detectability of scent-marks in natural environments [85,86]. In short, progress in this field will require integrative approaches linking chemical composition with perception, physiology, signal efficacy, and the spatial ecology of scent deposition [87,88].

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Tables

Table 1. Standardized path coefficients (Std. β) and 95% confidence intervals (CI_{95}) for direct and indirect effects estimated using bootstrapping (1,000 replicates). The table reports relationships among scent-mark composition and socio-spatial behaviour acting as mediators of male relative reproductive success as identified in the best-fitting piecewise SEM. Indirect effects are aggregated across all mediating pathways.

Response	Predictor	*Std. β*	Lower CI_{95}	Upper CI_{95}	Effect type
Reproductive success	Mating success	0.066	0.038	0.125	Direct
	Sperm competition intensity	-0.048	-0.130	-0.004	Direct
	High-quality residency	0.038	0.002	0.094	Direct
	Ergosterol	-0.005	-0.009	-0003	Indirect
	Campesterol	0.003	0.001	0.005	Indirect
	Dominance	0.004	0.001	0.007	Indirect
	High-quality residency	0.004	-0.019	0.013	Indirect
Mating success	Ergosterol	-0.051	-0.069	-0.030	Direct
Sperm competition intensity	High-quality residency	-0.079	-0.213	-0.034	Direct
	Ergosterol	0.002	0.001	0.008	Indirect
	Campesterol	-0.006	-0.021	-0.002	Indirect
	Dominance	-0.007	-0.017	-0.003	Indirect
Dominance	Ergosterol	-0.032	-0.043	-0.017	Direct
High-quality residency	Dominance	0.089	0.056	0.143	Direct
	Campesterol	0.074	0.035	0.147	Direct
	Ergosterol	-0.029	-0.038	-0.017	Indirect
Coperchings per female	Dominance	0.037	0.015	0.056	Direct
	High-quality residency	0.031	0.019	0.046	Direct
	Oleic acid	0.029	0.015	0.043	Direct
	Ergosterol	-0.013	-0.023	-0.005	Indirect
	Campesterol	0.002	0.001	0.004	Indirect
	High-quality residency	0.003	0.002	0.004	Indirect

Table 2. Predictors of per-egg fertilisation success. Model-averaged coefficients for the beta-binomial models testing whether realised fertilisation success is explained by male-female spatial proximity, male scent-mark composition, or dominance. Variance inflation factors (VIF) correspond to the saturated model. Standardized coefficients (Std. β; log-odds per 1 SD) are conditionally-averaged across top models (ΔAICc < 4), with CI_{95}, *Z*-values, and *P*-values. Relative importance (RIV) reflects summed Akaike weights across top models. Bold variables (RIV > 0.55; CI95 excluding zero) are considered strong predictors. "Same-site residency" indicates whether male and female shared a pallet or stone; "site-quality combination" is a four-level factor (i.e. high-high, low-low, high-low, low-high). Missing lipid values (8 males) were imputed as 0 (mean z-score) to retain full choice sets; results excluding these males are in **Table S12**.

Model					**Model including same-site residency**			
Response	**Predictors**	**VIF**	**Std. β**	**CI_{95}**	***Z***	***P*-value**	***N***	**RIV**
Fertilisation success (per-egg)	**Same-site residency**	**1.03**	**1.02**	**[0.41, 1.62]**	**3.27**	**0.001**	**37**	**1.00**
	Ergosterol	**1.83**	**−0.55**	**[−0.85, −0.26]**	**3.71**	**<0.001**	**37**	**1.00**
	Oleic acid	1.16	−0.19	[−0.45, 0.06]	1.47	0.142	19	0.49
	α-Tocopherol	1.22	0.10	[−0.16, 0.35]	0.73	0.463	12	0.26
	Sitosterol	1.26	0.12	[−0.16, 0.41]	0.84	0.401	10	0.24
	Cholesta-5,7-dien-3-ol	1.52	0.14	[−0.16, 0.45]	0.91	0.364	10	0.22
	Dominance	1.16	0.03	[−0.06, 0.12]	0.65	0.513	10	0.21
	Octadecanoic acid	1.32	0.08	[−0.17, 0.32]	0.63	0.531	10	0.19
	Campesterol	1.56	0.06	[−0.21, 0.33]	0.43	0.668	10	0.18
Model					**Model including parental site-quality combination**			
Response	**Predictors**	**VIF**	**Std. β**	**CI_{95}**	***Statistic***	***P*-value**	***N***	**RIV**
Fertilisation success (per-egg)	**Site-quality combination**	**1.30**	**-**	**-**	**$\chi^2 = 21.20$**	**<0.001**	**34**	**1.00**
	Ergosterol	**1.90**	**–0.57**	**[–0.87, –0.27]**	**$Z = 3.74$**	**<0.001**	**34**	**1.00**
	Oleic acid	1.19	–0.21	[–0.47, 0.05]	$Z = 1.60$	0.109	22	0.64
	Cholesta-5,7-dien-3-ol	1.58	0.15	[–0.16, 0.46]	$Z = 0.97$	0.333	13	0.31
	α-Tocopherol	1.24	0.11	[–0.16, 0.37]	$Z = 0.79$	0.429	9	0.22
	Sitosterol	1.28	0.09	[–0.20, 0.39]	$Z = 0.63$	0.529	9	0.20
	Dominance	1.32	0.03	[–0.07, 0.13]	$Z = 0.58$	0.565	8	0.18
	Campesterol	1.63	0.05	[–0.23, 0.32]	$Z = 0.34$	0.735	7	0.15
	Octadecanoic acid	1.36	0.02	[–0.23, 0.28]	$Z = 0.17$	0.864	7	0.15

Figures

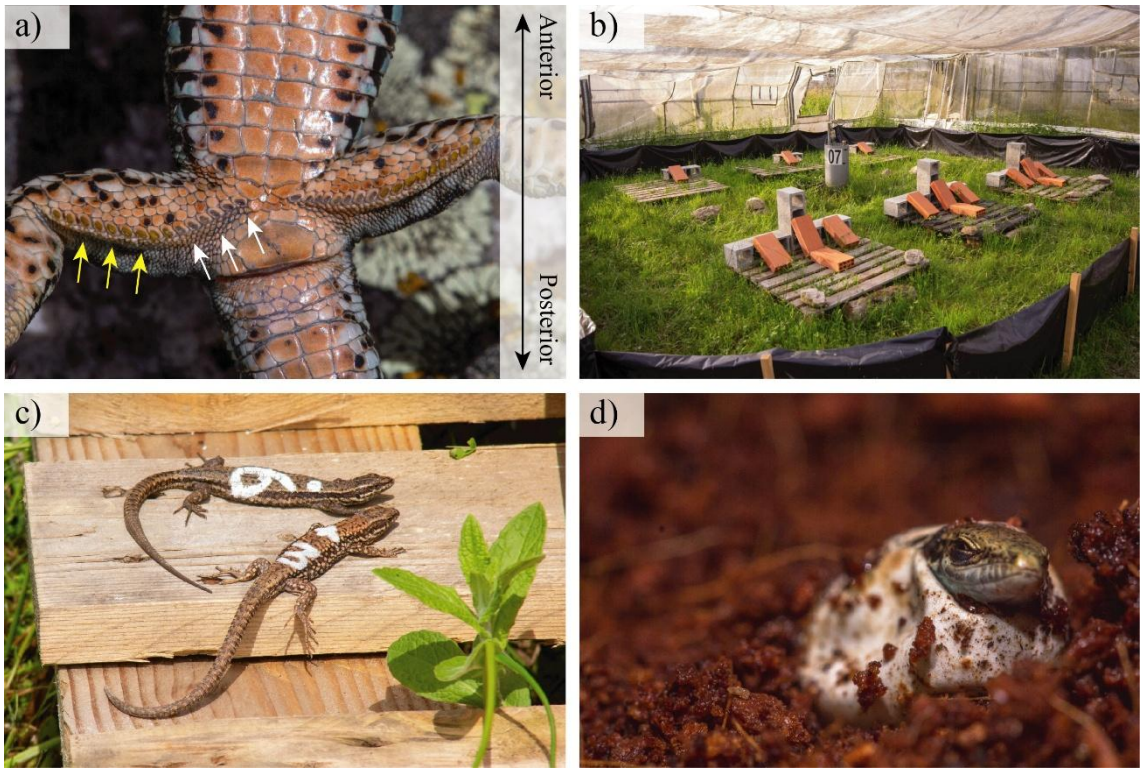

Figure 1. a) Detailed view of the pelvic region of an adult male *Podarcis muralis*, showing the femoral pore rows along the ventral surface of each hindlimb. A waxy secretion can be observed in the femoral pores indicated with yellow arrows, and is absent in pores indicated with white arrows. b) Arrangement of the experimental enclosures during the mesocosm experiment at the Metatron research facility (CNRS; Caumont, France). c) Male (marked with a number "3") and female (marked with a number "6") pair of *P. muralis* lizards engaged in co-perching behaviour in the experimental enclosures. d) Lizard hatching from one of the eggs resulting from clutches incubated in the laboratory. Parentage analyses of these offspring enabled us to reconstruct mating patterns, estimate sperm competition intensity, and quantify reproductive success, thereby identifying the behavioural and chemical traits that shaped male fitness within the enclosures.

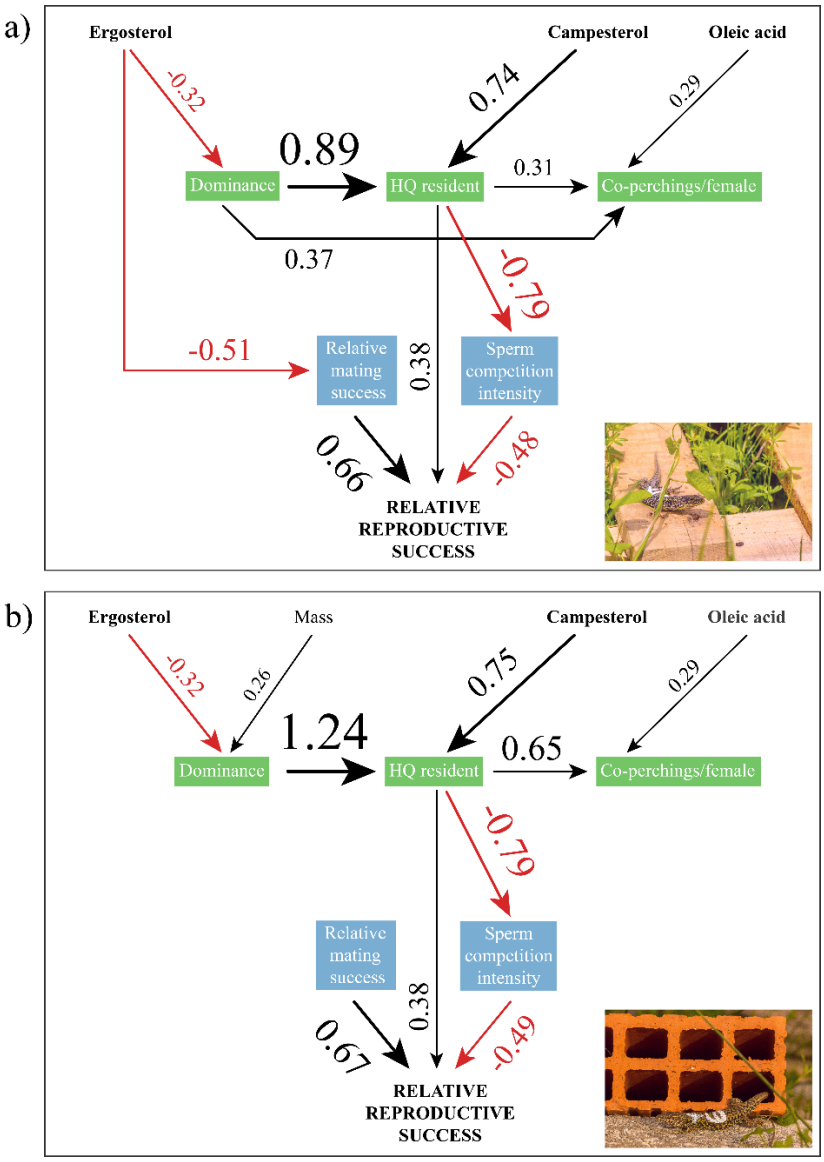

Fig. 2. Path diagrams illustrating the best-supported network of directional hypotheses from the piecewise structural equation modelling (pSEM) analysis fitted with the complete dataset (a) or excluding the males without offspring (b). Arrows represent supported causal relationships among morphological predictors, scent-mark composition, socio-spatial behaviour, and relative reproductive fitness. Arrow direction indicates the hypothesized causal flow; arrow thickness, font size, and accompanying values reflect standardized path coefficients from the pSEM, multiplied by 10 for visualization (a: **Table 2**; b: **Table 3**). Black arrows denote positive effects, while red arrows denote negative effects. Note that standardized coefficients obtained via bootstrapping differ in scale from the corresponding estimates in **Table 2** (a) and **Table S6** (b).

