# Synthesis of nature's extravaganza: an augmented meta-meta-analysis on (putative) sexual signals

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## Abstract

Why have conspicuous characteristics evolved? Our augmented meta-meta-analysis of 41 meta-analyses, encompassing 375 animal species and 7,428 individual effect sizes, shows that the conspicuousness of (putative) sexual signals is positively related to attractiveness and benefits to mates, as well as to the fitness, condition, and other traits (e.g. body size) of their bearers. These patterns are often consistent across taxa and seen in both sexes with a similar magnitude. Further, the strength of sexual selection on conspicuousness is positively associated with the relationship between conspicuousness and both benefits and individual condition, but not with other traits. Our study unifies several decades of knowledge on conspicuous traits, provides new insights about them, and lays a clear path for the future of this topic.

## Main text

Extravagant body parts and elaborate behaviours that apparently are not used to deter predators (e.g. aposematic traits) or to fight (e.g. weapons) have intrigued biologists for more than a century precisely because natural selection can rarely explain their evolution (*1*). These odd traits should be particularly conspicuous to conspecifics (hereby *conspicuous traits;* but see Supplementary material), even though some of them might be unnoticeable to us (e.g. pheromones, electromagnetic fields). The usual explanation for the existence of these conspicuous traits is that more noticeable individuals can attract more or better mates, generating sexual selection for greater trait conspicuousness via mate choice (*1–3*). Consequently, conspicuous traits are often deemed "sexual ornaments" or "sexual signals", especially if they are sexually dimorphic (*4*). Unsurprisingly, mate choice and sexual signals became popular topics within the sexual selection literature, culminating in the development of many theoretical models attempting to explain their evolution [reviewed in (*5*)]. Despite varying their expectations, these models usually predict that sexual signal conspicuousness increases the fitness of their bearers (e.g. by making them more attractive) and of their mates by signalling direct (in the same generation, with resources or good parenting) or indirect benefits (in subsequent generations, enhancing offspring fitness with greater viability - "good genes" - or attractiveness - "sexy genes") (*2, 5, 6*). The theory also predicts that sexual signal conspicuousness is condition-dependent as it ensures signal honesty (*6*) and that sexual signal conspicuousness covaries with the expression of other traits that can also represent benefits to prospective mates (e.g. body size, social dominance, traits related to sperm competition).

The veracity of the propositions above has been tested in the last 70 years by numerous empirical studies and, more recently, by various meta-analyses [reviewed in (*4*)]. However, our knowledge of conspicuous traits assumed to be sexual signals remains fragmented and far from satisfactory because studies (including meta-analytical ones) focus on one or few variables [e.g. parasite load (*7*); survival (*8*)], types of conspicuous traits [e.g. colourful plumage (*9, 10*); song traits (*11, 12*)], taxa [e.g. birds (*8, 13–16*)], and sex [e.g. males (*17–19*)]. The last one is particularly emblematic because most of the theory regarding sexual signals has been developed considering only males as their bearers, even though females possess conspicuous traits in many species (*20*) and males can express mate choice (*21*). Moreover, researchers often assume that conspicuous traits they investigate are attractive to prospective mates without evidence, potentially mixing sexual signals with other non-sexually selected traits and thus possibly drawing misleading conclusions on the evolution of conspicuous traits.

To resolve these outstanding issues and to provide a unified knowledge of (putative) sexual signals, we compiled and analysed 7,428 effect sizes from 1,196 empirical studies (used as data sources by 41 meta-analyses; i.e. second-order meta-analysis augmented with additional data) that investigate the relationship between these conspicuous traits and attractiveness, benefits to mates, and their bearers' fitness, individual condition, and other traits (Table S1; Fig. 1), comprising 375 animal species in total (Fig. 2). We also verified the role of two moderators in these relationships: sex (males *vs.* females) and trait type (behaviours, available only for males in our dataset, hereby *flexible traits, vs.* colour and morphology, hereby *fixed traits*). Furthermore, we test an implicit assumption commonly made by biologists that has never been systematically tested: that the strength of pre-copulatory sexual selection (from mate choice) on the conspicuousness of a trait is linked to the strength of the relationship between the conspicuousness of that trait and the benefits it signals (*22, 23*), and by extension to the relationship between the conspicuousness of that trait and the fitness, condition, and other traits of its bearer.

### Is the conspicuousness of putative sexual signals associated with attractiveness to prospective mates?

Empiricists commonly take different measurements from one or more conspicuous traits of individuals of a given species (Pollo et al. *in prep.*). They then verify the relationship between these measurements and success in mate choice trials or mating success in the field, which should roughly represent the strength of pre-copulatory sexual selection on conspicuous traits. Using this type of data, we found that putative sexual signal conspicuousness is, on average, (moderately) positively related to attractiveness to individuals of the opposite sex ($r = 0.329$, CI = 0.233 to 0.419; Table S2; Fig. 3). This result is consistent across species given the low heterogeneity at the level of species ($I^2_{[\text{species = species ID + phylogeny}]} = 2.3\%$) and therefore potentially generalisable, despite the high overall heterogeneity across effect sizes ($I^2_{\text{total}} = 91.5\%$; Table S3). Moreover, we found that the association between attractiveness and conspicuousness of male flexible putative sexual signals is greater than that of female fixed putative sexual signals (Table S4).

### Is the conspicuousness of putative sexual signals associated with benefits to their bearers and to their mates?

We found that putative sexual signal conspicuousness is, on average, (weakly) positively related to benefits to their bearers and to their mates ($r = 0.165$, CI = 0.133 to 0.197; Table S2; Fig. 3). However, we detected publication bias for these data, so the actual relationship might be even weaker as positive effect sizes were overrepresented (Fig. S1D-F, Table S6). This finding is potentially consistent across species ($I^2_{[\text{species = species ID + phylogeny}]} = 0.7\%$; Table S3). Furthermore, we found that males show, on average, a stronger relationship between putative sexual signal conspicuousness and benefits compared with females (Table S4). We note that these results come from an amalgamation of metrics (Fig. 1), so we discuss each of them in detail below.

First, more conspicuous putative sexual signals are, on average, (moderately) associated with earlier arrival at breeding sites, earlier pairing, or earlier reproduction (hereby simply *earlier timing*; $r = 0.213$, CI = 0.171 to 0.254; Table S2; Fig. 3). Earlier timing can represent individual quality and attractiveness, and may lead to more reproductive opportunities and a better environment for the offspring (*24*). We also found that the relationship between timing and putative sexual signal conspicuousness is stronger in males than in females (Table S4).

Second, putative sexual signal conspicuousness is, on average, (weakly) positively related to reproductive success (e.g. number of offspring; $r = 0.157$, CI = 0.121 to 0.193; Table S2; Fig. 3). Various mechanisms can produce a positive relationship between reproductive success and putative sexual signal conspicuousness. For instance, if individuals with traits that are more conspicuous are more attractive, these individuals should experience greater mating success and consequently increase their reproductive success if mating with multiple individuals is advantageous [i.e. when Bateman's gradient is positive, generally assumed for males but rarely for females (*25*)]. Moreover, individuals with more conspicuous sexual signals might be more likely to select mates that can provide them with more benefits (*21*), increasing their own fitness. Individuals with more conspicuous sexual signals may also receive greater reproductive investment from their partners than their counterparts (*26*). On the other hand, a positive relationship between sexual signal conspicuousness and reproductive success can arise from a positive association between putative sexual signal conspicuousness and (female) fecundity [e.g. (*27, 28*)] or reproductive investment beyond just gametes (e.g. parental care, see below), which would make these conspicuous traits signals of direct benefits to mates. Although we cannot determine which of these mechanisms more frequently explains why individuals with more conspicuous putative sexual signals show greater reproductive success, future studies should address this gap. We also note that the conspicuousness of flexible putative sexual signals is more strongly associated with reproductive success than that of fixed putative sexual signals (for males and females alike; Table S4).

Third, putative sexual signal conspicuousness is, on average, (weakly) positively related to offspring viability (e.g. proportion of eggs hatched) or quality (e.g. offspring size) ($r = 0.164$, CI = 0.123 to 0.205; Table S2; Fig. 3). More conspicuous sexual signals may indicate that their bearers possess "good genes" that can be passed to the offspring, possibly increasing offspring's viability and quality (*2*). However, the same arguments made for reproductive success (e.g. greater reproductive effort from partners) also apply to offspring's viability or quality because they result from genes and investment in the offspring from both parents.

Fourth, putative sexual signal conspicuousness is, on average, (weakly) positively related to greater extra-pair paternity and lower cuckoldry (collectively simply *paternity*; $r = 0.149$, CI = 0.092 to 0.204; Table S2; Fig. 3). While this relationship might occur because more ornamented males are more attractive (i.e. paternity may simply reflect male mating success or be a product of cryptic female choice favouring sperm from attractive males), it is also possible that more ornamented males obtain greater paternity when their conspicuous putative sexual signals signal sperm traits that increase success in sperm competition (*29*).

Fifth, putative sexual signal conspicuousness is, on average, (weakly) positively related to parental care ($r = 0.08$, CI = 0.022 to 0.136; Table S2; Fig. 3). This is perhaps the clearest evidence that conspicuous traits can signal direct benefits to mates. Still, this relationship might be complex in systems with biparental care if sexual signals from both parents affect parental care performed. This scenario becomes even more complicated when parental care provided by an individual can be modulated by the parental care provided by their social partner (*10*).

Sixth, putative sexual signal conspicuousness is, on average, (moderately) positively related to territory quality ($r = 0.241$, CI = 0.162 to 0.317; Table S2; Fig. 3). Given that territory quality represents resources that individuals use for their survival and reproduction, greater territory quality should enhance the fitness of the territory's owner as well as of their mates. Unfortunately, our dataset had no information for females regarding this relationship, revealing a dire need to investigate species in which females defend territories [e.g. (*30*)].

## Is the conspicuousness of putative sexual signals associated with the individual condition of their bearers?

We found that putative sexual signal conspicuousness is, on average, (weakly) positively related to distinct measures of individual condition ($r = 0.174$, CI = 0.124 to 0.224; Table S2; Fig. 4). Yet, this result can be overestimated as we found evidence of publication bias for these data (Fig. S1G-I; Table S6). Once more, this result is potentially generalisable across taxa ($I^2_{[\text{species = species ID + phylogeny}]} = 6.1\%$; Table S3). Moreover, we found that males show, on average, a stronger relationship between fixed putative sexual signal conspicuousness and individual condition compared with females (Table S4).

Individual condition can be measured in many ways (Fig. 1), so we also verified the relationship between each individual condition proxy and putative sexual signal conspicuousness separately. First, putative sexual signal conspicuousness is, on average, (moderately) positively associated with beneficial (external) conditions (e.g. better diet, lower reproductive effort, etc.; r = 0.263, CI = 0.215 to 0.31; Table S2; Fig. 4). Second, putative sexual signal conspicuousness is, on average, (weakly) positively associated with body condition [e.g. body mass controlled for structural body size (*31*); r = 0.198, CI = 0.161 to 0.235; Table S2; Fig. 4]. Yet, conspicuousness of fixed putative sexual signals is, on average, more strongly associated with body condition in males than in females (Table S4). Third, putative sexual signal conspicuousness is, on average, (weakly) positively associated with immune or antioxidant capacity (r = 0.129, CI = 0.084 to 0.174; Table S2; Fig. 4). Fourth, putative sexual signal conspicuousness is, on average, (weakly) positively associated with parasite resistance (i.e. opposite of parasite load; r = 0.119, CI = 0.078 to 0.159; Table S2; Fig. 4). Fifth, putative sexual signal conspicuousness is, on average, (weakly) positively associated with survival (r = 0.113, CI = 0.053 to 0.172; Table S2; Fig. 4). However, the relationship between putative sexual signal conspicuousness and survival was greater for males than for females, with the latter being essentially zero (Table S2; Table S4; Fig. 4).