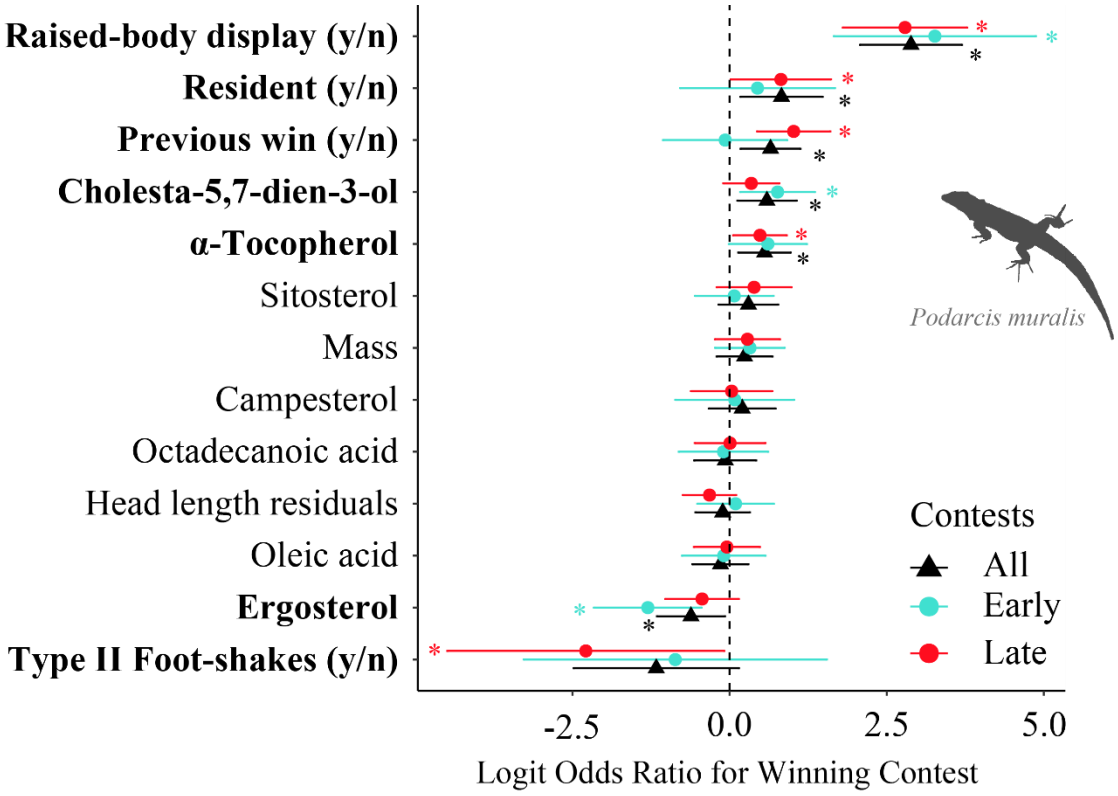

Figure 3. Forest plot showing model coefficients (logit-scale odd ratios ± CI_{95}) for each of the predictors considered in three Bradley-Terry models; an all-contests model on the full dataset of male-male competitive interactions (N = 544), an early-contests model on the interactions from days 1–9 (N = 137), and a late-contests model on the interactions observed from day 10 onwards (N = 407). Colour of the datapoints and error bars represent the different models. Bold letters and asterisks indicate significant predictors (α = 0.95, P-value < 0.05). Model coefficients correspond to the logarithm of odd ratios. Coefficients for chemical compounds and raised-body displays were higher in early contests, whereas the effects of type II foot shakes, residency status, and prior contest history became more pronounced in later contests.

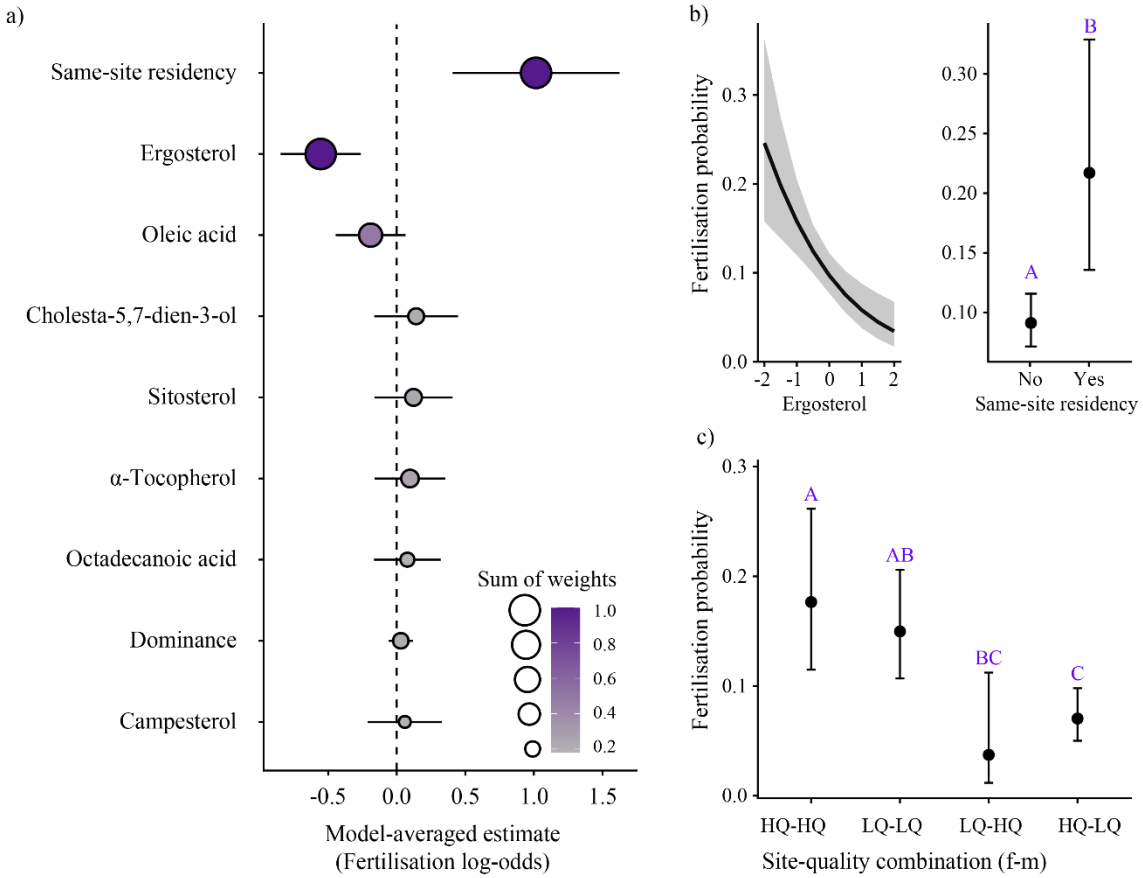

Figure 4. Predictors of per-egg fertilisation success in males. A) Forest plot of model-averaged conditional effects (points: log-scale odds ratios; bars: ± CI_{95}). Point size and colour reflect the summed model weights (SW). The analysis contrasts the effects of male–female spatial proximity and male traits (lipid abundances, dominance) on fertilization share. B) Effect plots for predictors with CI_{95} excluding zero and SW > 0.55. Left: fertilisation probability decreases with ergosterol (≈ 4% reduction per +1 SD). Right: males sharing a site with the female show higher fertilisation probability than males from other sites. C) To test whether this effect depends on site quality, we included parental site-quality combinations. Low–low pairs performed similarly to high–high pairs, indicating that the same-site advantage is not restricted to high-quality dyads. Blue letters show Tukey-adjusted comparisons: shared letters indicate no significant differences.

Appendix S1:

Supplementary material for the manuscript "Male scent-marks predict fitness via socio-spatial dominance, but not female choice, in a lacertid lizard".

Abalos, Javier [1,2]; Bartolomé, Alicia [1]; Pérez i de Lanuza, Guillem [1]; Aubret, Fabien [4,5]; Uller, Tobias [3]; Carazo, Pau [1]; Font, Enrique [1]; García-Roa, Roberto [1]

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Contents:

1. Expanded material and methods

1.1. Scent mark composition analyses

In the laboratory, femoral secretions were extracted from the left hindlimb of each *P. muralis* male following standardised protocols [1,2]. Samples were obtained by gently pressing around the femoral pores and collecting the resulting secretion in glass vials (1.1 ml). Blank control vials were included throughout the process to monitor potential contamination during handling. To minimise sample degradation, all vials were stored at −20 °C.

For a general characterisation and semiquantitative analysis of the chemical composition of male scent marks, each sample was treated with 100 µl of hexane containing 1 µg ml^{-1} of n-docosane D46 as an internal standard (IS). This internal standard allowed compound responses to be compared independently [2], which is crucial when examining inter-individual variation in compound abundance. Samples were agitated for 15 minutes in an orbital shaker, and the resulting extract was transferred to a conical glass insert using a Pasteur pipette for immediate analysis. Chemical analyses were conducted using gas chromatography–mass spectrometry (GC–MS). We used an Agilent 6890N gas chromatograph equipped with an HP-5MS UI capillary column (30 m × 0.25 mm × 0.25 µm), coupled to a TSQ Quantum XLS triple quadrupole mass spectrometer for quantification. A 1 µl aliquot of each extract was injected via an Agilent 7683B auto-injector into a 270 °C inlet in split-less mode (with the split valve opened after 2 minutes). The oven temperature programme was: 50 °C for 1 minute, then ramped at 40 °C min^{-1} to 150 °C, followed by 5 °C min^{-1} to 320 °C, and held for 9 minutes. Helium was used as the carrier gas at a constant flow rate of 1.4 ml min^{-1}. Mass spectra were acquired in scan mode (m/z 33–450) using electron impact ionisation at 70 eV. The ion source and quadrupole temperatures were set to 150 °C and 230 °C, respectively, and the transfer line was maintained at 300 °C. Compound identification followed standard procedures widely used in chemical studies of European lizards [3–5], using: (1) retention time comparisons with available authentic standards analysed under similar conditions, and (2) mass spectral matches against the NIST 2017 library using the Mass Spectral Search Program. A compound was considered positively identified when the match score exceeded 80%. All analyses were conducted at the Advanced Research Facilities of the University of the Basque Country (SGIker, UPV–EHU, Spain).

While this methodology provides a tentative broad overview of the scent mark composition, it is not optimal for the fine-scale identification and quantification of target compounds (see **Section 2.1.**, **Table S1**, and **Fig S1** for comparison between scan and targeted analyses). Therefore, we implemented a second step focused on specific compounds of interest: cholesterol, α-tocopherol, ergosterol (provitamin D2), oleic acid, hexadecanoic acid, octadecanoic acid, campesterol, cholesta-5,7-dien-3-ol, and ergosta-5,8-dien-3-ol. These compounds were selected on the base of their alleged role in sexual selection according to the literature (reviewed in [6]. Using the mass spectra of each compound, we used diagnostic fragment ions (m/z) that allowed us to confirm their presence in scan-mode chromatograms. Then, we extracted their signal intensities and retention times (tR) from each sample (i.e. set of fragment ions) to confirm compound identity and quantify relative abundance.

1.2. Preprocessing of scent mark composition data

Graphical exploration of the data from the targeted analysis of scent mark composition revealed a pronounced positive skew across all examined compounds, characterized by an excess of low-value readings relative to a normal distribution. Additionally, many compounds exhibited both positive skew and extreme high-value observations (outliers), complicating statistical analyses. To mitigate the impact of these outliers, Winsorization was applied to all compound levels, capping values at the 95th percentile (**Fig. S2**). To address zeros across varying scales (which is essential for logarithmic transformations), we applied adaptive pseudo-count addition by identifying the smallest nonzero value for each compound and adding 10% of across individuals [7,8]. We then applied a logarithmic transformation to attenuate skewness in the data. Finally, to enable comparisons across variables with differing scales, z-scores were computed by standardizing each variable to have a mean of zero and a standard deviation of one.

We found considerable levels of covariation between the ten examined compounds, with α-tocopherol and oleic acid showing the highest levels of independent variation (**Fig. S3**). To reduce problems resulting from multicollinearity in statistical modelling we used the *findCorrelation* function in the caret R package to select a subset of compound concentration variables showing no pairwise Pearson correlation coefficient higher than ± 0.6 [9]. This resulted in keeping seven out of ten examined compounds (i.e. cholesta-5,7-dien-3-ol, ergosterol, octadecanoic acid, campesterol, oleic acid, α-tocopherol, and sitosterol). The three excluded compounds are well represented by variation in other retained compounds (**Fig. S3**). More specifically, ergosta-5,8-dien-3-ol is well represented by ergosterol, cholesterol is well represented by variation in cholesta-5,7-dien-3-ol, and hexadecanoic acid is well represented by variation in octadecanoic acid (**Table S2**).

1.3. Behavioural observations

From May 23 to June 22, we conducted observations of spatial and social behaviour during peak activity hours (9.00-19.30), waiting at least1 h between consecutive visits to the same enclosure. One observer performed sequential rounds visiting all the enclosures every 2.5 h to collect data on the lizards' spatial behaviour (i.e. positional data). Using scan sampling, we determined the identity and location of every lizard in sight on a scale map of the enclosure that included the six wooden pallets. To balance sampling effort across enclosures, scanning of a single enclosure was restricted to a maximum period of 15 min after the first lizard was spotted. Meanwhile, two researchers recorded the identity, position and behaviours of the lizards participating in social interactions using a behaviour sampling rule in recording sessions lasting 40 min. A social interaction was considered to occur whenever a marked lizard in our visual range directed any of the behaviours listed in **Table S3** toward a conspecific. Consecutive interactions involving the same lizards were recorded as different events whenever the participants remained further than 30 cm apart for longer than 2 min. For further details, see [10,11].

1.4. Spatial behaviour analysis

We analyzed positional data using kernel density estimation (KDE) as implemented in the R package adehabitatHR [12,13], with spatial objects handled using the sp package [14]. To determine an appropriate smoothing parameter (h) for the kernel density estimates, we initially applied the least-squares cross-validation (LSCV) method (h = "LSCV"). This method minimizes the mean integrated squared error by evaluating the prediction error of each point using leave-one-out cross-validation. Although some individual models failed to converge using LSCV, we successfully obtained optimal h values for a majority of individuals (N = 161). We calculated the mean LSCV-derived h across converged models, which yielded an average value of approximately 0.24 (± 0.17 SD). Based on this result, and to maintain consistency and comparability across individuals, we used a fixed bandwidth of h = 0.2 for all kernel estimations. Using this common smoothing parameter, we estimated utilization distributions (UDs) for each lizard with the kernelUD() function and extracted the 95% and 50% probability contours using the getverticeshr() function. These contours were interpreted as the individual's home range and core area, respectively.

1.5. Parentage analyses

Parentage was assigned using multilocus microsatellite genotypes [15,16] and likelihood-based methods [17,18]. We isolated DNA from tail-tip samples using the DNeasy 96 Blood & Tissue Kit (Qiagen, Valencia, CA, USA), obtaining a final elution volume of 150 µl in AE buffer. We then combined the primers of six microsatellite loci described in *P. muralis* [15,16] into two different multiplexes (MPA: Pm16, Pm09, PmurC168; MPB: Pm19, Pm14, PmurC038) and ran standard PCR with 26 cycles and a final extension step of 30 min at 60°C. Forward primers were labeled with different fluorescent dyes (FAM, NED, HEX). Diluted PCR products (1:5) were genotyped together with an internal ladder (Red ROX-500) on an ABI 3130 genetic analyzer (Applied Biosystems Inc.). One researcher scored the alleles for every adult and juvenile lizard in Geneious 7.0.4 (Biomatters, available at http://www.geneious.com), which we used to conduct parentage analysis in Cervus 3.0 [17,18]. We assigned paternity based on the log-likelihood statistic of each mother–father–offspring trio (LOD scores), using two confidence levels (strict: 95%, relaxed: 80%) and the nine males within each enclosure as candidate fathers. Critical LOD scores were determined by running a simulation paternity analysis based on 100,000 offspring with known mothers and nine candidate fathers. We could reliably assign paternity to every offspring examined (strict: 208 juveniles, relaxed: 230 juveniles).

1.6. Piecewise structured equation modelling

Piecewise SEM is a form of path analysis particularly suited for evaluating direct and indirect relationships among multiple interrelated variables in complex systems [19]. This approach allows for flexible model specification, including random effects and non-Gaussian error distributions, making it well-suited for hierarchical data with complex dependency structures [20]. To avoid problems of reduced statistical power and overparameterization, we first examined the relationships among potential predictor variables using a Spearman correlation

matrix, calculated with the *chart.Correlation* function from the PerformanceAnalytics package in R [21]. Spearman's rank correlation was used because it is robust to non-normal distributions and non-linear relationships. To control for the false discovery rate across multiple correlation tests, we adjusted *P*-values using the *p.adjust* function with the Benjamini–Yekutieli procedure [22] implemented in the stats package. We explored the relationship among dominance rank index (DRI), core range size, number of females courted (tail-grabs), number of females guarded (co-perching), co-perchings per female (CP/F), HQ residency (HQr; HQ = 1, LQ or rocks = 0), relative mating success (RMS), sperm competition intensity (SCI), and relative reproductive success (RRS) (**Fig. S4**).

The initial pSEM (**Fig. S5**) specified direct effects of dominance (DRI), habitat residency (HQr), co-perching per female (CP/F), and relative mating success (RMS) on relative reproductive success (RRS). Direct effects of DRI, HQr, and CP/F on RMS and SCI were also included. Male chemical traits and morphology (mass, head-length residuals) were modelled as predictors of DRI, HQr, and CP/F. Mass and HL res were selected as morphological predictors because lizards were paired within each enclosure to minimize variation in SVL differences, and BCI was highly correlated with mass (**Fig. S3**). GLMMs for RMS, RRS, and SCI were fitted using a negative binomial error distribution to account for overdispersion, while the model for DRI was fitted as a linear mixed model (LMM) with a Gaussian error distribution, and the model for HQr used a binomial error distribution.

1.7. Bradley-Terry models on male-male competition

Individuals with missing data for specific predictors were handled using the null model framework, which assigns separate ability scores [23,24]. For each male, the first contest was assigned a prior contest outcome value of 0, as no individual had previous wins [25,26]. Model selection was conducted using backwards single term deletions (*P-value* < 0.05) of the saturated model followed by model comparisons via likelihood ratio tests (at $\alpha = 0.05$) using the function *drop1* included in `base` R [27]. Day nine was chosen as a cutoff point between early and late contests based on a marked increase in male–male confrontations observed thereafter [11].

1.8. Model fitting

All models were fitted using functions available in the glmmTMB and lme4 packages of R [28]. All numerical variables were centered and scaled before running the models [29]. To account for the mesocosm design of the experiment, we included the experimental cell as a random factor in all GLMM models. We graphically explored that residuals conformed to homoscedasticity and normality assumptions using the function *simulateResiduals* from the package DHARMa [30]. We also tested for zero-inflation, overdispersion and collinearity using functions available in the DHARMa and Performance packages in R [30,31]. Model selection was conducted using the corrected Akaike's information criterion (AICc) [32]. As model selection methods for piecewise SEMs do not yet accommodate the full set of models nested within a saturated structure, for the pSEM procedure we conducted model selection using backwards single term deletions of the saturated model until we obtained the model showing the lowest value of AICc [33,34]. Because the piecewiseSEM package does not provide measures of uncertainty for standardized path coefficients, we complemented our

analysis by using the *semEff* function from the homonym R package [35]. This function summarizes the direct, indirect, and total effects in the SEM and estimates bootstrapped CI_{95} for standardized coefficients. Importantly, these estimates are computed on a different scale than the standardized coefficients returned by *coefs* in piecewiseSEM, and thus are not directly comparable in magnitude. Bootstrapped estimates were obtained using *bootEff* with 1,000 replicates, incorporating the random effects structure of the original models.

To further refine inference on individual pathways, we complemented the pSEM-based selection with an exhaustive model selection approach for each of its component models, implemented via the *dredge* function in the MuMIn package [36]. This same method for model selection was applied to beta-binomial mixed models on fertilisation success. We considered models with AICc differences (ΔAICc) < 4 to have substantial support, extending the conventional threshold of ΔAICc < 2 to better capture alternative plausible models [27,32,37]. We examined multiple comparisons among factor levels in the top-ranked models using estimated marginal means (EMMs), computed with the *emmeans* function in the homonym R package [38]. Pairwise contrasts were performed with Tukey-adjusted *p*-values to account for multiple comparisons [39]. We calculated the model averaged coefficients and 95% confidence intervals (CI) along with the relative importance of variables (RIV) for each variable by summing the normalized AIC_C weights of the models in this subset where a given variable was present. We considered a variable to be biologically significant if its CI_{95} did not include 0 and it had RIV $\geq$ 0.55 [34]. All analysis were conducted in R v.4.2.2. [40].

2. Expanded results

2.1. Scent mark composition analyses

Compared to results from the scan analysis, the targeted methodology resulted in a much lower number of blank readings, with the exception of α-Tocopherol and Oleic acid (**Table S1**). To compare results from the scan and the targeted analysis, we plotted against each other the corresponding individual readings obtained in both analyses for the nine compounds present in both results. Blank readings from the scan analysis were substituted with zeroes, while blank readings in the targeted analysis were left as NA. To deal with deviations from normality, we added a constant of 0.01 to all values and then extracted the corresponding logarithm. Graphical examination of the resulting scatterplots reveals that blank readings in the scan analysis did not generally correspond to low concentration levels in the targeted analysis, arguing against the common practice of substituting blank readings from scan analysis with zeroes (**Fig. S1**). Consequently, we deemed unreliable the results from the scan analysis and based all subsequent analysis on results from the targeted methodology, where blank readings can confidently be assumed to reflect low concentration levels.