Two hypotheses in the literature explain how condition-dependent sexual signals represent honesty: the costly signalling principle [first proposed by (*32*)] and the index hypothesis [e.g. (*33*)]. The former states that the expression and maintenance of sexual signals require resources that could be spent elsewhere (*32*), with higher-quality individuals being expected to deal more effectively with metabolic trade-offs and thus being able to be more ornamented (*34, 35*). On the other hand, the index hypothesis does not invoke resource trade-offs to explain sexual signals' condition-dependency, but rather posits that these traits evolve as honest signals of condition by sharing pathways with basic physiological processes (*36–38*). These hypotheses are contentious as each has different underlying concepts, with multiple authors proposing distinct features and predictions [see (*39*)]. Our results support that (putative) sexual signal conspicuousness is, on average, condition-dependent, but we cannot elucidate which of these two hypotheses is more likely to explain this pattern.

### Is the conspicuousness of putative sexual signals associated with the expression of other traits of their bearers?

We found that putative sexual signal conspicuousness is, on average, (moderately) positively related to body size (r = 0.23, CI = 0.144 to 0.312; Table S2; Fig. 4), an apparently generalisable finding across species ($I^2_{[\text{species = species ID + phylogeny}]} = 3.6\%$; Table S3). Body size can be under positive directional selection if larger individuals are more fecund (*40*) or experience greater success in intrasexual competition (*2*). Given that sexual signal conspicuousness is also predicted to be under positive directional sexual selection (*41*), a positive relationship between sexual signal conspicuousness and body size can occur. In such a scenario, trait conspicuousness would signal direct benefits to prospective mates. However, larger body size can be constrained or even disfavoured in some taxa [e.g. (*42*)], so this rationale is not universal.

We found that putative sexual signal conspicuousness is, on average, (moderately) positively related to aggression and social dominance (e.g. greater number of aggressive behaviours performed to hetero- and conspecific intruders; r = 0.205, CI = 0.047 to 0.354; Table S2; Fig. 4). However, this result is not as generalisable across species as our other findings ($I^2_{[\text{species = species ID + phylogeny}]} = 14.6\%$; Table S3). Greater trait conspicuousness then may signal one's status to others interested in battling for resources, ultimately deterring costly fights (*43*). Note that, *a priori*, if these resources are not mates, these signals have no connection to sexual selection, highlighting that conspicuous traits might not necessarily be sexual signals. Yet, conspicuous traits that signal to rivals can also be used for mate selection, even if this is not their primary function. After all, greater success in competition for resources should be related to greater access to resources, meaning possible benefits to mates (e.g. territory quality, more competitive offspring if heritable).

We found that putative sexual signal conspicuousness is, on average, (weakly) positively related to the expression of traits that increase success in sperm competition (e.g. more or better sperm, larger testes; r = 0.107, CI = 0.029 to 0.185; Table S2; Fig. 4). This result appears to be generalisable across taxa, but not across studies ($I^2_{[\text{species = species ID + phylogeny}]} = 1.2\%$, $I^2_{\text{across-studies}} = 43\%$; Table S3). Highly ornamented males could be wasting resources by investing in traits related to sperm competition if, being more attractive, they can experience a lower risk of sperm competition by biassing cryptic female choice in their favour [e.g. (*44*)] or reducing the chances that females they mate with remate with another male [e.g. (*45*)]. However, traits that enhance sperm competition success are potentially under positive directional selection for all males [(*46*); but see (*47*)], and thus may be expected to covary with sexual signal conspicuousness. Alternatively, this pattern can occur if male ornamentation honestly signals their fertilisation ability to females (*46*). Interestingly, we also detected that flexible putative sexual signals were more strongly related to the expression of sperm competition-related traits than fixed putative sexual signals (Table S4).

Lastly, we found that putative sexual signal conspicuousness is, on average, (weakly) positively related to age (r = 0.196, CI = 0.043 to 0.34; Table S2; Fig. 4), a result that may be generalisable across species ($I^2_{[\text{species = species ID + phylogeny}]} = 7.4\%$; Table S3). Sexual signal conspicuousness should increase with age [but see (*48*)] as older individuals are under greater terminal investment selection [i.e. to increase reproductive effort before dying (*49, 50*)]. Moreover, when sexual signal conspicuousness is positively related to age, trait conspicuousness essentially signals individual ability to survive for longer (*51*). We note, however, that our results regarding age might be conflated by mating experience (i.e. older individuals are more likely to have mated than their younger counterparts), although a meta-analysis controlling for this showed a similar result (*48*).

### Is the strength of sexual selection on the conspicuousness of a trait associated with the relationship between the conspicuousness of the same trait and other variables?

The relationships between conspicuous traits and multiple variables we explored in previous sections involved traits *assumed* to be preferred by mates (i.e. putative sexual signals). Still, these traits could actually be unattractive to mates or attractive in the opposite direction than the one predicted (e.g. mates prefer dull colours instead of vivid colours). To provide insights into sexual signals, we sought putative sexual signals in our dataset for which we had two pieces of information: how their conspicuousness was related to attractiveness to mates and how their conspicuousness was related to other variables within our framework (e.g. benefits, individual condition, etc.; Fig. 1). For each putative sexual signal of each species, we calculated an overall effect size for the former (hereby *Zr-attractiveness*) and an overall effect size for the latter (hereby *Zr-benefits*, *Zr-condition*, etc.). We then were able to perform meta-regressions to verify how the strength of sexual selection on a putative sexual signal (i.e. Zr-attractiveness) relates to the strength of the association between the conspicuousness of that putative sexual signal and either benefits (Zr-benefits), individual condition (Zr-condition), or other traits (Zr-size, Zr-dominance, Zr-sperm, Zr-age).

We found that sexual selection on putative sexual signal conspicuousness is positively associated with the relationship between putative sexual signal conspicuousness and both the benefits they provide (Fig. 5A; Fig. S3A) and bearers' individual condition (Fig. 5B; Fig. S3B; Table S7). However, we found no evidence that sexual selection on putative sexual signal conspicuousness is associated with the relationship between putative sexual signal conspicuousness and other traits (Fig. 5C-F; Fig. S3C-E; Table S7). Nonetheless, data for these analyses were scarce, so these results require extra caution as they might not be generalisable.

Theory predicts that mate choosiness, and thus pre-copulatory sexual selection, increases with variation in mate quality (*22, 23*). Therefore, the positive relationship we found between Zr-attractiveness and Zr-benefits is expected, but what about other variables? It seems plausible that greater sexual selection on conspicuousness intensifies its condition-dependence as an escalation of honest signalling (generating the positive relationship between Zr-attractiveness and Zr-condition we found). By contrast, the relationship between conspicuousness and other traits might be more variable because greater body size, social dominance, expression of traits related to sperm competition, and age may lead to benefits to their bearers only in certain situations. Perhaps the most valuable insight from these results is that even when Zr-attractiveness is zero or negative (representing mate preference for lower conspicuousness), other relationships between conspicuousness and distinct variables (e.g. Zr-benefits, Zr-condition) can be positive (and vice-versa). This means that researchers should not assume that positive relationships between putative sexual signal conspicuousness and different variables attest that they are, indeed, sexually selected.

### Future opportunities for research on putative sexual signals

Given that the relationship between the conspicuousness of putative sexual signals and attractiveness to mates represents the core of the theory on mate choice, and that our dataset represents the information collected by most meta-analyses on putative sexual signals, it is astonishing that this relationship was available for only a quarter of the species (Fig. 2) and represented less than 8% of all effect sizes in our dataset. The scarcity of data on attractiveness suggests that biologists may inspect associations between conspicuous traits and their potential benefits or costs without attesting to the attractive function of these traits in the first place. However, we remind researchers that conspicuous traits can serve purposes other than mate attraction, such as to signal status to conspecifics regardless of sex (see previous sections), to deter (*52*) or confuse predators (*53, 54*), or to avoid sexual harassment (*55*). Therefore, it is imperative to first examine the primary function of conspicuous traits, as making assumptions about them can hamper our knowledge about their evolution.

In addition to the dismal amount of information related to the attractiveness of conspicuous traits, our dataset contains other limitations inherited from the primary meta-analyses that we used as sources, which largely represent deficits in the literature on sexual selection (*4*). More specifically, most meta-analyses that we collected data from focus on bird colouration [e.g. (*8–10, 13–18, 56–65*)], resulting in a dataset where other traits and animal groups (e.g. invertebrates) are underrepresented (Figs. S4 and S5). Notably, female behaviours as putative sexual signals were almost absent from our dataset despite being ubiquitous in nature [e.g. pheromones; (*66*)] and potentially subjected to sexual selection (*67*), possibly leading to similar patterns to the ones we found for other putative sexual signals [e.g. condition-dependence, (*68*)]. Although more data may have become available after the primary meta-analyses we used as data sources were published (i.e. data not included in our dataset), information on female behavioural sexual signals and other neglected topics likely remains scarce. Collecting data on overlooked traits and taxa should address these gaps and may even challenge our perceptions, such as of stereotypical sex roles (*69–71*). However, stronger incentives may be necessary to achieve this goal (*4*).

While our study represents a solid advancement for the theory of sexual selection by testing many of its predictions, and most of our results appear consistent across taxa, we stress that conspicuous traits in nature are extremely diverse. This means that existing and future primary studies and meta-analyses on sexual signals remain valuable if they provide in-depth investigations on factors that are unique to certain conspicuous traits [e.g. type of pigment for colourful traits; (*57*)]. More importantly, the diversity we see in nature reinforces the urgency in acquiring data beyond certain conspicuous traits and taxonomic groups. Failing to do so risks leaving us with biassed and stagnant evidence, dimming the spark that Darwin ignited over 150 years ago.

## Acknowledgements

We thank László Zsolt Garamszegi, Sarah Guindre-Parker, América Hernández Martínez, and Tim Parker for sending us data from their meta-analyses. We also thank Yong Zhi Foo for contributing to the conceptualisation of this project and both Russell Bonduriansky and Michael Kasumovic for feedback on the manuscript.

## Funding

ARC (Australian Research Council) Discovery Project grants DP210100812 and DP230101248 (PP, ML, YY, SN)

Canada Excellence Research Chair Program CERC-2022-00074 (SN)

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) as part of the Programa de Desenvolvimento da Pós-Graduação PDPG 88887.803974/2023-00 (RCMR)

## Author contributions

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Formal analysis: PP

Funding acquisition: SN

Investigation: PP, ML, RCMR, AM, YY, SN

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Project administration: PP

Software: PP

Supervision: SN

Visualisation: PP

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Writing – review & editing: PP, ML, RCMR, AM, YY, SN.

## Competing interests

We declare no competing interests.

## Data and code availability

All data and code used in this study are available at: https://osf.io/6njem/?view_only=7b01538fb32e4f78b7130b6e8f303649.

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# Figures

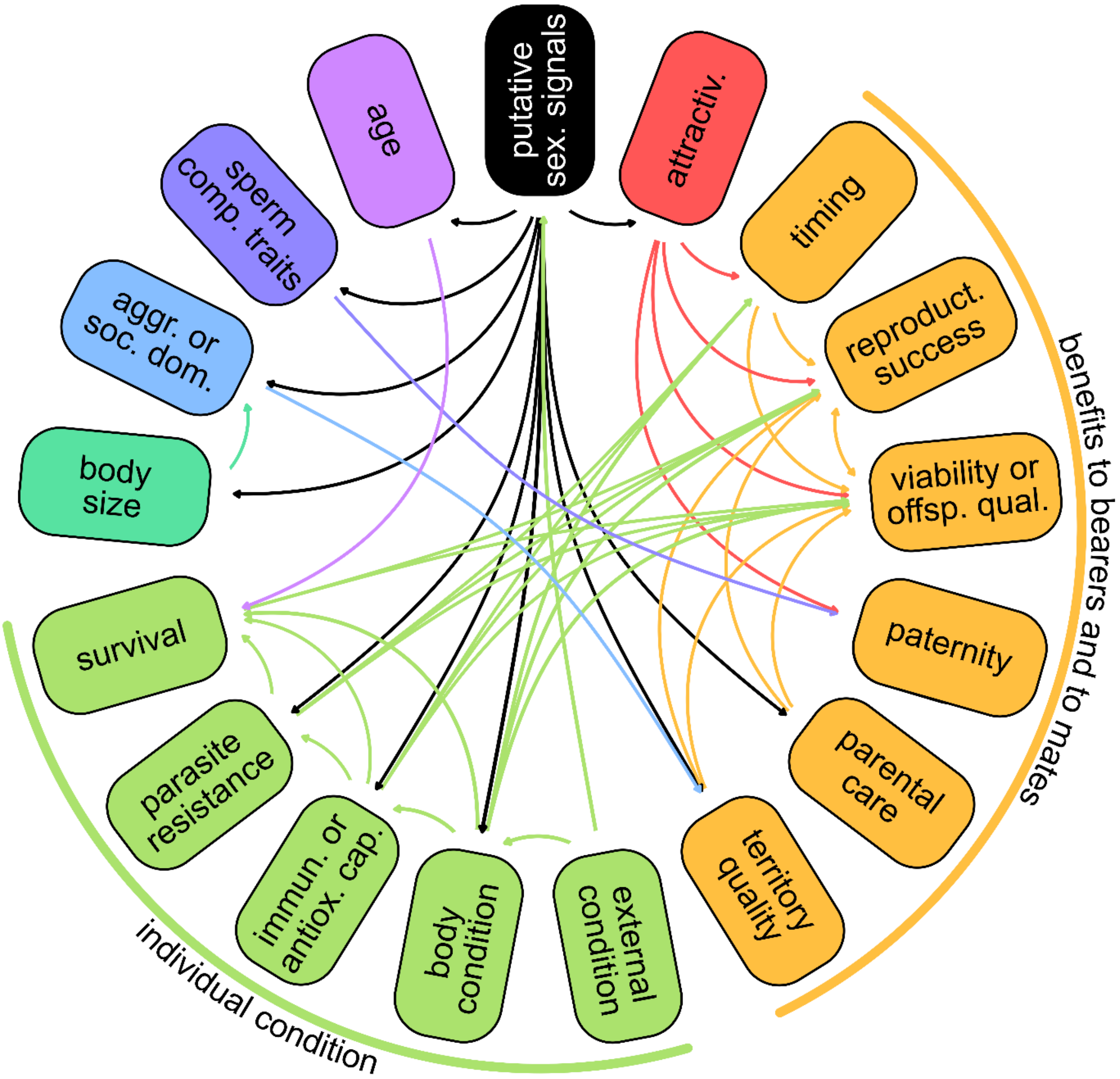

**Figure 1**. Framework for the relationship between putative sexual signals and different variables (clockwise from the top): conspicuousness of putative sexual signals, attractiveness, benefits to bearers and to mates (timing, reproductive success, viability or offspring quality, paternity, parental care, territory quality), individual condition (external condition, body condition, immunological or antioxidant capacity, parasite resistance, survival), body size, aggression or social dominance, traits related to sperm competition, and age (see also Table S1). Arrows represent that a variable potentially influences or signals another variable (see text for details).

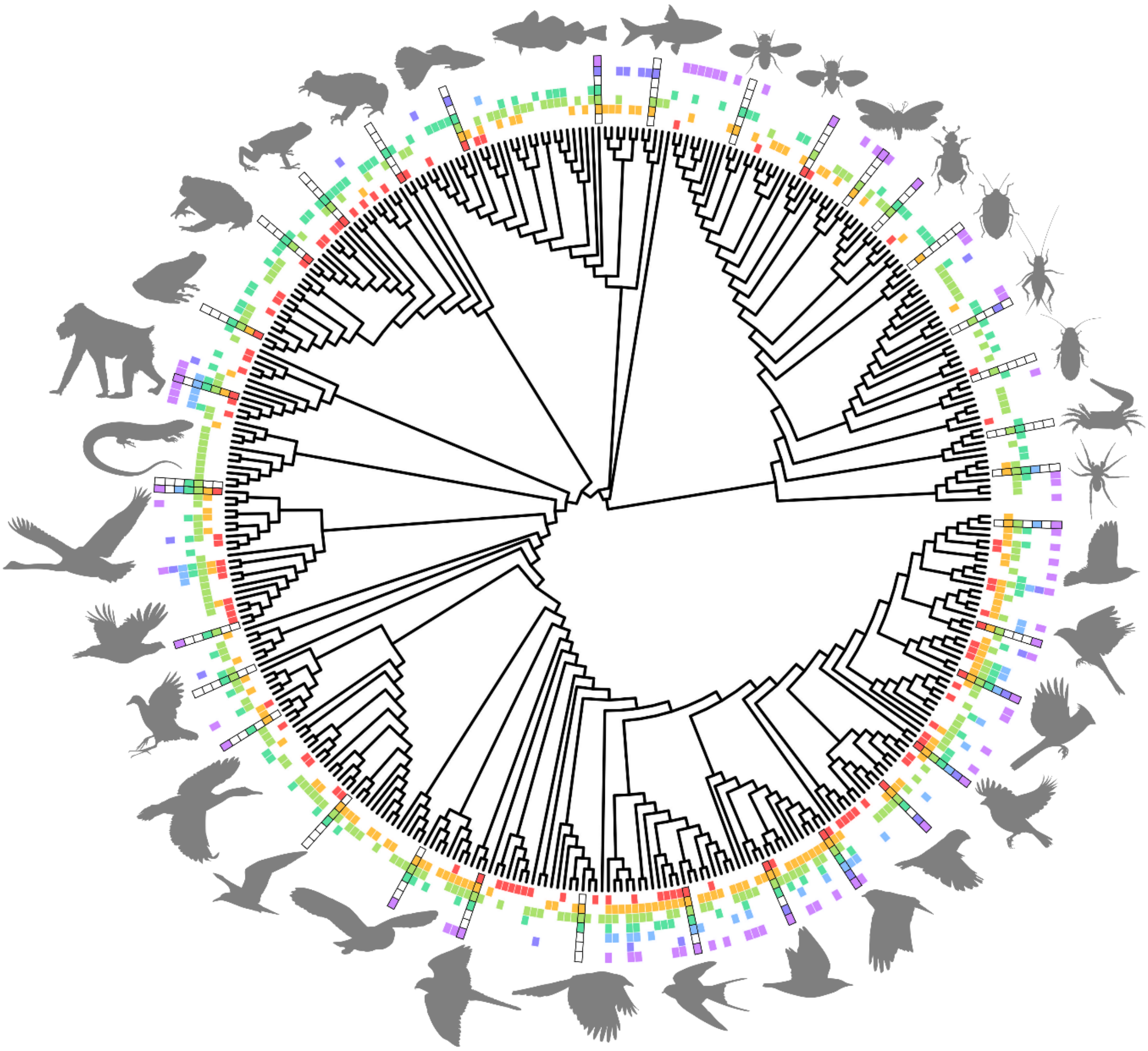

**Figure 2**. Phylogeny of the 375 animal species present in our dataset. Each ring around the phylogenetic tree indicates the existence (colourful cells) or absence (blank cells) of data on the relationship between the conspicuousness of one or more putative sexual signals of a given species and a variable assessed in our study (red: attractiveness, orange: benefits to bearers and to mates, green: individual condition, aquamarine: body size, blue: aggression or social dominance, indigo: traits related to sperm competition, violet: age). Silhouettes represent species whose nearby cells have black edges.

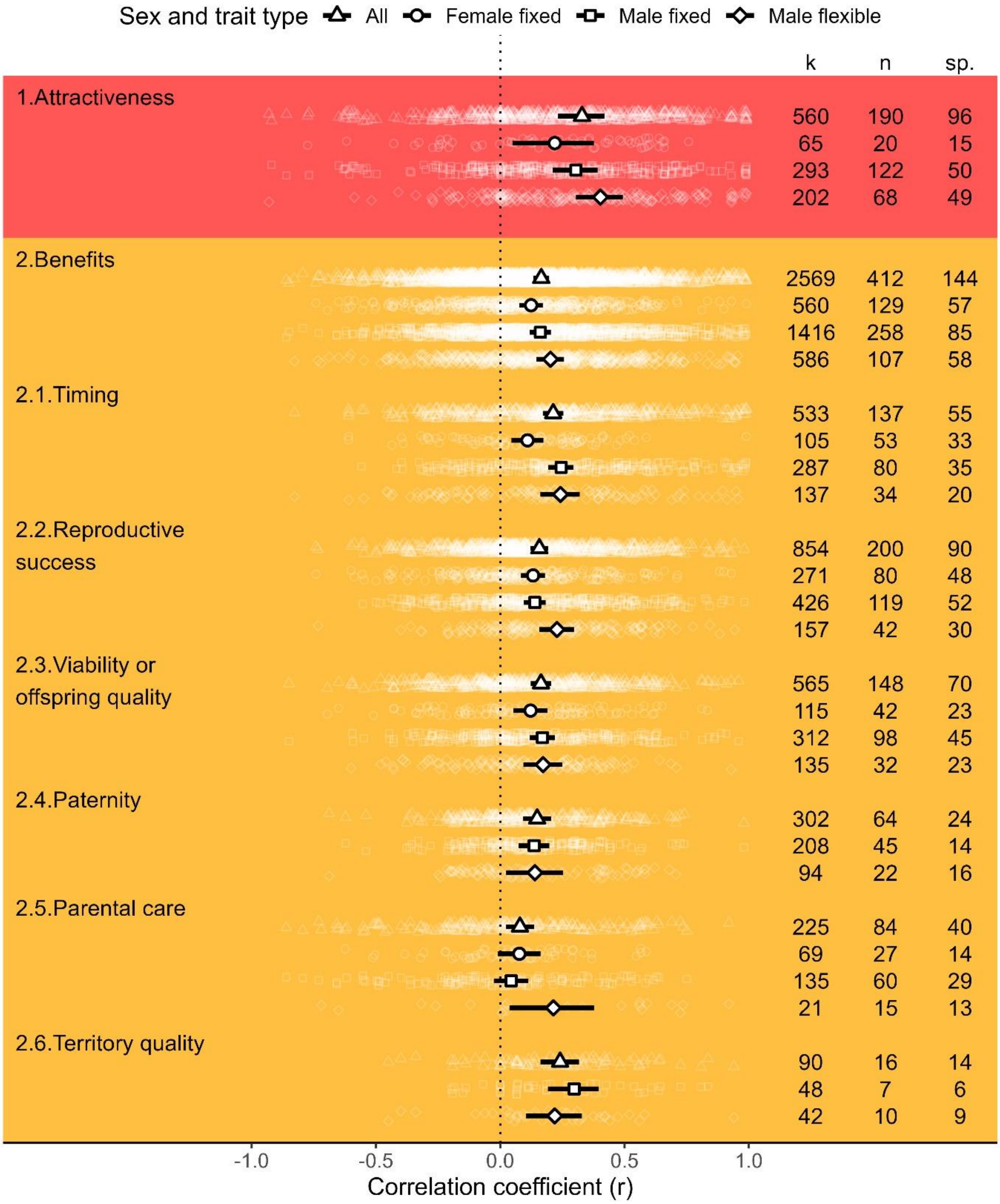

Figure 3. Mean effect sizes for relationship between the conspicuousness of putative sexual signals and their bearers' attractiveness (red zone) and benefits (to bearers and to their mates; orange zone). Variance explained by fixed factors in these models (marginal $R^2$) were, respectively, 2.3% and 4.1% (see Table S5). The vertical black dotted line highlights zero (no relationship). k, n, and sp. represent, respectively, the number of effect sizes, empirical studies, and species for each set.