Graphical exploration of the data from the targeted analysis revealed a pronounced positive skew across all examined compounds, characterized by an excess of low-value readings relative to a normal distribution. Additionally, many compounds exhibited both positive skew and extreme high-value observations (outliers), complicating statistical analyses (**Fig. S2**). To mitigate the impact of these outliers, Winsorization was applied to all

compound levels, capping values at the 95th percentile (**Fig. S2**). To address zeros across varying scales (which is essential for logarithmic transformations), we applied adaptive pseudo-count addition by identifying the smallest nonzero value for each compound and adding 10% of across individuals [7,8]. We then applied a logarithmic transformation to attenuate skewness in the data. Finally, to enable comparisons across variables with differing scales, z-scores were computed by standardizing each variable to have a mean of zero and a standard deviation of one.

2.2. Socio-spatial behaviour and fitness

Spearman correlation analyses revealed several significant associations between male dominance, socio-spatial behaviour, and male fitness (**Fig. S4**). Dominance rank was negatively associated with core range size (ϱ = –0.45) and sperm competition intensity (ϱ = –0.13), but positively with the number of females guarded (co-perching; ϱ = 0.35), the number of females courted (tail-grab; ϱ = 0.46), and the probability of settling in a HQ site (ϱ = 0.44). These patterns suggest that dominant males had more restricted ranges, encountered more females, and faced reduced sperm competition intensity, overall showing higher relative mating (ϱ = 0.20) and reproductive success (ϱ = 0.27). Core range size was negatively correlated with both average sperm competition intensity (ϱ = –0.47) and relative reproductive success (ϱ = –0.44), while being positively related to relative mating success (ϱ = 0.27). The number of females guarded showed strong positive correlations with number of females courted (ϱ = 0.31) and both mating (ϱ = 0.27) and reproductive success (ϱ = 0.27). Expectedly, relative mating success was highly positively associated with reproductive success (ϱ = 0.82) and negatively with average sperm competitors (ϱ = -0.51), confirming that exclusive access to multiple mates is a key determinant of male fitness in this system.

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4. Tables

Table S1. Chemical compounds (lipidic fraction) in the femoral secretions of 78 *Podarcis muralis* males, ranked in descending order according to their prevalence of blank readings in the sweep analysis.

	Scan analysis		Targeted analysis	
Variable	**Blank**	**Proportion**	**Blank**	**Proportion**
Cholesterol	1	0.013	1	0.013
Cholesta-5,7-dien-3-ol	11	0.141	0	0.000
Squalene	12	0.154		
α-Tocopherol	15	0.192	32	0.410
Docosemide13	19	0.244		
Hexadecanoic acid	22	0.282	15	0.192
Ester acid	27	0.346		
Ester – no id	27	0.346		
Octadecanoic acid-9-ester	31	0.397	1	0.013
Ergosta-5,7,2,5-trienol	32	0.41		
Campesterol	32	0.41	9	0.115
Ergosta-5,8-dien-3-ol	36	0.462	1	0.013
Ergosterol	37	0.474	0	0.000
No id	39	0.5		
Alkene	42	0.538		
Oleic acid	44	0.564	47	0.603
Cholesta-4,6-dien-3-one	44	0.564		
Cholesta-3,5-diene	48	0.615		
No id	51	0.654		
Alkene	53	0.679		
Hexadecal	54	0.692		
No id	56	0.718		
Octadecanoic acid	63	0.808		
No id	70	0.897		
No id	72	0.923		
Sitosterol	-	-	6	0.077

Table S2. Pearson correlation coefficients and *P-value*s corresponding to the compound concentration variables dropped from the analysis due to them being well represented by other retained variables (Pearson R > 0.6). Correlation coefficients were estimated after winsorization, adaptive pseudocount addition, logarithmic transformation, and Z-transformation.

Retained_Variable	**Correlated_Variable**	**Correlation**	***P-value***
Cholesta-5,7-dien-3-ol	Cholesterol	0.633	4.83E-10
Ergosterol	Ergosta-5,8-dien-3-ol	0.694	1.89E-12
Octadecanoic acid	Hexadecanoic acid	0.643	2.18E-10

1236 **Table S3.** Partial ethogram of *Podarcis muralis* including social behaviours used to collect
1237 data on interactions during behavioural observations within the experimental enclosures.

Behaviour	Description
Approach*	Movement toward a non-fleeing conspecific
Raised-body display	Gular extension, back-arching, shoulders raised, head down, sagittal compression (any combination)
Bite	One or more bites to another individual (excluding tail grab)
Retreat*	Movement away from a non-chasing conspecific
Chase	Rapidly following another FLEEING lizard
Flight	Fast-paced movement to withdraw from a CHASING lizard
Type II foot shakes	Rapid large amplitude vertical movements of forelimbs (belly down, head up posture), often accompanied by TAIL WAVE/SHAKE
Tail grab	A male bites the tail or inguinal region of a female. Often followed by copulation
Tail wave/shake	Vibrating entire tail (or its distal portion) swiftly from side to side
Mating	Two lizards engage in copulation
Co-perching	Two or more lizards lying together in close vicinity (<15 cm; >30 s)

* We classified the mode of locomotion used as either running (fast-paced) or any other mode of locomotion (slow-paced).

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Table S4. Model selection results from the binomial GLMM assessing sex differences on the probability of settling in high-quality (HQ) versus low-quality (LQ) sites. Model # refers to the model ID used for reference. Fixed effects included in each model are indicated by their estimated coefficients (Intercept, Mass, Sex). df is the number of estimated parameters, AICc is the corrected Akaike Information Criterion, ΔAICc indicates the difference in AICc between model *i* and the top-ranked model, and Weight represents the relative probability that model *i* is the best model given the data.

Model #	Intercept	Mass	Sex	df	AICc	ΔAICc	Weight
3	-0.09		+	3	208.3	0.00	0.625
4	-1.19	0.18	+	4	209.3	1.02	0.375
2	1.48	-0.24		3	252.2	43.92	0.000
1	-0.07			2	253.4	45.09	0.000

Table S5. Summary of results from the piecewise SEM assessing relationships among male scent mark composition, socio-spatial behaviour, and relative fitness. Unstandardized coefficients (β), standard errors (SE), standardized coefficients (Std. β), and marginal pseudo-R^2 (R^2m) coefficients are provided. Bolded variables were retained in the best-ranked model (AICc = 1010.656). Coefficients for non-included variables are shown at their point of removal. RRS = relative reproductive success, RMS = relative mating success, SCI = sperm competition intensity, HQr = residency at high-quality site, CP/F = co-perchings per female guarded, DRI = dominance rank index, HL res = residuals of head length against SVL.

Response	Predictor	*β*	SE	Std. *β*	*F*	Df	*P*-value	R^2m
RRS	**RMS**	**0.34**	**0.10**	**0.51**	**3.42**	**53**	**<0.001**	
	SCI	**-0.27**	**0.16**	**-0.38**	**-1.63**	**53**	**0.103**	**0.15**
	HQr	**0.44**	**0.26**	**0.28**	**1.67**	**53**	**0.094**	
	CP/F	0.09	0.09	0.17	0.98	53	0.325	
	DRI	0.07	0.15	0.10	0.47	53	0.641	
RMS	**Ergosterol**	**-0.42**	**0.13**	**-0.37**	**-3.26**	**78**	**0.001**	
	DRI	-0.03	0.13	-0.03	-0.24	78	0.810	
	CP/F	0.02	0.09	0.03	0.27	78	0.787	0.10
	HQr	0.05	0.32	0.02	0.16	78	0.872	
SCI	**HQr**	**-0.71**	**0.31**	**-0.44**	**-2.28**	**53**	**0.022**	
	CP/F	-0.00	0.12	-0.01	-0.04	53	0.971	0.10
	DRI	-0.00	0.12	-0.00	-0.00	53	0.998	
DRI	**Ergosterol**	**-0.32**	**0.11**	**-0.32**	**-2.97**	**76**	**0.004**	
	α-Tocopherol	0.19	0.11	0.19	1.68	75	0.097	
	Cholesta-5,7-dien-3-ol	0.25	0.13	0.25	1.97	74	0.052	
	Oleic_acid	-0.18	0.11	-0.18	-1.61	73	0.112	
	Campesterol	0.12	0.12	0.12	1.10	72	0.276	0.10
	Octadecanoic acid	-0.11	0.12	0.11	-0.93	71	0.356	
	Mass	0.09	0.12	0.10	0.79	70	0.431	
	HL res	0.04	0.12	0.04	0.34	69	0.736	
	Sitosterol	0.02	0.12	0.02	0.16	68	0.870	
HQr	**DRI**	**1.68**	**0.22**	**0.60**	**3.64**	**78**	**<0.001**	
	Campesterol	**1.40**	**0.34**	**0.50**	**1.97**	**78**	**0.0483**	
	α-Tocopherol	-0.59	0.38	-0.21	-1.55	78	0.122	
	Sitosterol	0.37	0.51	0.12	0.73	78	0.463	0.58
	Oleic_acid	-0.29	0.40	-0.10	-0.73	78	0.466	
	HL res	-0.28	0.39	-0.09	-0.72	78	0.474	
	Cholesta-5,7-dien-3-ol	-0.21	0.44	-0.07	-0.48	78	0.634	
	Mass	0.20	0.42	0.06	0.46	78	0.642	
	Octadecanoic acid	-0.17	0.46	-0.06	-0.38	78	0.705	
	Ergosterol	-0.07	0.70	-0.02	-0.10	78	0.917	
CP/F	**DRI**	**0.30**	**0.06**	**0.38**	**2.60**	**78**	**0.010**	
	HQr	**0.59**	**0.11**	**0.32**	**2.57**	**78**	**0.010**	
	Oleic_acid	**0.21**	**0.05**	**0.26**	**2.16**	**78**	**0.031**	
	α-Tocopherol	-0.09	0.11	-0.12	-0.87	78	0.383	
	Cholesta-5,7-dien-3-ol	-0.06	0.10	-0.08	-0.64	78	0.521	0.18
	Sitosterol	0.06	0.11	0.08	0.54	78	0.590	
	Campesterol	-0.08	0.12	0.08	-0.64	78	0.520	
	HL res	0.03	0.11	0.04	0.257	78	0.798	
	Mass	0.01	0.11	0.01	0.05	78	0.964	
	Ergosterol	-0.00	0.14	-0.00	-0.01	78	0.992	
	Octadecanoic acid	-0.00	0.11	-0.00	-0.01	78	0.993	

Table S6. Summary of model-averaged coefficients from the individual GLMMs nested as component models in the piecewise SEM. Variance inflation factors (VIF) correspond to the saturated model. Standardized coefficients (Std. β) represent the conditionally-averaged effect sizes across the subset of top models (ΔAICc < 4), with CI_{95}, *Z*-values, and *P*-values. Relative importance values (RIV) represent the summed Akaike weights across all top models in which each predictor was retained, reflecting their relative support in explaining variation. Bolded letters highlight variables with RIV > 0.55. which are considered strong predictors. RRS = relative reproductive success, RMS = relative mating success, HQr = residency at HQ site, CP/F = co-perchings per female guarded, DRI = dominance rank index, HL res = residuals of head length against SVL.