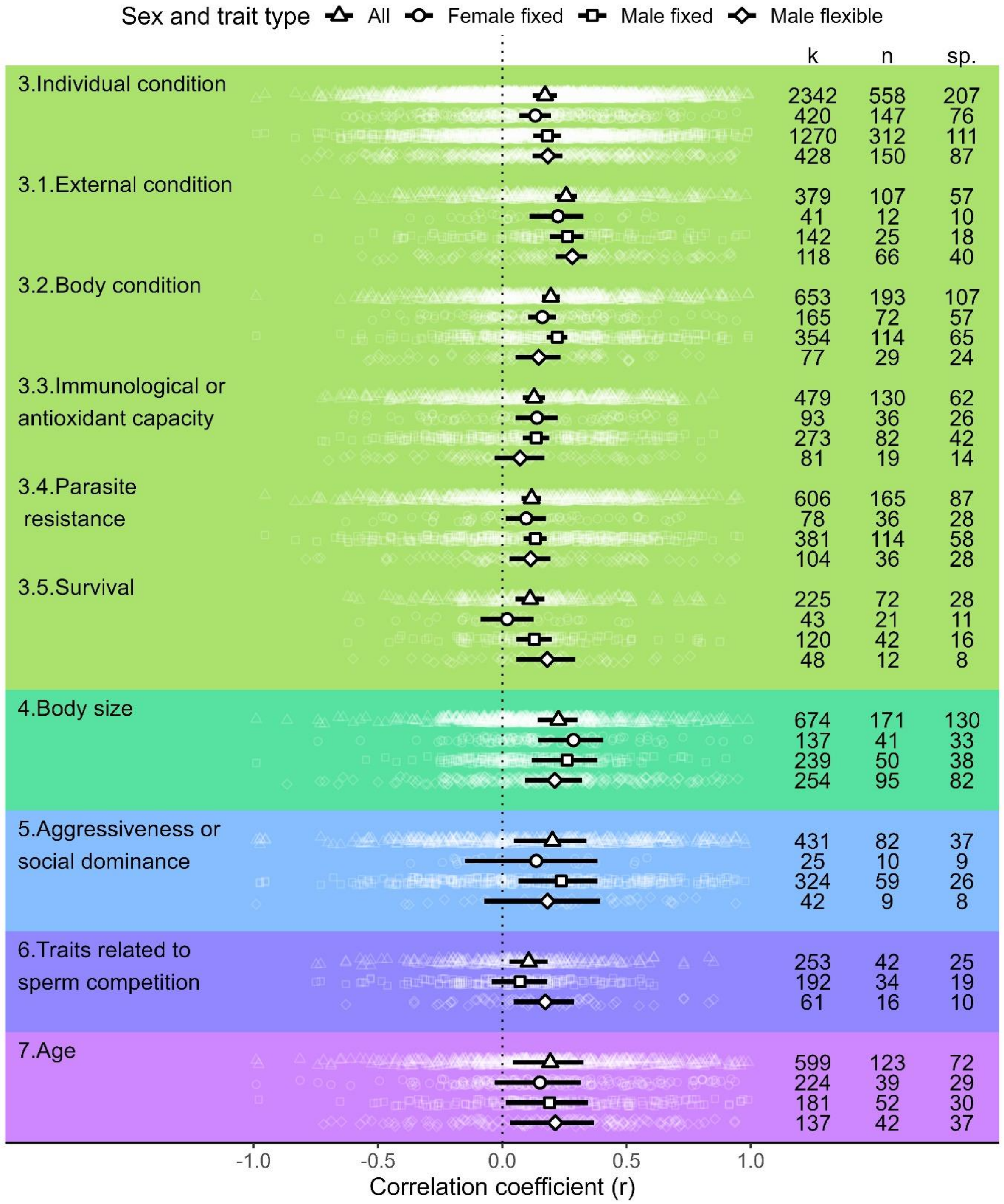

**Figure 4**. Mean effect sizes for the relationship between the conspicuousness of putative sexual signals and their bearers' condition, body size, aggressiveness or social dominance, traits related to sperm competition, or age. Variance explained by fixed factors in these models (marginal $R^2$) were, respectively, 4.9%, 1.2%, 1.9%, 3.3%, and 0.5% (see Table S5). k, n, and sp. represent, respectively, the number of effect sizes, empirical studies, and species for each set.

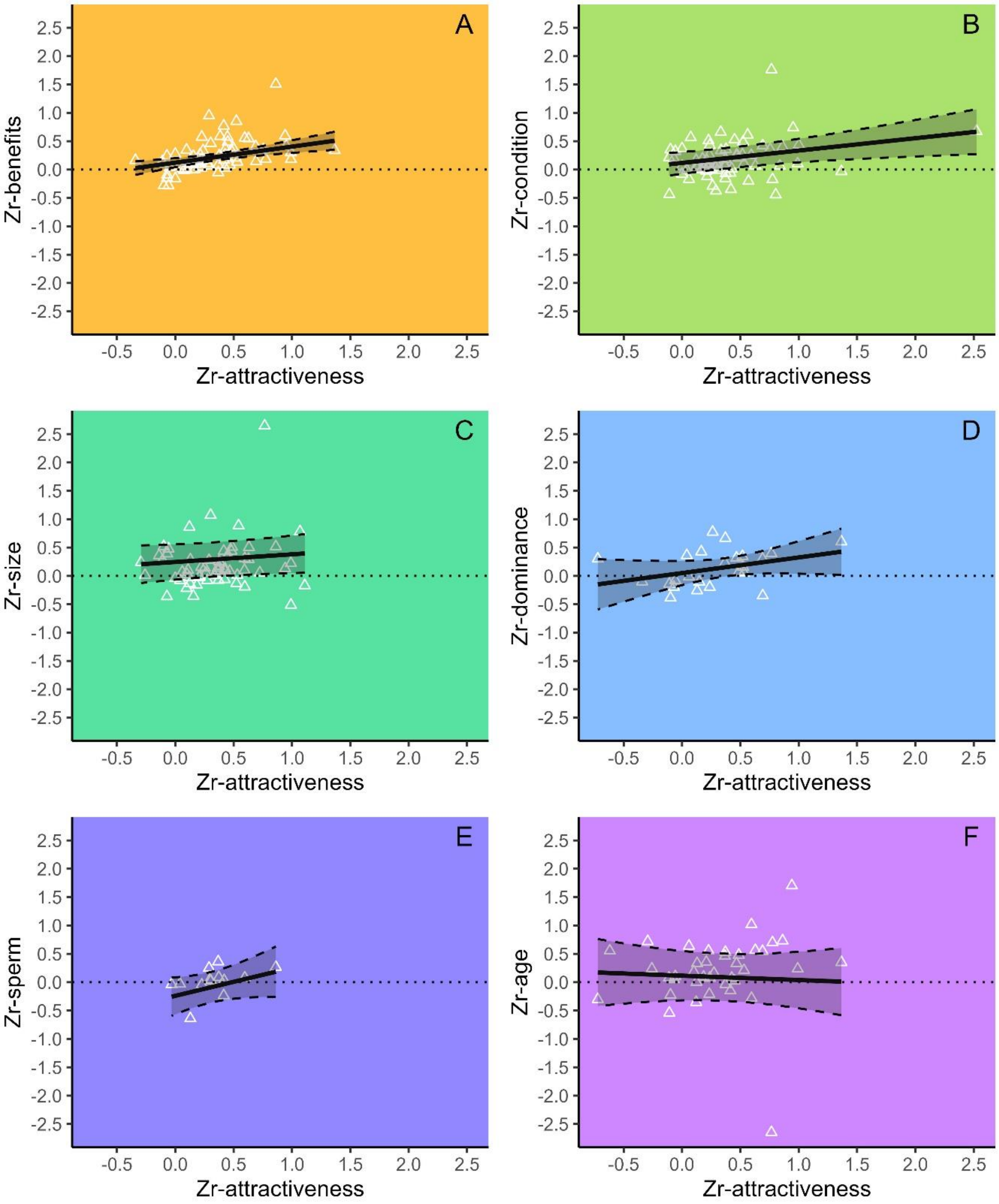

Figure 5. Meta-regressions between two relationships: putative sexual signal conspicuousness and attractiveness to mates (x-axis, i.e. Zr-attractiveness) and putative sexual signal conspicuousness and other variables from our framework (y-axis; A: benefits, B: individual condition, C: body size, D: aggression or social dominance, E: traits related to sperm competition, F: age). Solid lines represent slopes, hashed areas between dashed lines represent slopes' 95% confidence interval, and dotted lines highlight zero.

## Supplementary material

## Material and Methods

### General

Our methodology was described in our pre-registration (*72*) and in a twin study that essentially used the same dataset as we did in the present study (*73*). We report author contributions using MeRIT guidelines (*74*) and the CRediT statement (*75*).

### Deviations from the pre-registration

We planned to use the modality of putative sexual signals (i.e. whether they were visual, acoustic, or other types of signals) as a moderator in meta-analytical models but we preferred not to proceed with this decision because this variable overlapped with trait type (e.g. most fixed putative sexual signals were visual traits). We did not verify the effect of re-extracted *vs*. originally reported data as our related study using the same dataset showed that data replicability was high (*73*). PP adjusted variables within our framework from our pre-registration [compare Table S1 with Table 1 from (*72*), see also (*73*)].

### Putative sexual signal conspicuousness and variables within our framework

Our dataset contains information on the relationship between putative sexual signal conspicuousness and many variables (Table S1; Fig. 1). To clarify, putative sexual signals refer to traits thought to be involved in mate attraction [by authors of empirical papers or of primary meta-analyses that we used as data sources, see next section; weapons or body size were not considered valid putative sexual signals; see also (*76*)]. On the other hand, conspicuousness refers to the expected direction of attractiveness to mates regarding the expression of putative sexual signals. For instance, more colourful traits are expected to be more attractive, and thus greater values of certain colour metrics that reflect this (e.g. chroma) are deemed more conspicuous. However, despite using conspicuousness throughout the manuscript for all putative sexual signals, other terms could be more appropriate in many cases. For example, more symmetric traits are often expected to be more appealing to mates, so they were deemed more conspicuous, even though this term may be misleading here. Conspicuousness for other putative sexual signals may be even more confusing as the expectations on the direction of their appeal is expected to differ across taxa or scenarios, e.g. sounds with higher frequency are expected to be more appealing for birds (*11*) but less appealing for amphibians (*19*). PP ascertained the expected direction of attractiveness (i.e. conspicuousness) based on information provided by authors of empirical and primary meta-analyses but we note that what is considered more appealing to mates according to these authors has often not been tested. In fact, PP was not able to infer the expected direction of attractiveness for certain traits when we directly extracted data from empirical studies. PP then made additional analyses (see below) in which effect sizes with ambiguous direction were removed or changed to their opposite value to ensure our results were robust (see Table S2).

Variables within our framework are explained throughout the manuscript as results are reported, while their direction and more examples are given in Table S1. Meta-analyses' authors were often vague regarding the exact data they extracted, so interconnected proxies, such as reproductive success and viability measures, were difficult to separate. For instance, whether "fledgling success" means number of fledglings (reproductive success) or proportion of offspring that fledged from all eggs laid (viability) was unclear in many cases, so PP deemed most of them as reproductive success given that this is a more diverse measure.

Data collection

We used Fisher's Zr as our effect size, transforming it to correlation coefficient (r) when reporting most of our results. Details on the calculation of effect sizes, including all equations used, are reported in (*73*).

As previously stated, our data collection is fully reported in (*73*). Briefly, PP compiled individual effect sizes from 41 primary meta-analyses (*7–19, 46, 48, 56–65, 77–92*), which contained relevant data for our study from 1,196 empirical sources. Then, all authors (re-)extracted all data related to putative sexual signals from 243 empirical studies that these meta-analyses used as sources (*93–338*). This was done as part of a reproducibility and replicability project (*73*) but also provided the base to the present study (see below). After data re-extractions, PP replaced the individual effect sizes reported by meta-analyses with re-extracted effect sizes for these 243 empirical studies. Other effect sizes reported by meta-analyses (from empirical studies whose data we did not re-extract) were maintained in the dataset. Despite these 243 empirical studies being cited as data sources by meta-analyses, many of the effect sizes re-extracted by us were not actually reported by primary meta-analyses or, alternatively, were reported by primary meta-analyses with a different value from the ones we obtained during re-extraction [see (*73*)]. Thus, to some extent, our dataset contains data that have not been used in previous meta-analyses. PP additionally removed identically reported effect sizes (both in description and in value) from other duplicated empirical studies (those that we did not extract data from). This process ensured that all individual effect sizes in our dataset were unique, in contrast to meta-meta-analyses that analyse mean effect sizes from primary meta-analyses [e.g. (*339–341*)], which can encompass repeated data (as the same empirical studies can be used by multiple primary meta-analyses). PP further removed from the dataset data that were unfit to verify the relationship between putative sexual signal conspicuousness and distinct variables, such as measurements of parental care after manipulation of putative sexual signals [e.g. (*231*)]. After these procedures, our dataset tallied 7,428 effect sizes, with 4,237 of them (57% of the dataset) being extracted by us and the remaining effect sizes being originally reported by primary meta-analyses (*7–19, 46, 48, 56–65, 77–92*).

Analyses

PP constructed separate meta-analytical models to verify the relationship between putative sexual signal conspicuousness and each variable within our framework, resulting in seven sets of models (one set for each background colour in Figs. 3 and 4). PP used multilevel meta-analytical models because effect sizes were not independent of one another. Different effect sizes could share the same (empirical) study ID, species ID, and trait type ID (i.e. flexible or fixed trait, nested within-species). Thus, in addition to effect size ID, PP used these variables as random factors in our models to control for non-independence. PP also included a correlation matrix related to phylogenetic relatedness for the species in our model as a random factor (*342*). From meta-analytical models with all these random factors, PP quantified $I^2_{total}$ [a measure of heterogeneity not attributed to sampling error; (*343*)] and how much of it each random factor explained (partial $I^2$; see Table S3). PP fitted meta-analytical models with the following fixed factors: none (only intercept, showing the average relationship), sub variable (only models involving benefits and individual condition, see Table S1), sex (male, female, or unknown) and trait type (fixed or flexible). We followed (*344*) to interpret the magnitude to mean effect sizes (as *Zr*, before converting them to *r*, "weak" for values up to 0.2, "moderate" for values up to 0.5, and "high" for greater values).

We also constructed additional versions of all models described above, in which we removed or inverted the value of data points whose direction was ambiguous (e.g. putative sexual signals without information on expected direction for mate attraction or data with direction not clearly reported in empirical studies). The results of these analyses were very similar to the ones with data points as originally extracted (Table S2).

We tested for signs of publication bias in meta-analytical models using three approaches (see Table S6, Figs. S1 and S2). First, we visually evaluated funnel asymmetry for each model using funnel plots, which show the residuals of meta-analytical models containing all moderators against effect sizes' precision (i.e. inverse of standard error). Second, we further assessed funnel asymmetry with an alternative approach to Egger's regression: using the inverse of the effective sample size as a moderator in a multilevel meta-analytical model (*345*). Third, in the same meta-analytical models of the second approach, we verified time-lag bias using publication year as a moderator (*346*).

To verify whether the relationship between putative sexual signal conspicuousness and attractiveness is associated with the relationship between putative sexual signal conspicuousness and other variables within our framework, we sought conspicuous traits in our dataset with both of these relationships. We used two approaches to collect and link these data. In the first approach (hereby *across-studies*, Fig. 5), we calculated a mean effect size for each putative sexual signal (across different empirical studies examining a given species) regarding the relationship between its conspicuousness and attractiveness to mates (Zr-attractiveness). We then linked these estimates to mean effect sizes regarding the relationship between the conspicuousness of that same putative sexual signal and another variable (Zr-benefits, Zr-condition, etc.), also across different empirical studies examining a given species. This first approach assumes that the relationship between attractiveness and putative sexual conspicuousness across time and populations is consistent, which is not necessarily true (*347*). To ameliorate this issue, our second approach (hereby *within-studies*; Fig. S3) only links these relationships (Zr-attractiveness with either Zr-benefits, Zr-condition, Zr-size, Zr-dominance, Zr-sperm, or Zr-age) extracted from the same empirical study. This second approach is more reliable but yields fewer data points, such that the relationship between Zr-attractiveness and Zr-sperm could not be analysed with this second approach as a single data point was available. We only show the results of the first approach in the manuscript as both approaches generated similar qualitative results.

Meta-regressions described above accounted for the variation of effect sizes serving as the response variables (i.e. Zr-benefits, Zr-condition, etc.), but disregarded the dispersal of effect sizes serving as predictor variables (i.e. Zr-attractiveness). In other words, they are univariate models. To correct this, we conducted bivariate models, in which the dispersal of both response and predictor variables is considered. However, this approach yields much larger confidence intervals and estimates generated may not be reliable as we could not preclude divergent transitions when running these analyses. Thus, we preferred to show results of only univariate models (with the across-studies approach) in the manuscript, but results for other approaches and models can be found in Table S7.

All statistical analyses were conducted in the software R 4.4.0 (*348*). We fitted meta-analytical models (except for bivariate models) using the *rma.mv* function from the package *metafor* (*349*). Bivariate models were fitted using the package *brms* (*350*), in which we ran three chains, each with 10,000 iterations plus another 10,000 burn-in iterations. In these analyses, we adopted Stan's standard uninformative priors, and set the maximum tree depth to 12 and the adaptive delta to 0.999. We calculated $R^2$ (*351*) and $I^2$ using, respectively, the *r2_ml* and *i2_ml* function from the package *orchaRd* (*352*). Phylogenetic trees were built using the packages *ape* (*353*) and *rotl* (*354*), which uses data from (*355*). We performed pairwise comparisons (two-tailed z-tests) using the function *glht* from the package *multcomp* (*356*).

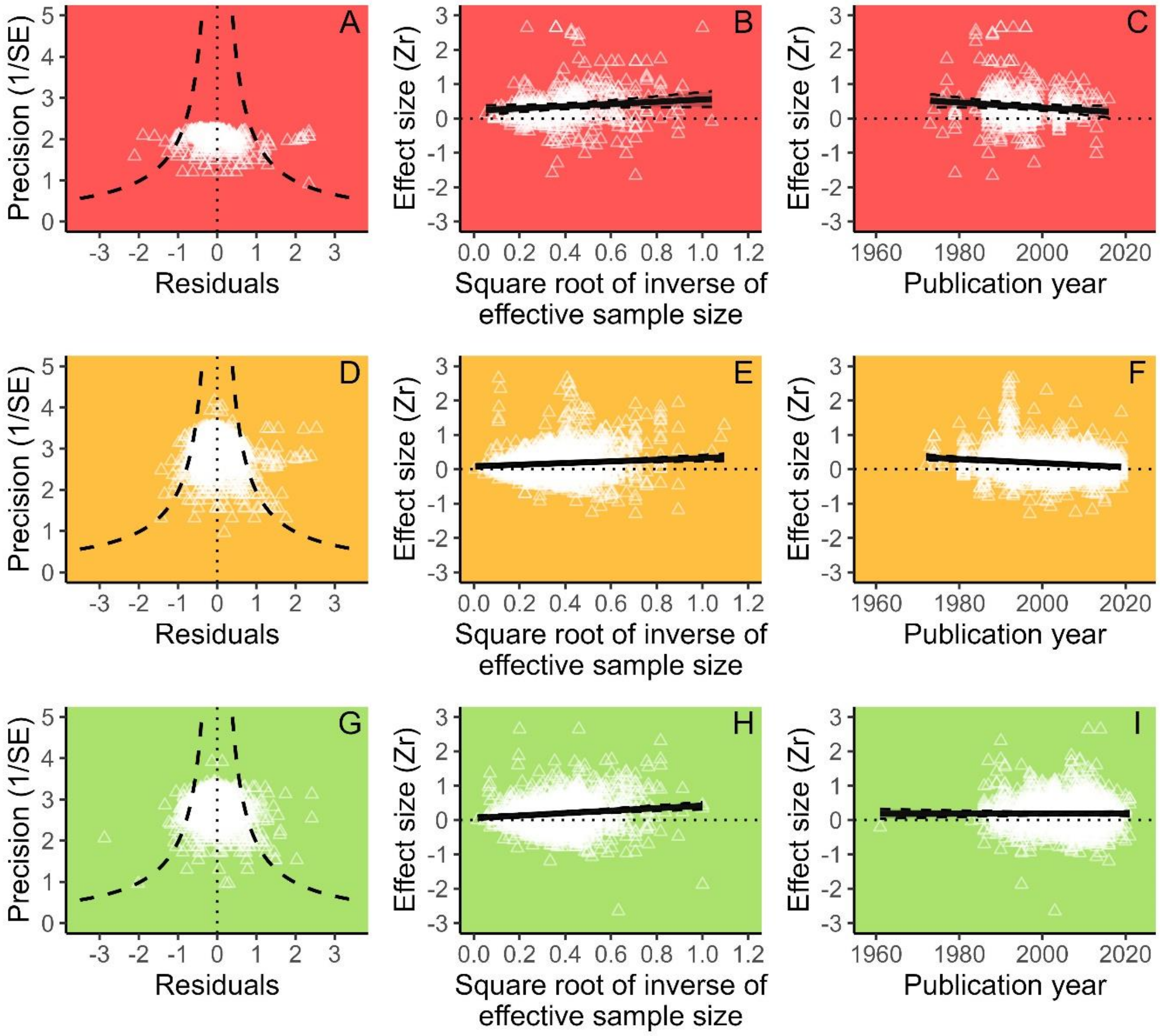

**Figure S1.**

Assessments of publication bias: funnel plots of the residuals of meta-analytical models with all moderators used (1st column), relationship between effect size (Zr) and square root of inverse of effective sample size (2nd column), and relationship between effect size (Zr) and publication year (3rd column). Dashed lines represent 95% confidence intervals for expected values (1st column) or for regression estimates (2nd and 3rd columns). Panels refer to attractiveness (A-C), benefits (D-F), or individual condition (G-I).