Respose	Predictor	*N*	VIF	Std. β	CI_{95}	*Z*	*P*-value	RIV
RRS	**RMS**		**1.19**	**0.38**	**[0.16, 0.60]**	**3.37**	**<0.001**	**1.00**
	SCI		**1.47**	**-0.30**	**[-0.62, 0.01]**	**1.87**	**0.061**	**0.64**
	HQr	14	2.21	0.50	[-0.10, 1.10]	1.61	0.103	0.50
	CP/F		1.51	0.16	[-0.07, 0.38	1.35	0.178	0.39
	DRI		1.62	0.14	[-0.16, 0.44]	0.93	0.354	0.30
RMS	**Ergosterol**		**1.13**	**-0.05**	**[-0.67, -0.16]**	**3.17**	**0.002**	**1.00**
	CP/F	4	1.56	0.03	[-0.19, 0.24]	0.27	0.791	0.17
	HQr		1.52	0.06	[-0.46, 0.57]	0.21	0.831	0.17
	DRI		1.53	-0.01	[-0.25, 0.23]	0.09	0.927	0.16
SCI	**HQr**		**1.45**	**-0.71**	**[-1.39, -0.04]**	**2.07**	**0.038**	**0.84**
	CP/F	5	1.43	-0.04	[-0.28, 0.19]	0.35	0.725	0.23
	DRI		1.25	-0.00	[-0.24, 0.24]	0.01	0.992	0.16
DRI	**Ergosterol**		**1.75**	**-0.92**	**[-1.62, -0.22]**	**2.59**	**0.010**	**0.98**
	α-Tocopherol		**1.49**	**0.65**	**[0.01, 1.30]**	**1.99**	**0.047**	**0.67**
	Cholesta-5,7-dien-3-ol		**1.75**	**0.60**	**[-0.07, 1.28]**	**1.74**	**0.081**	**0.55**
	Oleic acid	40	1.33	-0.49	[-1.11, 0.13]	1.54	0.124	0.36
	Mass		1.27	0.35	[-0.27, 0.98]	1.12	0.265	0.20
	Campesterol		1.53	0.32	[-0.30, 0.94]	1.01	0.311	0.19
	HL res		1.11	0.18	[-0.42, 0.78]	0.59	0.555	0.10
	Octadecanoic acid		1.39	-0.17	[-0.78, 0.44]	0.56	0.579	0.09
	Sitosterol		1.31	0.03	[-0.54, 0.59]	0.09	0.926	0.06
HQr	**DRI**		**2.05**	**1.81**	**[0.77, 2.84]**	**3.43**	**0.001**	**1.00**
	Campesterol		**3.27**	**1.33**	**[-0.08, 2.73]**	**1.85**	**0.064**	**1.00**
	α-Tocopherol	33	2.29	-0.57	[-1.37, 0.23]	1.4	0.161	0.43
	Oleic acid		1.42	-0.42	[-1.21, 0.38]	1.03	0.302	0.28
	HL res		1.19	-0.35	[-1.08, 0.38]	0.93	0.352	0.28
	Sitosterol		1.46	0.34	[-0.59, 1.27]	0.71	0.476	0.17
	Mass		1.89	0.08	[-0.68, 0.84]	0.2	0.839	0.11
	Octadecanoic acid		1.27	-0.03	[-0.75, 0.70]	0.08	0.94	0.11
	Cholesta-5,7-dien-3-ol		1.58	-0.1	[-0.85, 0.66]	0.25	0.804	0.10
	Ergosterol		3.60	-0.07	[-1.03, 0.88]	0.15	0.883	0.09
CP/F	**HQr**		**1.62**	**0.57**	**[0.11, 1.03]**	**2.42**	**0.016**	**1.00**
	DRI		**1.8**	**0.31**	**[0.07, 0.54]**	**2.55**	**0.011**	**1.00**
	Oleic acid		**1.4**	**0.21**	**[0.01, 0.40]**	**2.11**	**0.035**	**0.87**
	α-Tocopherol	16	1.74	-0.09	[-0.31, 0.12]	0.86	0.388	0.20
	Sitosterol		1.48	0.07	[-0.15, 0.30]	0.66	0.511	0.14
	Ergosterol		2.32	-0.05	[-0.26, 0.15]	0.53	0.593	0.10
	Cholesta-5,7-dien-3-ol		1.91	-0.05	[-0.25, 0.15]	0.51	0.612	0.10
	Mass		1.63	-0.05	[-0.24, 0.14]	0.54	0.588	0.09
	Campesterol		1.85	-0.05	[-0.27, 0.17]	0.44	0.658	0.09
	Octadecanoic acid		1.4	0.01	[-0.19, 0.20]	0.05	0.958	0.06
	HL res		1.18	0	[-0.22, 0.21]	0.04	0.966	0.06

Table S7. Summary of results from the piecewise SEM assessing relationships among male scent mark composition, socio-spatial behaviour, and relative fitness (excluding males without offspring). Unstandardized coefficients (β), standard errors (SE), standardized coefficients (Std. β), and marginal pseudo-R^2 (R^2m) coefficients are provided. Bolded variables were retained in the best-ranked model (AICc = 654.069). Coefficients for non-included variables are shown at their point of removal. RRS = relative reproductive success, RMS = relative mating success, HQr = residency at HQ site, CP/F = co-perchings per female guarded, DRI = dominance rank index, HL res = residuals of head length against SVL.

Respose	Predictor	*β*	SE	Std. *β*	*F*	Df	*P*-value	*R²m*
RRS	**RMS**	**0.34**	**0.10**	**0.25**	**3.49**	**53**	**<0.001**	
	SCI	**-0.27**	**0.16**	**-0.21**	**-1.68**	**53**	**0.093**	**0.23**
	HQr	**0.44**	**0.26**	**0.16**	**1.71**	**53**	**0.089**	
	CP/F	0.09	0.09	0.10	0.98	53	0.325	
	DRI	0.07	0.15	0.06	0.47	53	0.641	
RMS	Ergosterol	-0.11	0.13	-0.11	-0.86	53	0.392	
	DRI	-0.10	-0.10	-0.11	-0.72	53	0.471	
	CP/F	-0.04	0.11	-0.06	-0.36	53	0.715	0.00
	HQr	0.10	0.26	0.05	0.40	53	0.692	
SCI	**HQr**	**-0.71**	**0.31**	**-0.32**	**-2.28**	**53**	**0.022**	
	CP/F	-0.00	0.11	-0.00	0.03	53	0.972	0.10
	DRI	-0.00	0.12	-0.00	-0.00	53	0.998	
DRI	**Ergosterol**	**-0.39**	**0.14**	-0.35	**-2.74**	**50**	**0.008**	
	Mass	**0.26**	**0.13**	**0.26**	**2.01**	**50**	**0.050**	
	Cholesta-5,7-dien-3-ol	0.21	0.15	0.22	1.42	49	0.162	
	Sitosterol	0.15	0.14	0.14	1.05	48	0.299	
	Octadecanoic acid	0.08	0.15	0.09	0.55	47	0.586	0.17
	HL res	0.07	0.15	0.06	0.44	46	0.661	
	Campesterol	0.08	0.20	0.07	0.39	45	0.700	
	α-Tocopherol	-0.02	0.16	-0.02	1.68	44	0.097	
	Oleic_acid	0.01	0.17	0.01	0.06	43	0.953	
HQr	**DRI**	**2.28**	**0.74**	**0.74**	**3.09**	**53**	**0.002**	
	Campesterol	**1.51**	**0.98**	**0.45**	**1.53**	**53**	**0.125**	
	Ergosterol	-1.50	1.11	-0.32	-1.34	53	0.181	
	Sitosterol	1.39	1.30	0.29	1.07	53	0.283	
	Mass	0.50	0.51	0.15	0.98	53	0.327	
	α-Tocopherol	-0.42	0.47	-0.13	-0.90	53	0.370	0.64
	HL res	0.24	0.56	0.05	0.43	53	0.670	
	Octadecanoic acid	-0.20	0.63	-0.04	0.32	53	0.750	
	Cholesta-5,7-dien-3-ol	-0.11	0.79	-0.02	-0.13	53	0.895	
	Oleic_acid	-0.13	0.73	-0.03	-0.18	53	0.861	
CP/F	**HQr**	**0.96**	**0.23**	**0.32**	**4.26**	**53**	**<0.001**	
	DRI	**0.20**	**0.14**	**0.16**	**1.38**	**53**	**0.166**	
	Oleic_acid	**0.19**	**0.11**	**0.15**	**1.71**	**53**	**0.087**	
	Campesterol	-0.15	0.19	-0.11	-0.79	53	0.431	
	Ergosterol	0.14	0.17	0.10	0.83	53	0.408	0.17
	HL res	0.12	0.13	0.09	0.91	53	0.362	
	Sitosterol	0.10	0.18	0.08	0.54	53	0.586	
	Octadecanoic acid	0.09	0.13	0.07	0.69	53	0.489	
	Cholesta-5,7-dien-3-ol	-0.07	0.12	-0.06	0.54	53	0.584	
	Mass	-0.06	0.14	-0.05	-0.42	53	0.674	
	α-Tocopherol	0.04	0.17	0.03	0.27	53	0.787	

Table S8. Standardized path coefficients (Std. β) and 95% confidence intervals (CI_{95}) for direct and indirect effects estimated using bootstrapping (1,000 replicates). The table reports relationships among scent mark composition and socio-spatial behaviour acting as mediators of male relative reproductive success (RRS) as identified in the best-fitting piecewise SEM (excluding males without offspring). Indirect effects are aggregated across all mediating pathways.

Response	Predictor	*Std. β*	Lower CI_{95}	Upper CI_{95}	Effect type
Reproductive success	Mating success	0.067	0.040	0.130	Direct
	Sperm competition intensity	-0.049	-0.130	-0.004	Direct
	High-quality residency	0.038	0.002	0.096	Direct
	Dominance	0.005	0.002	0.014	Indirect
	High-quality residency	0.004	-0.025	0.014	Indirect
	Campesterol	0.003	0.001	0.008	Indirect
	Ergosterol	-0.002	-0.005	-0.000	Indirect
	Mass	0.001	0.000	0.004	Indirect
Sperm competition intensity	High-quality residency	-0.079	-0.213	-0.034	Direct
	Dominance	-0.010	-0.030	-0.002	Indirect
	Campesterol	-0.006	-0.032	-0.001	Indirect
	Ergosterol	0.003	0.000	0.022	Indirect
	Mass	-0.003	-0.013	0.050	Indirect
Dominance	Ergosterol	-0.035	-0.056	-0.014	Direct
	Mass	0.026	0.002	0.046	Direct
High-quality residency	Dominance	0.124	0.074	0.275	Direct
	Campesterol	0.075	0.024	0.225	Direct
	Ergosterol	-0.044	-0.189	-0.023	Indirect
	Mass	0.032	0.008	0.123	Indirect
Copercbings per female	Oleic_acid	0.029	0.08	0.049	Direct
	High-quality residency	0.065	0.047	0.086	Direct
	Dominance	0.008	0.004	0.018	Indirect
	Campesterol	0.005	0.001	0.017	Indirect
	Ergosterol	-0.003	-0.009	-0.001	Indirect
	Mass	0.002	0.001	0.009	Indirect

Table S9. Summary of model-averaged coefficients from the individual GLMMs nested as component models in the piecewise SEM (excluding males without offspring). Variance inflation factors (VIF) correspond to the saturated model. Standardized coefficients (Std. β) represent the conditionally-averaged effect sizes across the subset of top models (ΔAICc < 4), with CI_{95}, *Z*-values, and *P*-values. Relative importance values (RIV) represent the summed Akaike weights across all top models in which each predictor was retained, reflecting their relative support in explaining variation. Bolded letters highlight variables with RIV > 0.55, which are considered strong predictors. RRS = relative reproductive success, RMS = relative mating success, HQr = residency at HQ site, CP/F = co-perchings per female guarded, DRI = dominance rank index, HL res = residuals of head length against SVL.