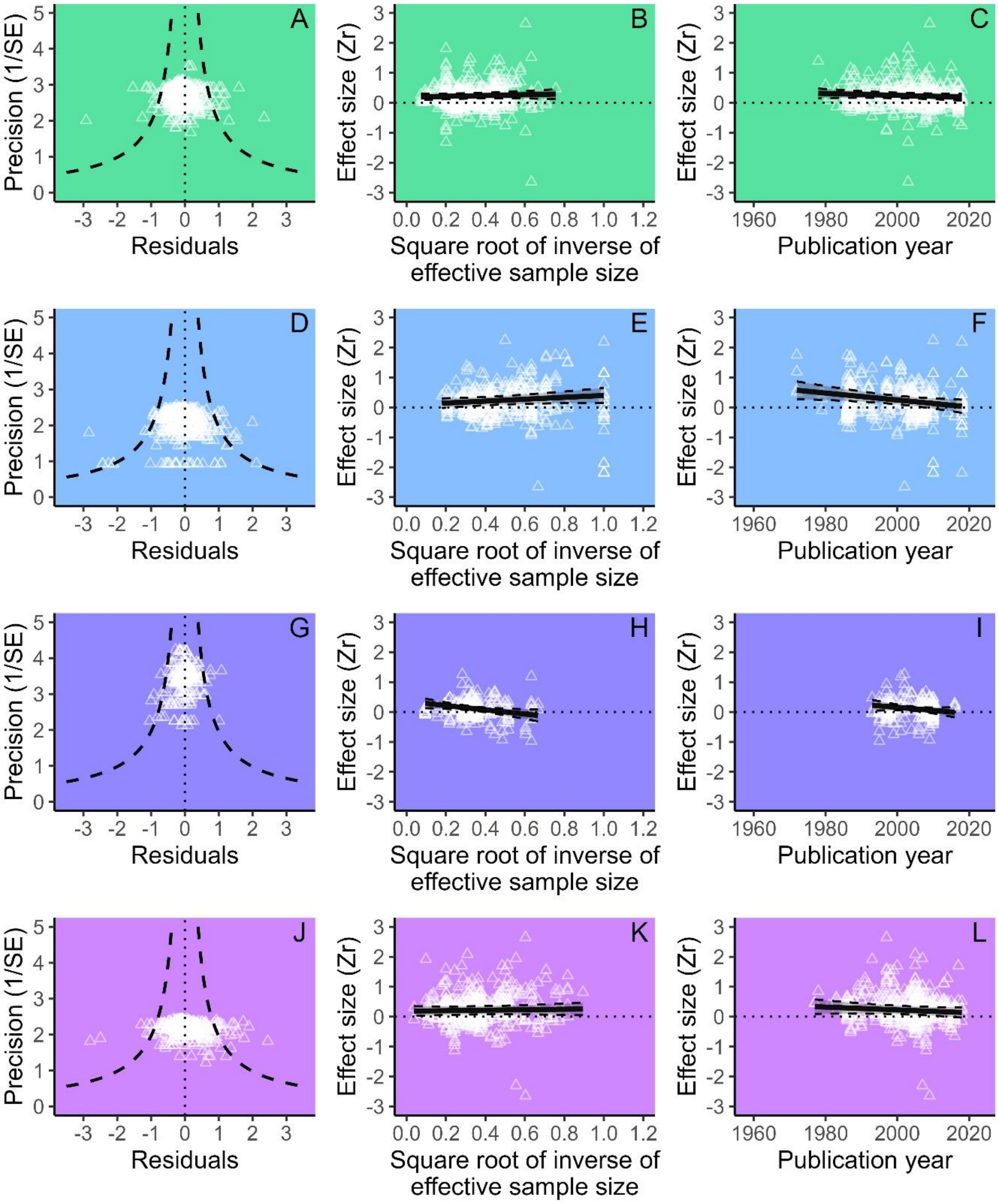

**Figure S2.**

Assessments of publication bias: funnel plots of the residuals of meta-analytical models with all moderators used (A, D, G, J), relationship between effect size (Zr) and square root of inverse of effective sample size (B, E, H, K), and relationship between effect size (Zr) and publication year (C, F, I, L). Dashed lines represent 95% confidence intervals for expected values (A, D, G, J) or for regression estimates (B, C, E, F, H, I, K, L). Panels refer to body size (A-C), aggressiveness or social dominance (D-F), traits related to sperm competition (G-I), or age (J-L).

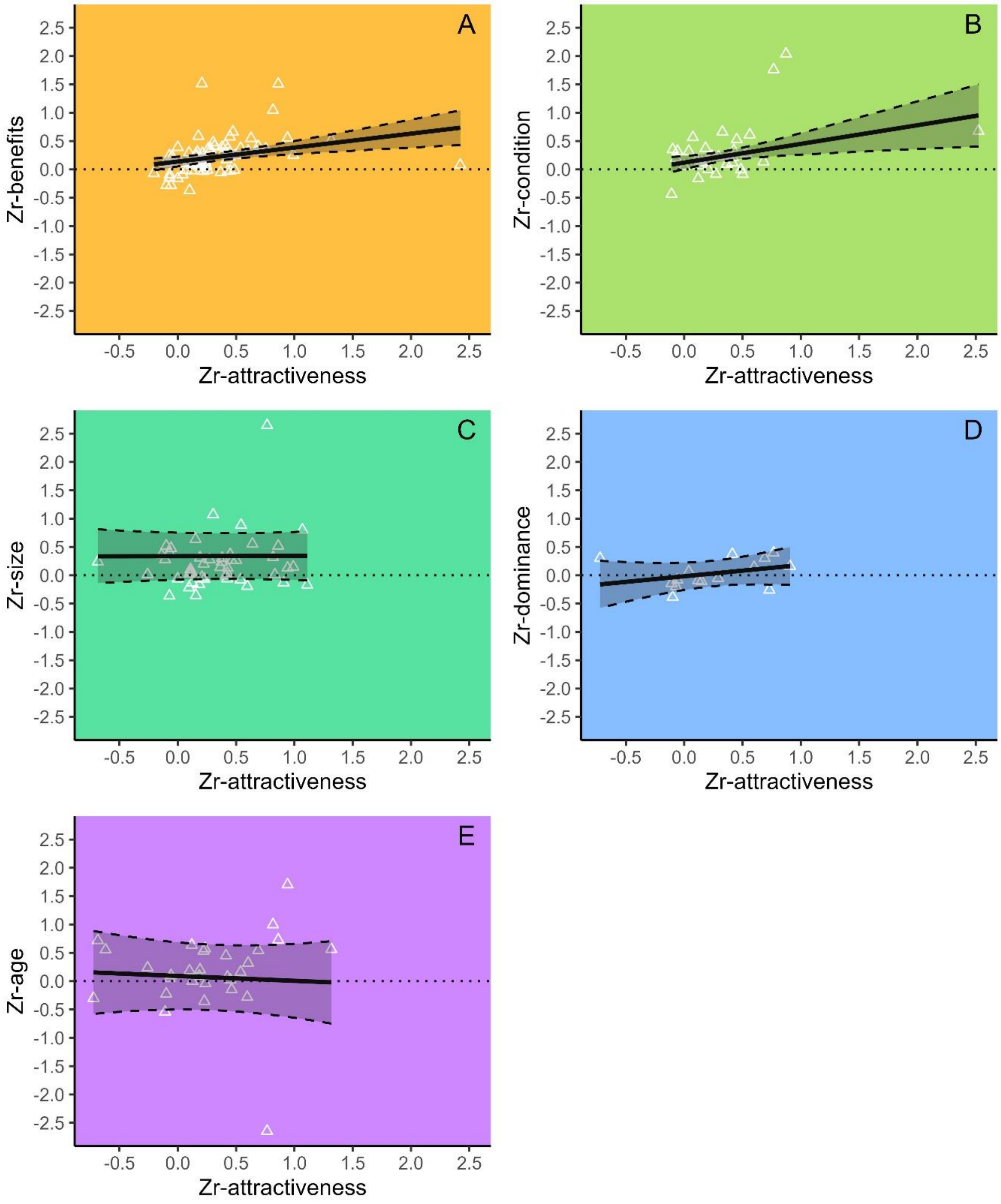

**Figure S3.**

Meta-regressions between two relationships (considering only information from the same study, i.e. within-study approach): putative sexual signal conspicuousness and attractiveness to mates (x-axis, i.e. Zr-attractiveness) and putative sexual signal conspicuousness and other variables from our framework (y-axis; A: benefits, B: individual condition, C: body size, D: aggression of social dominance, E: age). Solid lines represent slopes, hashed areas between dashed lines represent slopes' 95% confidence interval, and dotted lines highlight zero.

**Figure S4.**

Proportion (x-axis) and number (inside bars) of species for which we had information on the relationship between putative sexual signal conspicuousness and several variables (y-axis) assessed in our study, for each sex (left panel) and trait type (right panel).

**Figure S5.**

Proportion (x-axis) and number (inside bars) of effect sizes for which we had information on the relationship between putative sexual signal conspicuousness and several variables (y-axis) assessed in our study, for each sex (left panel) and trait type (right panel).