Respose	Predictor	*N*	VIF	Std. β	CI_{95}	*Z*	*P*-value	RIV
RRS	**RMS**		**1.19**	**0.38**	**[0.16, 0.60]**	**3.37**	**<0.001**	**1.00**
	SCI		**1.47**	**-0.30**	**[-0.62, 0.01]**	**1.87**	**0.061**	**0.64**
	HQr	14	1.52	0.50	[-0.10, 1.10]	1.61	0.103	0.50
	CP/F		1.56	0.16	[-0.07, 0.38	1.35	0.178	0.39
	DRI		1.53	0.14	[-0.16, 0.44]	0.93	0.354	0.30
RMS	Ergosterol		1.14	-0.12	[-0.38, 0.15]	0.85	0.398	0.27
	HQr		1.72	0.11	[-0.41, 0.63]	0.42	0.674	0.18
	DRI	7	1.65	-0.02	[-0.26, 0.21]	0.19	0.849	0.17
	CP/F		1.58	-0.02	[-0.24, 0.21]	0.14	0.891	0.12
SCI	**HQr**		**1.45**	**-0.71**	**[-1.39, -0.04]**	**2.07**	**0.038**	**0.84**
	CP/F	5	1.43	-0.04	[-0.28, 0.19]	0.35	0.725	0.23
	DRI		1.25	-0.00	[-0.24, 0.24]	0.01	0.992	0.16
DRI	**Ergosterol**		**2.60**	**-1.20**	**[-2.12, -0.27]**	**2.53**	**0.014**	**0.98**
	Mass		**1.42**	**0.72**	**[0.01, 1.42]**	**2.00**	**0.046**	**0.69**
	Cholesta-5,7-dien-3-ol		2.35	0.57	[-0.26, 1.39]	1.35	0.178	0.38
	Octadecanoic acid	32	1.74	0.41	[-0.32, 1.13]	1.11	0.269	0.23
	Campesterol		1.99	0.18	[-0.74, 1.11]	0.39	0.700	0.13
	Sitosterol		1.49	0.31	[-0.46, 1.07]	0.79	0.432	0.12
	HL res		1.26	0.13	[-0.63, 0.88]	0.33	0.743	0.10
	Oleic acid		1.62	-0.11	[-0.87, 0.66]	0.27	0.786	0.10
	α-Tocopherol		1.71	-0.00	[-0.79, 0.79]	0.01	0.995	0.10
HQr	**DRI**		**2.23**	**2.31**	**[0.72, 3.90]**	**2.85**	**0.004**	**1.00**
	Campesterol		**5.37**	**1.53**	**[-0.86, 3.92]**	**1.26**	**0.209**	**0.67**
	Sitosterol		2.69	1.29	[-0.81, 3.38]	1.20	0.229	0.50
	Mass		2.22	0.65	[-0.61, 1.90]	1.01	0.311	0.24
	Oleic acid		2.25	-0.45	[-1.42, 0.53]	0.90	0.370	0.19
	α-Tocopherol	44	3.38	-0.44	[-1.51, 0.63]	0.80	0.422	0.17
	Ergosterol		5.76	-0.37	[-2.17, 1.43]	0.41	0.685	0.14
	Octadecanoic acid		2.08	0.28	[-0.69, 1.26]	0.57	0.568	0.11
	Cholesta-5,7-dien-3-ol		2.30	-0.08	[-1.16, 1.01]	0.14	0.892	0.08
	HL res		1.47	-0.18	[-1.08, 0.72]	0.39	0.698	0.06
CP/F	**HQr**		**1.71**	**0.85**	**[0.30, 1.40]**	**3.03**	**0.002**	**1.00**
	Oleic acid		1.72	0.19	[-0.04, 0.42]	1.60	0.110	0.48
	DRI		1.70	0.21	[-0.09, 0.50]	1.39	0.165	0.42
	HL res		1.27	0.13	[-0.13, 0.40]	1.00	0.320	0.17
	Cholesta-5,7-dien-3-ol		2.39	-0.07	[-0.31, 0.17]	0.58	0.562	0.11
	Mass		2.03	-0.05	[-0.30, 0.18]	0.45	0.654	0.10
	α-Tocopherol	40	2.04	0.03	[-0.22, 0.28]	0.25	0.803	0.09
	Sitosterol		1.83	0.04	[-0.24, 0.31]	0.14	0.262	0.08
	Ergosterol		2.94	0.03	[-0.25, 0.30]	0.19	0.853	0.08
	Campesterol		2.41	-0.03	[-0.33, 0.26]	0.23	0.822	0.08
	Octadecanoic acid		1.76	0.01	[-0.22, 0.24]	0.11	0.916	0.08

Table S10. Results from Bradley–Terry models examining the effects of morphology, chemical compounds, behavioural displays, prior contest history and residency on the log odds of winning a contest. M1 was fitted on the full dataset of contests. M2 was fitted on the early contests observed before Day 10. M3 included every late contest observed from day 10 onwards. Significant predictors are highlighted in bold ($\alpha = 0.95$, *P-value* < 0.05). Statistics for non-significant factors are included at the point of their deletion from the model.

Model	Predicted	Variable	Estimate	SE	VIF	*Z*	*P*-value
M1 All contests 544 fights	83.8%	Mass	0.24	0.23	1.47	1.04	0.296
		HL res	-0.11	0.22	1.27	-0.50	0.620
		Cholesta-5,7-dien-3-ol	**0.59**	**0.24**	**2.17**	**2.47**	**0.013**
		Ergosterol	**-0.61**	**0.28**	**2.35**	**-2.22**	**0.026**
		Octadecanoic acid	-0.07	0.25	1.52	-0.27	0.785
		Campesterol	0.20	0.27	1.81	0.74	0.459
		Oleic acid	-0.14	0.23	1.41	-0.64	0.523
		α-Tocopherol	**0.56**	**0.21**	**1.78**	**2.60**	**0.009**
		Sitosterol	0.30	0.24	1.59	1.24	0.213
		Raised-body display	**2.89**	**0.41**	**1.24**	**6.97**	**< 0.001**
		Type II foot shakes	-1.17	0.67	1.06	1.74	0.082
		Prior contest history	**0.65**	**0.24**	**1.10**	**2.68**	**0.007**
		Resident	**0.83**	**0.33**	**1.22**	**2.48**	**0.013**
		ID (Std. dev)	1.08	0.19		5.76	<0.001
M2 Early ≤ Day 9 137 fights	71.5%	Mass	0.32	0.28	1.39	1.15	0.250
		HL res	0.09	0.31	1.50	0.31	0.760
		Cholesta-5,7-dien-3-ol	**0.76**	**0.30**	**2.86**	**2.52**	**0.012**
		Ergosterol	**-1.30**	**0.44**	**2.58**	**-2.98**	**0.003**
		Octadecanoic acid	-0.10	0.36	1.74	-0.27	0.790
		Campesterol	0.08	0.48	1.78	0.17	0.863
		Oleic acid	-0.09	0.34	1.61	-0.28	0.784
		α-Tocopherol	0.61	0.31	2.49	1.93	0.053
		Sitosterol	0.07	0.32	1.52	0.23	0.815
		Raised-body display	**3.27**	**0.44**	**1.19**	**4.00**	**< 0.001**
		Type II foot shakes	-0.86	1.22	1.24	-0.70	0.481
		Prior contest history	-0.07	0.50	1.28	-0.14	0.889
		Resident	0.44	0.63	1.10	0.71	0.480
		ID (Std. dev)	0.71	0.33		2.14	0.033
M3 Late > Day 9 407 fights	84.8%	Mass	2.84	0.26	1.56	1.08	0.281
		HL res	-0.32	0.22	1.29	-1.48	0.140
		Cholesta-5,7-dien-3-ol	0.35	0.23	2.06	1.52	0.129
		Ergosterol	-0.44	0.30	2.19	-1.47	0.143
		Octadecanoic acid	0.01	0.28	1.51	0.03	0.980
		Campesterol	0.03	0.33	1.91	0.10	0.922
		Oleic acid	0.04	0.27	1.52	-0.16	0.871
		α-Tocopherol	0.48	0.22	1.83	2.22	0.026
		Sitosterol	0.39	0.30	1.63	1.29	0.198
		Raised-body display	**2.79**	**0.50**	**1.28**	**5.53**	**< 0.001**
		Type II foot shakes	**-2.29**	**1.12**	**1.17**	**-2.04**	**0.042**
		Prior contest history	**1.02**	**0.30**	**1.14**	**3.43**	**< 0.001**
		Resident	**0.82**	**0.41**	**1.28**	**2.01**	**0.044**
		ID (Std. dev)	1.08	0.22		4.92	< 0.001

Table S11. Results of robust one-way ANOVAs (bootstrapped trimmed means) testing differences in ten chemical compounds among males settled in HQ sites, LQ sites, and the rocks in between. Each test reflects 10,000 bootstrap iterations. Reported are the mean ± SEM for each compound (as Z-scores) in each site quality category, test statistic, *P*-value, proportion of variance explained (% Var.), and effect size (ξ; ES).

Compound	HQ $N = 18$	LQ $N = 24$	Rocks $N = 36$	Statistic	*P*-value	% Var.	ES
Cholesta-5,7-dien-3-ol	0.10 ± 0.27	-0.18 ± 0.15	0.07 ± 0.18	0.31	0.732	0.021	0.146
Ergosterol	-0.02 ± 0.27	-0.18 ± 0.20	0.13 ± 0.16	0.91	0.409	0.030	0.172
Hexadecanoic_acid	0.26 ± 0.16	-0.10 ± 0.21	-0.07 ± 0.19	0.29	0.776	0.047	0.216
Octadecanoic acid	0.11 ± 0.24	-0.19 ± 0.20	0.07 ± 0.17	0.57	0.568	0.030	0.172
Campesterol	0.35 ± 0.13	-0.15 ± 0.23	-0.08 ± 0.18	0.31	0.745	0.044	0.209
Ergosta-5,8-dien-3-ol	0.13 ± 0.29	-0.09 ± 0.18	-0.00 ± 0.16	0.04	0.964	0.012	0.109
Oleic acid	-0.24 ± 0.22	-0.07 ± 0.20	0.17 ± 0.17	0.98	0.301	0.052	0.227
α-Tocopherol	-0.08 ± 0.24	0.16 ± 0.20	-0.07 ± 0.17	0.39	0.670	0.022	0.147
Cholesterol	0.07 ± 0.25	0.05 ± 0.21	-0.07 ± 0.16	0.21	0.816	0.013	0.116
Sitosterol	0.24 ± 0.23	-0.11 ± 0.20	-0.05 ± 0.17	0.49	0.624	0.048	0.218

Table S12. Predictors of per-egg fertilisation success. Summary of model-averaged coefficients for the beta-binomial models excluding eight reproducing males with unknown lipids. Variance inflation factors (VIF) correspond to the saturated model. Standardized coefficients (Std. β) represent the conditionally-averaged effect sizes (change in log-odds per 1 SD predictor) across the subset of top models (ΔAICc < 4), with CI_{95}, *Z*-values, and *P*-values. Relative importance values (RIV) represent the summed Akaike weights across all top models in which each predictor was retained, reflecting their relative support in explaining variation. Bold letters highlight variables with RIV > 0.55 and CI_{95} excluding zero, which are considered strong predictors. "Same-site residency" is a binary indicator of whether male and female occupied the same pallet or stone. "Site-quality combination" is a four-level factor indicating the site-quality assigned to each of the possible female-male pair combinations. For results with the full set of males (imputing lacking lipid values as 0, the mean of the z-distribution) see **Table 2**.

Model					**Model including same-site residency**			
Response	**Predictors**	**VIF**	**Std. β**	**CI_{95}**	***Z***	***P*-value**	***N***	**RIV**
Fertlisation success (per-egg)	**Same-site residency**	**1.04**	**1.59**	**[1.10, 2.09]**	**6.32**	**<0.001**	**44**	**1.00**
	Ergosterol	**1.86**	**–0.66**	**[–1.02, –0.30]**	**3.61**	**<0.001**	**44**	**1.00**
	Oleic acid	1.17	–0.21	[–0.51, 0.09]	1.37	0.172	21	0.47
	Campesterol	1.56	0.19	[–0.15, 0.53]	1.08	0.279	13	0.30
	Dominance Rank Index	1.21	0.05	[–0.06, 0.17]	0.87	0.385	13	0.25
	Cholesta-5,7-dien-3-ol	1.55	0.12	[–0.24, 0.48]	0.66	0.509	12	0.21
	Sitosterol	1.26	0.11	[–0.20, 0.43]	0.70	0.486	12	0.22
	α-Tocopherol	1.24	0.07	[–0.25, 0.40]	0.44	0.657	12	0.19
	Octadecanoic acid	1.32	0.04	[–0.26, 0.33]	0.24	0.808	11	0.17
Model					**Model including parental site-quality combination**			
Response	**Predictors**	**VIF**	**Std. β**	**CI_{95}**	***Statistic***	***P*-value**	***N***	**RIV**
Fertlisation success (per-egg)	**Site-quality combination**	**1.33**	**-**	**-**	**$\chi^2 = 18.94$**	**<0.001**	**31**	**1.00**
	Ergosterol	**1.94**	**–0.57**	**[–0.87, –0.27]**	**$Z = 3.74$**	**0.00018**	**31**	**1.00**
	Oleic acid	1.20	–0.21	[–0.47, 0.05]	$Z = 1.60$	0.109	21	0.66
	Cholesta-5,7-dien-3-ol	1.61	0.15	[–0.16, 0.46]	$Z = 0.97$	0.334	12	0.31
	α-Tocopherol	1.27	0.11	[–0.16, 0.37]	$Z = 0.79$	0.429	9	0.24
	Sitosterol	1.28	0.09	[–0.20, 0.39]	$Z = 0.63$	0.529	9	0.21
	Campesterol	1.63	0.05	[–0.23, 0.33]	$Z = 0.36$	0.716	6	0.13
	Octadecanoic acid	1.37	0.02	[–0.23, 0.28]	$Z = 0.17$	0.867	6	0.14
	Dominance Rank Index	1.39	0.03	[–0.07, 0.13]	$Z = 0.58$	0.562	6	0.16

Table S13. Relationship between hatchling mass at birth and father scent mark composition, including mother clutch size as a covariate. Summary of conditionally averaged coefficients for 208 hatchlings of known parentage. Variance inflation factors (VIF) correspond to the saturated global model. Standardized coefficients (Std. β) represent the conditionally-averaged effect sizes (change in per 1 SD predictor) across the subset of top models (ΔAICc < 4), with CI_{95}, *Z*-values, and *P*-values. Relative importance values (RIV) represent the summed Akaike weights across all top models in which each predictor was retained, reflecting their relative support in explaining variation.

Response	Predictors	VIF	Std. β	CI_{95}	*Z*	*P*-value	*N*	RIV
Hatchling mass	Mother clutch size	1.06	–0.004	[–0.009, 0.001]	1.74	0.081	40	0.68
	Octadecanoic acid	1.68	–0.006	[–0.015, 0.003]	1.33	0.185	26	0.42
	Oleic acid	1.37	0.004	[–0.005, 0.013]	0.90	0.369	19	0.26
	Cholesta-5,7-dien-3-ol	2.10	–0.004	[–0.013, 0.006]	0.72	0.470	16	0.21
	Sitosterol	1.42	0.002	[–0.008, 0.012]	0.44	0.657	15	0.18
	α-Tocopherol	1.38	0.003	[–0.007, 0.012]	0.55	0.583	14	0.18
	Campesterol	1.78	0.003	[–0.008, 0.013]	0.52	0.603	15	0.18
	Ergosterol	2.35	–0.002	[–0.013, 0.008]	0.43	0.666	13	0.16

5. Figures

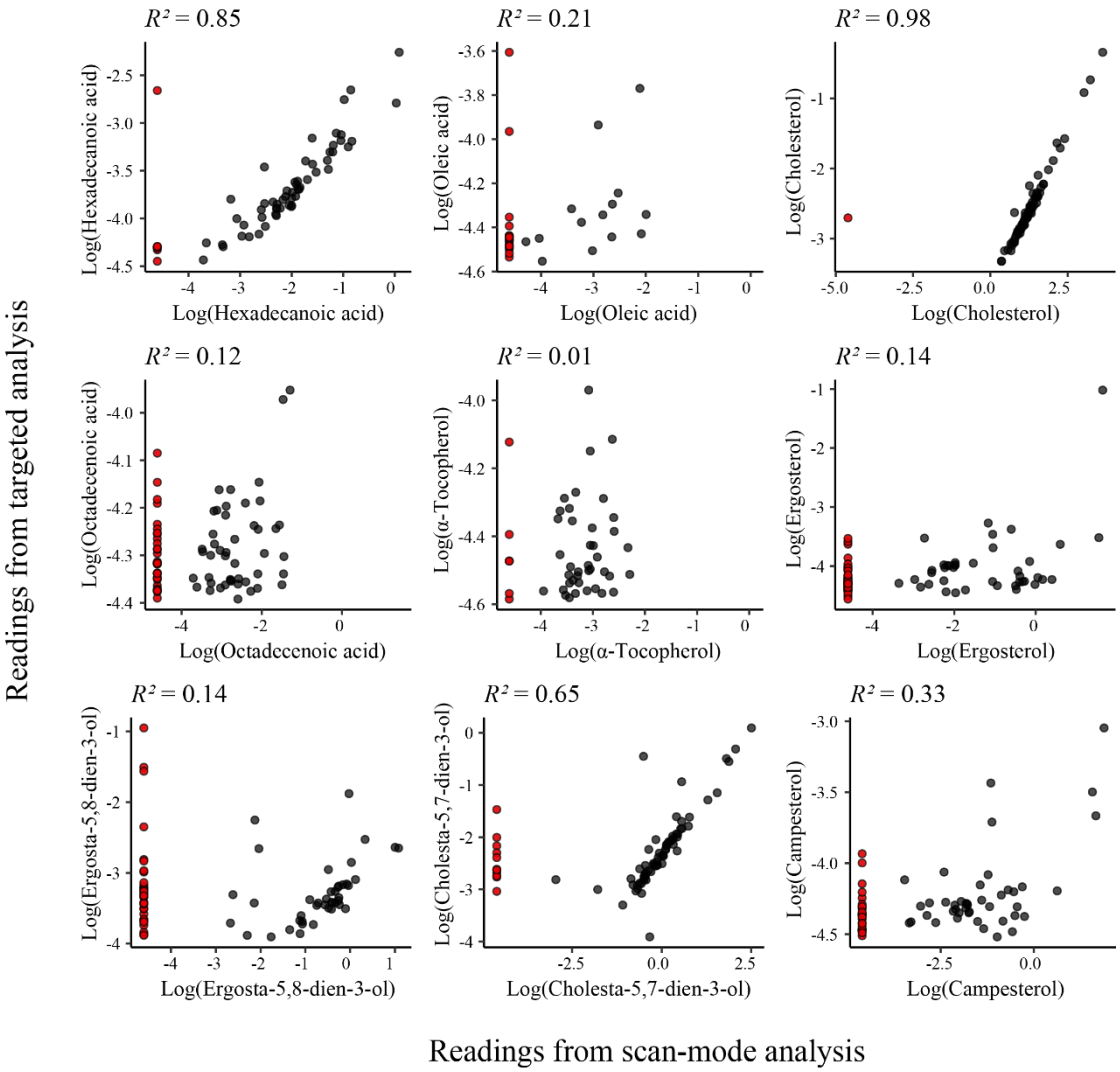

Figure S1. Scatterplots showing the relationship between the logarithm of corresponding concentration levels in the scan-mode (X axis) and targeted analysis (Y axis), for each of the nine repeatedly analysed compounds. Black dots represent readings for the same individual. Blank readings in the scan-mode analysis (in red) have been substituted with zeroes and hence form a column close to the X axis origin. The wide span of these red datapoints in the Y axis suggests that these blank readings do not necessarily correspond to low concentration levels, and hence argues against the common practice of substituting these blank readings from scan-mode analysis with zeroes. R^2 values correspond to Pearson correlation coefficients between non-zero values from the scan mode analysis and corresponding individual readings from the targeted analysis (excluding the red datapoints).

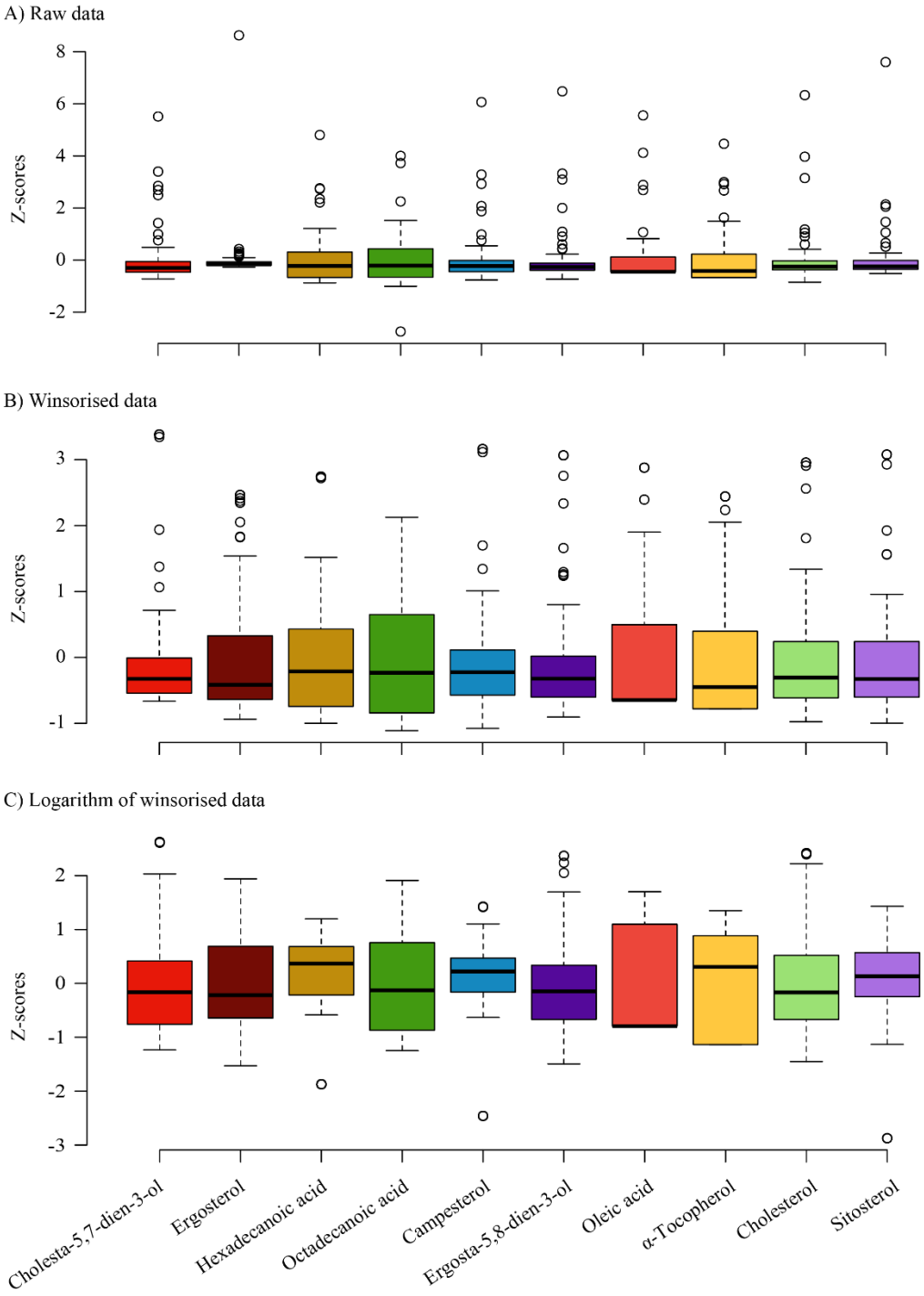

Figure S2. Boxplots showing the distribution of the relative concentration levels (corrected by individual secretion volume) estimated for 10 selected lipidic compounds. All variables have been transformed to z-scores to enable meaningful comparison among variables with differing scales. A) Untransformed readings relative to standard show both positive skew and extreme high-value outliers. B) Winsorized data capped at the 95th percentile. C) Increased normality in the distribution of datapoints after adaptive pseudo-count addition and logarithmic transformation of the winsorized data.