**Table S1.**

Variables within our framework, for which we verified the relationship with putative sexual signal conspicuousness. *N* represents the number of primary meta-analyses in our dataset that explored these variables. Underlined examples are predicted to have a negative relationship with sexual signal conspicuousness, while others are predicted to have a positive relationship with sexual signal conspicuousness.

| Variable | Sub variable | *N* | Examples |
|---|---|---|---|
| Attractiveness | - | 15 | Copulation success, harem size, success in mate choice trials, divorce, pairing success or status |
| Benefits to sexual signal bearers or to their mates | Timing | 9 | Latency to arrive at breeding site, latency to nest, latency to pair, latency to mate, latency to breed, latency to lay eggs, latency for eggs to hatch, latency for offspring to fledge |
| | Reproductive success | 12 | Clutch size, breeding success, number of fledglings, total offspring sired, number of recruits |
| | Offspring quality or viability | 9 | Antioxidants or hormones in yolk, offspring growth rate, offspring attractiveness, offspring reproductive success, proportion of eggs hatched, fledging success, offspring size |
| | Paternity | 10 | Within and extra-pair paternity, cuckoldry occurrence |
| | Parental care | 7 | Feeding rate, incubation frequency |
| | Territory | 2 | Territory quality or size |
| Individual condition | External condition | 7 | Increase in brood size or reproductive effort, decrease in brood size or reproductive effort, habitat quality, mother's condition, date when reared, diet supplementation, dietary deprivation, nutritional stress |
| | Body condition | 11 | Carotenoid, protein, or lipid amount in plasma or in feathers, unspecified body condition, feather quality, subcutaneous fat score, residual mass, pectoral score |
| | Immune or antioxidant capacity | 10 | Antibody response, glucocorticoids, hematocrit, heterophil-to-lymphocyte ratio, oxidative damage, white blood cells |
| | Parasite resistance | 10 | Abundance of parasites, infection with a pathogen, pathogen richness, parasite removal |
| | Survival | 9 | Days alive, seen or re-captured after a given period |
| Body size | - | 8 | Body (or part of it) mass, length, width, depth, area, or volume |
| Aggression or social dominance | - | 7 | Performed aggression, received aggression, dominance, fights initiated, social rank, nest defence, distance from intruder, territory tenure |
| Traits related to sperm competition | - | 1 | Quantity of seminal fluid, sperm size, sperm viability, testes size |
| Age | - | 8 | Age, ontogenetic stage (e.g. adult *vs*. juveniles) |

**Table S2.**

Estimated correlation coefficients from meta-analytical models. Three types of analyses are reported regarding how we dealt with data points with ambiguous direction: (1) “original” refers to results reported in the manuscript, which used data points as originally extracted; (2) “opposite” instead uses the opposite value of these data points; (3) “removed” refers to analyses without these data points.

| Variable | Sub variable | Set | Analysis | Estimate | Standard error | 95% CI lower bound | 95% CI upper bound |
|---|---|---|---|---|---|---|---|
| Attractiveness | - | All | Original | 0.329 | 0.053 | 0.233 | 0.419 |
| | | | Opposite | 0.330 | 0.054 | 0.233 | 0.420 |
| | | | Removed | 0.333 | 0.054 | 0.235 | 0.423 |
| | | Female fixed | Original | 0.220 | 0.088 | 0.050 | 0.377 |
| | | | Opposite | 0.234 | 0.090 | 0.062 | 0.393 |
| | | | Removed | 0.226 | 0.089 | 0.054 | 0.385 |
| | | Male fixed | Original | 0.304 | 0.051 | 0.211 | 0.392 |
| | | | Opposite | 0.306 | 0.053 | 0.208 | 0.397 |
| | | | Removed | 0.309 | 0.053 | 0.212 | 0.400 |
| | | Male flexible | Original | 0.403 | 0.057 | 0.304 | 0.493 |
| | | | Opposite | 0.394 | 0.060 | 0.291 | 0.488 |
| | | | Removed | 0.402 | 0.059 | 0.299 | 0.495 |
| Benefits to sexual signal bearers or to their mates | - | All | Original | 0.165 | 0.017 | 0.133 | 0.197 |
| | | | Opposite | 0.158 | 0.017 | 0.125 | 0.191 |
| | | | Removed | 0.170 | 0.017 | 0.137 | 0.203 |
| | | Female fixed | Original | 0.124 | 0.025 | 0.077 | 0.171 |
| | | | Opposite | 0.126 | 0.029 | 0.070 | 0.181 |
| | | | Removed | 0.133 | 0.026 | 0.084 | 0.182 |
| | | Male fixed | Original | 0.161 | 0.022 | 0.118 | 0.204 |
| | | | Opposite | 0.155 | 0.027 | 0.103 | 0.206 |
| | | | Removed | 0.164 | 0.023 | 0.120 | 0.208 |
| | | Male flexible | Original | 0.202 | 0.029 | 0.146 | 0.257 |
| | | | Opposite | 0.194 | 0.033 | 0.131 | 0.256 |
| | | | Removed | 0.209 | 0.031 | 0.152 | 0.266 |
| | Timing | All | Original | 0.213 | 0.022 | 0.171 | 0.254 |
| | | | Opposite | 0.223 | 0.023 | 0.181 | 0.265 |
| | | | Removed | 0.219 | 0.023 | 0.176 | 0.262 |
| | | Female fixed | Original | 0.110 | 0.033 | 0.045 | 0.174 |
| | | | Opposite | 0.144 | 0.034 | 0.079 | 0.209 |
| | | | Removed | 0.126 | 0.035 | 0.059 | 0.193 |
| | | Male fixed | Original | 0.245 | 0.028 | 0.194 | 0.295 |
| | | | Opposite | 0.254 | 0.028 | 0.201 | 0.305 |
| | | | Removed | 0.242 | 0.028 | 0.190 | 0.294 |
| | | Male flexible | Original | 0.242 | 0.043 | 0.161 | 0.320 |
| | | | Opposite | 0.219 | 0.044 | 0.136 | 0.300 |
| | | | Removed | 0.247 | 0.044 | 0.165 | 0.326 |
| | Reproductive success | All | Original | 0.157 | 0.019 | 0.121 | 0.193 |
| | | | Opposite | 0.152 | 0.019 | 0.115 | 0.189 |
| | | | Removed | 0.166 | 0.020 | 0.128 | 0.203 |
| | | | Original | 0.132 | 0.025 | 0.084 | 0.180 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | Female fixed | Opposite | 0.134 | 0.026 | 0.084 | 0.183 |
| | | | Removed | 0.140 | 0.026 | 0.089 | 0.190 |
| | | Male fixed | Original | 0.139 | 0.023 | 0.094 | 0.183 |
| | | | Opposite | 0.131 | 0.024 | 0.085 | 0.176 |
| | | | Removed | 0.142 | 0.024 | 0.097 | 0.188 |
| | | Male flexible | Original | 0.228 | 0.038 | 0.157 | 0.297 |
| | | | Opposite | 0.224 | 0.038 | 0.152 | 0.295 |
| | | | Removed | 0.245 | 0.039 | 0.172 | 0.315 |
| | Offspring quality or viability | All | Original | 0.164 | 0.022 | 0.123 | 0.205 |
| | | | Opposite | 0.149 | 0.022 | 0.106 | 0.190 |
| | | | Removed | 0.171 | 0.022 | 0.128 | 0.214 |
| | | Female fixed | Original | 0.122 | 0.036 | 0.053 | 0.190 |
| | | | Opposite | 0.107 | 0.036 | 0.037 | 0.177 |
| | | | Removed | 0.132 | 0.038 | 0.058 | 0.204 |
| | | Male fixed | Original | 0.170 | 0.026 | 0.119 | 0.219 |
| | | | Opposite | 0.155 | 0.027 | 0.103 | 0.206 |
| | | | Removed | 0.178 | 0.027 | 0.127 | 0.229 |
| | | Male flexible | Original | 0.172 | 0.041 | 0.093 | 0.250 |
| | | | Opposite | 0.157 | 0.042 | 0.075 | 0.236 |
| | | | Removed | 0.171 | 0.043 | 0.088 | 0.252 |
| | Paternity | All | Original | 0.149 | 0.029 | 0.092 | 0.204 |
| | | | Opposite | 0.143 | 0.030 | 0.085 | 0.199 |
| | | | Removed | 0.151 | 0.030 | 0.094 | 0.208 |
| | | Male fixed | Original | 0.136 | 0.032 | 0.074 | 0.198 |
| | | | Opposite | 0.133 | 0.033 | 0.070 | 0.196 |
| | | | Removed | 0.136 | 0.032 | 0.073 | 0.197 |
| | | Male flexible | Original | 0.140 | 0.060 | 0.022 | 0.253 |
| | | | Opposite | 0.119 | 0.062 | -0.003 | 0.237 |
| | | | Removed | 0.140 | 0.061 | 0.022 | 0.254 |
| | Parental care | All | Original | 0.079 | 0.029 | 0.022 | 0.136 |
| | | | Opposite | 0.052 | 0.030 | -0.006 | 0.110 |
| | | | Removed | 0.069 | 0.031 | 0.008 | 0.130 |
| | | Female fixed | Original | 0.077 | 0.044 | -0.009 | 0.162 |
| | | | Opposite | 0.030 | 0.045 | -0.057 | 0.117 |
| | | | Removed | 0.070 | 0.049 | -0.025 | 0.164 |
| | | Male fixed | Original | 0.044 | 0.036 | -0.026 | 0.113 |
| | | | Opposite | 0.020 | 0.036 | -0.051 | 0.091 |
| | | | Removed | 0.027 | 0.037 | -0.046 | 0.100 |
| | | Male flexible | Original | 0.214 | 0.092 | 0.037 | 0.378 |
| | | | Opposite | 0.248 | 0.092 | 0.071 | 0.409 |
| | | | Removed | 0.253 | 0.095 | 0.072 | 0.418 |
| | Territory | All | Original | 0.241 | 0.042 | 0.162 | 0.317 |
| | | | Opposite | 0.241 | 0.043 | 0.161 | 0.318 |
| | | | Removed | 0.236 | 0.043 | 0.156 | 0.314 |
| | | Male fixed | Original | 0.298 | 0.057 | 0.192 | 0.397 |
| | | | Opposite | 0.300 | 0.058 | 0.193 | 0.400 |
| | | | Removed | 0.285 | 0.058 | 0.176 | 0.387 |
| | | Male flexible | Original | 0.219 | 0.060 | 0.104 | 0.329 |
| | | | Opposite | 0.213 | 0.061 | 0.096 | 0.324 |
| | | | Removed | 0.229 | 0.061 | 0.113 | 0.338 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Individual condition | - | All | Original | 0.174 | 0.026 | 0.124 | 0.224 |
| | | | Opposite | 0.174 | 0.027 | 0.121 | 0.225 |
| | | | Removed | 0.177 | 0.026 | 0.128 | 0.226 |
| | | Female fixed | Original | 0.134 | 0.034 | 0.069 | 0.198 |
| | | | Opposite | 0.137 | 0.035 | 0.070 | 0.203 |
| | | | Removed | 0.137 | 0.034 | 0.072 | 0.201 |
| | | Male fixed | Original | 0.184 | 0.030 | 0.126 | 0.241 |
| | | | Opposite | 0.182 | 0.032 | 0.121 | 0.241 |
| | | | Removed | 0.187 | 0.030 | 0.129 | 0.244 |
| | | Male flexible | Original | 0.186 | 0.033 | 0.123 | 0.247 |
| | | | Opposite | 0.184 | 0.034 | 0.119 | 0.248 |
| | | | Removed | 0.186 | 0.033 | 0.124 | 0.248 |
| | External condition | All | Original | 0.263 | 0.026 | 0.215 | 0.310 |
| | | | Opposite | 0.265 | 0.029 | 0.211 | 0.318 |
| | | | Removed | 0.274 | 0.028 | 0.222 | 0.325 |
| | | Female fixed | Original | 0.228 | 0.062 | 0.110 | 0.339 |
| | | | Opposite | 0.222 | 0.062 | 0.104 | 0.334 |
| | | | Removed | 0.227 | 0.065 | 0.104 | 0.343 |
| | | Male fixed | Original | 0.269 | 0.041 | 0.194 | 0.341 |
| | | | Opposite | 0.278 | 0.041 | 0.203 | 0.350 |
| | | | Removed | 0.289 | 0.043 | 0.210 | 0.364 |
| | | Male flexible | Original | 0.290 | 0.038 | 0.219 | 0.357 |
| | | | Opposite | 0.293 | 0.039 | 0.222 | 0.360 |
| | | | Removed | 0.296 | 0.039 | 0.226 | 0.364 |
| | Body condition | All | Original | 0.198 | 0.020 | 0.161 | 0.235 |
| | | | Opposite | 0.199 | 0.024 | 0.153 | 0.244 |
| | | | Removed | 0.202 | 0.022 | 0.160 | 0.244 |
| | | Female fixed | Original | 0.163 | 0.030 | 0.105 | 0.220 |
| | | | Opposite | 0.171 | 0.030 | 0.113 | 0.228 |
| | | | Removed | 0.168 | 0.031 | 0.108 | 0.227 |
| | | Male fixed | Original | 0.225 | 0.024 | 0.180 | 0.269 |
| | | | Opposite | 0.220 | 0.024 | 0.175 | 0.265 |
| | | | Removed | 0.228 | 0.025 | 0.181 | 0.273 |
| | | Male flexible | Original | 0.148 | 0.048 | 0.054 | 0.238 |
| | | | Opposite | 0.147 | 0.049 | 0.053 | 0.239 |
| | | | Removed | 0.145 | 0.049 | 0.051 | 0.237 |
| | Immune or antioxidant capacity | All | Original | 0.129 | 0.023 | 0.084 | 0.174 |
| | | | Opposite | 0.126 | 0.028 | 0.073 | 0.179 |
| | | | Removed | 0.128 | 0.026 | 0.078 | 0.178 |
| | | Female fixed | Original | 0.141 | 0.045 | 0.054 | 0.227 |
| | | | Opposite | 0.142 | 0.045 | 0.054 | 0.228 |
| | | | Removed | 0.144 | 0.046 | 0.056 | 0.230 |
| | | Male fixed | Original | 0.138 | 0.028 | 0.084 | 0.191 |
| | | | Opposite | 0.135 | 0.028 | 0.081 | 0.189 |
| | | | Removed | 0.140 | 0.029 | 0.084 | 0.195 |
| | | Male flexible | Original | 0.072 | 0.052 | -0.030 | 0.172 |
| | | | Opposite | 0.081 | 0.053 | -0.022 | 0.182 |
| | | | Removed | 0.073 | 0.053 | -0.030 | 0.175 |
| | Parasite resistance | All | Original | 0.119 | 0.021 | 0.078 | 0.159 |
| | | | Opposite | 0.123 | 0.025 | 0.074 | 0.171 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | Removed | 0.128 | 0.023 | 0.082 | 0.172 |
| | | Female fixed | Original | 0.097 | 0.042 | 0.015 | 0.178 |
| | | | Opposite | 0.108 | 0.042 | 0.025 | 0.189 |
| | | | Removed | 0.110 | 0.044 | 0.023 | 0.195 |
| | | Male fixed | Original | 0.134 | 0.025 | 0.086 | 0.181 |
| | | | Opposite | 0.136 | 0.025 | 0.088 | 0.183 |
| | | | Removed | 0.141 | 0.025 | 0.092 | 0.189 |
| | | Male flexible | Original | 0.115 | 0.043 | 0.030 | 0.197 |
| | | | Opposite | 0.100 | 0.044 | 0.015 | 0.184 |
| | | | Removed | 0.111 | 0.044 | 0.026 | 0.196 |
| | Survival | All | Original | 0.113 | 0.031 | 0.053 | 0.172 |
| | | | Opposite | 0.100 | 0.034 | 0.034 | 0.166 |
| | | | Removed | 0.108 | 0.033 | 0.044 | 0.172 |
| | | Female fixed | Original | 0.020 | 0.055 | -0.088 | 0.127 |
| | | | Opposite | 0.003 | 0.055 | -0.105 | 0.111 |
| | | | Removed | 0.013 | 0.057 | -0.098 | 0.123 |
| | | Male fixed | Original | 0.130 | 0.038 | 0.057 | 0.202 |
| | | | Opposite | 0.125 | 0.038 | 0.051 | 0.197 |
| | | | Removed | 0.133 | 0.039 | 0.058 | 0.206 |
| | | Male flexible | Original | 0.183 | 0.065 | 0.057 | 0.302 |
| | | | Opposite | 0.147 | 0.066 | 0.019 | 0.271 |
| | | | Removed | 0.162 | 0.066 | 0.033 | 0.286 |
| Body size | - | All | Original | 0.230 | 0.045 | 0.144 | 0.312 |
| | | | Opposite | 0.228 | 0.051 | 0.132 | 0.319 |
| | | | Removed | 0.232 | 0.041 | 0.155 | 0.307 |
| | | Female fixed | Original | 0.295 | 0.080 | 0.147 | 0.431 |
| | | | Opposite | 0.297 | 0.084 | 0.140 | 0.440 |
| | | | Removed | 0.295 | 0.077 | 0.152 | 0.426 |
| | | Male fixed | Original | 0.267 | 0.078 | 0.119 | 0.403 |
| | | | Opposite | 0.269 | 0.083 | 0.113 | 0.413 |
| | | | Removed | 0.262 | 0.075 | 0.120 | 0.394 |
| | | Male flexible | Original | 0.215 | 0.065 | 0.092 | 0.333 |
| | | | Opposite | 0.212 | 0.069 | 0.079 | 0.337 |
| | | | Removed | 0.221 | 0.061 | 0.105 | 0.331 |
| Aggression or social dominance | - | All | Original | 0.205 | 0.082 | 0.047 | 0.354 |
| | | | Opposite | 0.202 | 0.087 | 0.034 | 0.358 |
| | | | Removed | 0.206 | 0.084 | 0.044 | 0.358 |
| | | Female fixed | Original | 0.138 | 0.147 | -0.151 | 0.404 |
| | | | Opposite | 0.114 | 0.147 | -0.174 | 0.383 |
| | | | Removed | 0.131 | 0.148 | -0.159 | 0.401 |
| | | Male fixed | Original | 0.242 | 0.092 | 0.065 | 0.404 |
| | | | Opposite | 0.245 | 0.095 | 0.064 | 0.410 |
| | | | Removed | 0.245 | 0.093 | 0.066 | 0.409 |
| | | Male flexible | Original | 0.184 | 0.131 | -0.072 | 0.416 |
| | | | Opposite | 0.188 | 0.130 | -0.066 | 0.420 |
| | | | Removed | 0.189 | 0.130 | -0.064 | 0.419 |
| Traits related to sperm competition | - | All | Original | 0.107 | 0.040 | 0.029 | 0.185 |
| | | | Opposite | 0.103 | 0.044 | 0.017 | 0.188 |
| | | | Removed | 0.108 | 0.040 | 0.031 | 0.184 |
| | | Male fixed | Original | 0.072 | 0.058 | -0.043 | 0.184 |
| | | | Opposite | 0.068 | 0.059 | -0.048 | 0.183 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | Removed | 0.072 | 0.058 | -0.042 | 0.185 |
| | | Male flexible | Original | 0.175 | 0.066 | 0.046 | 0.297 |
| | | | Opposite | 0.170 | 0.067 | 0.041 | 0.294 |
| | | | Removed | 0.176 | 0.066 | 0.047 | 0.299 |
| Age | - | All | Original | 0.196 | 0.079 | 0.043 | 0.340 |
| | | | Opposite | 0.201 | 0.054 | 0.099 | 0.300 |
| | | | Removed | 0.197 | 0.085 | 0.032 | 0.350 |
| | | Female fixed | Original | 0.153 | 0.094 | -0.030 | 0.326 |
| | | | Opposite | 0.174 | 0.075 | 0.028 | 0.313 |
| | | | Removed | 0.163 | 0.100 | -0.032 | 0.346 |
| | | Male fixed | Original | 0.193 | 0.092 | 0.014 | 0.360 |
| | | | Opposite | 0.208 | 0.074 | 0.067 | 0.342 |
| | | | Removed | 0.203 | 0.098 | 0.013 | 0.380 |
| | | Male flexible | Original | 0.217 | 0.096 | 0.032 | 0.387 |
| | | | Opposite | 0.198 | 0.078 | 0.047 | 0.341 |
| | | | Removed | 0.206 | 0.102 | 0.009 | 0.388 |