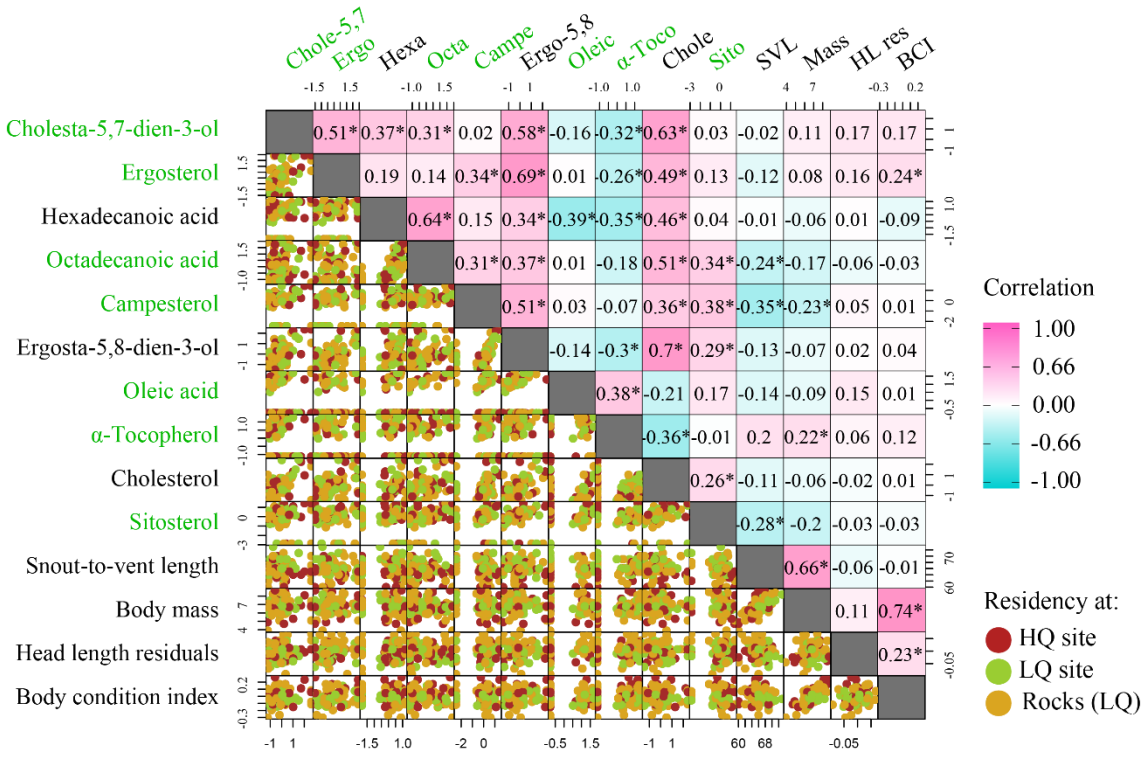

Figure S3. Morphological predictors of male fitness. Correlation plot showing the relationship between the lipidic compound levels examined, and the four morphological variables measured for each individual male. Numbers and gradient cell colour in the upper panel indicate Pearson correlation coefficients, with asterisks representing significant pairwise correlations at the 95% confidence level. Compounds included in the subset showing no pairwise Pearson coefficient higher than 0.6 are indicated in green. Scatter plots in the lower panel correspond to individual datapoints, with colour fill representing alternative throat colours.

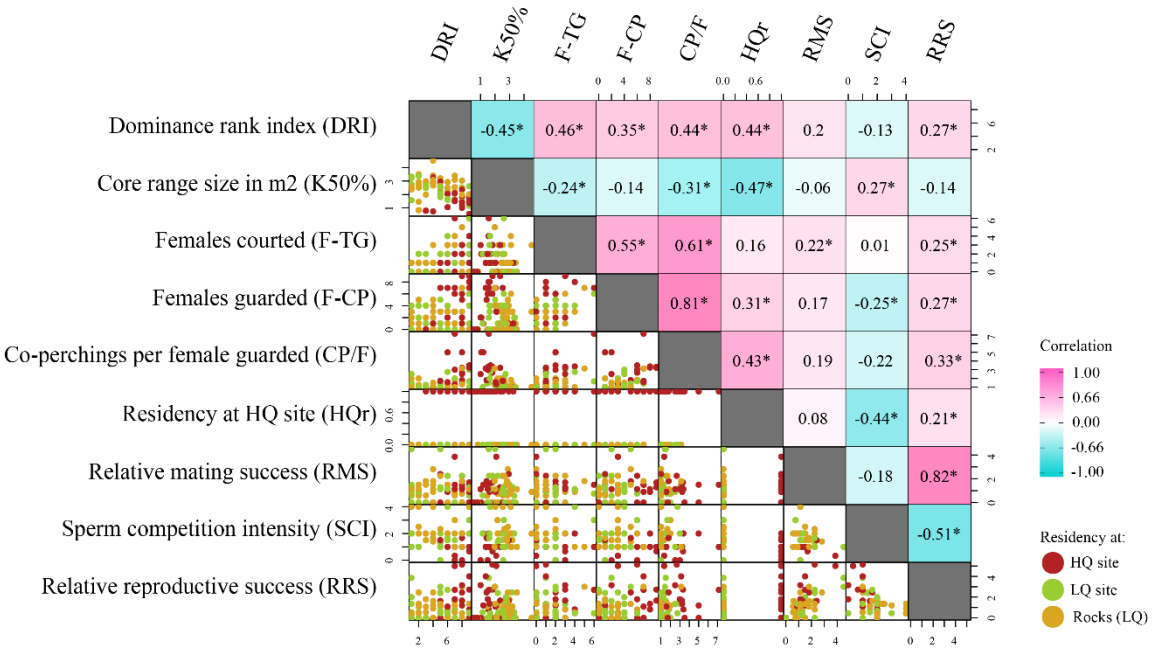

Figure S4. Correlation plot showing the relationship between male dominance rank, socio-spatial behaviour, and fitness variables. Numbers and gradient cell colour in the upper panel indicate Spearman correlation coefficients, with asterisks representing significant pairwise correlations at the 95% confidence level after correction for multiple comparisons. Scatter plots in the lower panel correspond to individual datapoints, with colour fill representing residency status at high-quality sites, low-quality sites, or the rocks in between (also considered low-quality sites).

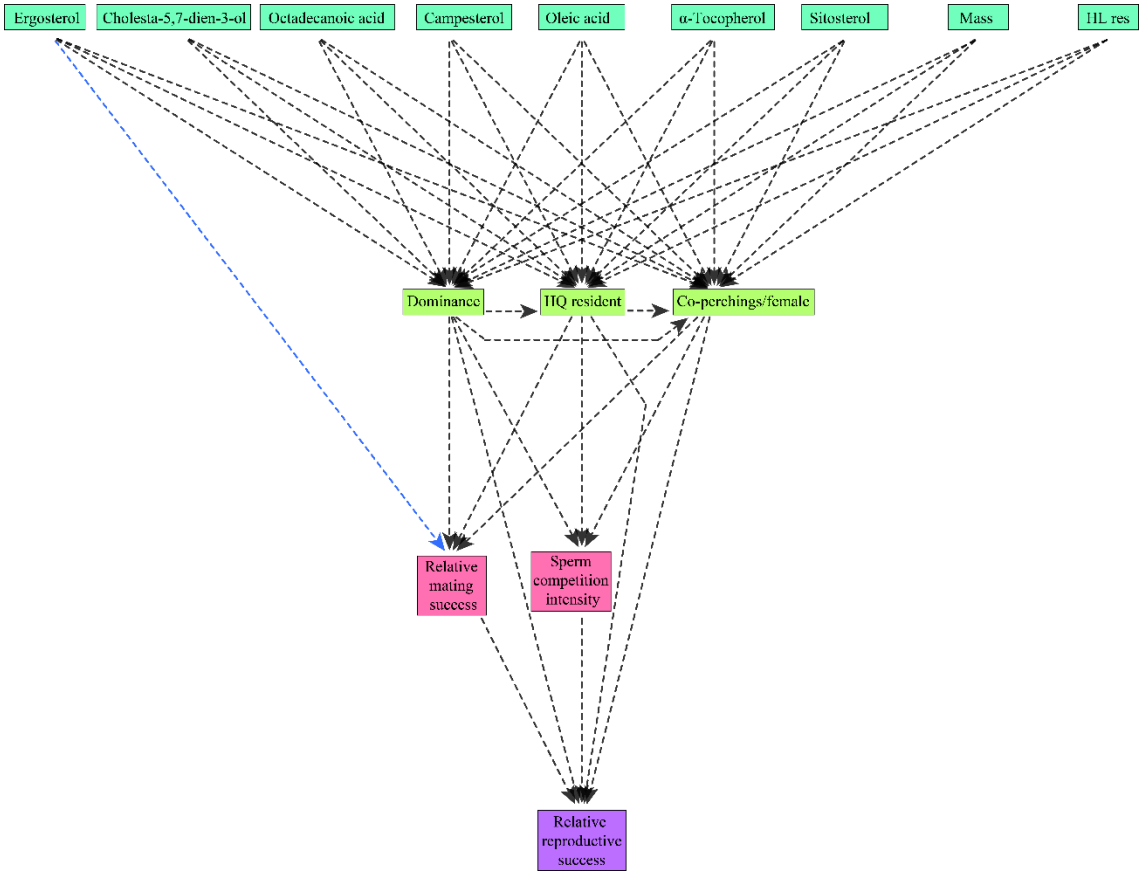

Figure S5. Network of causal pathways fitted in the initial piecewise structural equation modelling (pSEM) procedure, representing the directional hypotheses relating morphological predictors, scent mark composition, socio-spatial behaviour, and relative reproductive fitness in male *Podarcis muralis*. Black arrows indicate paths specified in the original model formula. The blue arrow was added based on significant results from tests of *d*-separation. Additionally, a second model excluding sperm competition intensity (SCI) was run to assess its influence on the network.