**Table S3.**

Heterogeneity ($I^2$) observed in meta-analytical models on the relationship between the expression of putative sexual signals and different variables within our framework.

| **Variable** | $I^2_{total}$ | $I^2_{within\text{-}study}$ **(effect size ID)** | $I^2_{across\text{-}study}$ **(study ID)** | $I^2_{across\text{-}species}$ **(species ID)** | $I^2_{phylogeny}$ | $\mathrm{I}^2_{\text{within-species}}$ **trait type** |
|---|---|---|---|---|---|---|
| **Attractiveness** | 91.537 | 55.947 | 25.180 | <00.001 | 2.252 | 8.158 |
| **Benefits to sexual signal bearers or to their mates** | 88.017 | 51.591 | 25.048 | 0.684 | <0.001 | 10.694 |
| **Individual condition** | 85.176 | 52.427 | 26.649 | 4.778 | 1.321 | <0.001 |
| **Body size** | 87.193 | 35.080 | 04.278 | <0.001 | 3.599 | 44.236 |
| **Aggression or social dominance** | 78.527 | 19.885 | 43.136 | 9.353 | 5.237 | 0.916 |
| **Traits related to sperm competition** | 75.923 | 31.769 | 42.970 | <0.001 | 1.183 | 0.000 |
| **Age** | 93.585 | 44.460 | 28.500 | <0.001 | 7.395 | 13.230 |

**Table S4.**

Pairwise comparisons (two-tailed test) among combinations of sex and trait type. Shaded cells highlight significant comparisons (*p-value* < 0.05).

| **Variable** | **Sub variable** | **Female fixed *vs.* male fixed** | | **Female fixed *vs.* male flexible** | | **Male fixed *vs.* male flexible** | |
|---|---|---|---|---|---|---|---|
| | | *z-value* | *p-value* | *z-value* | *p-value* | *z-value* | *p-value* |
| Attractiveness | – | -1.048 | 0.294 | -2.070 | 0.038 | -1.735 | 0.083 |
| Benefits to sexual signal bearers or to their mates | – | -2.068 | 0.039 | -2.229 | 0.026 | -1.227 | 0.220 |
| | Timing | -3.975 | <0.001 | -2.538 | 0.011 | 0.058 | 0.954 |
| | Reproductive success | -0.276 | 0.783 | -2.214 | 0.027 | -2.120 | 0.034 |
| | Offspring quality or viability | -1.321 | 0.186 | -0.949 | 0.343 | -0.058 | 0.953 |
| | Paternity | – | – | – | – | -0.050 | 0.960 |
| | Parental care | 0.664 | 0.507 | -1.380 | 0.168 | -1.774 | 0.076 |
| | Territory | – | – | – | – | -1.024 | 0.306 |
| Individual condition | – | -2.484 | 0.013 | -1.662 | 0.097 | -0.071 | 0.943 |
| | External condition | -0.718 | 0.472 | -0.924 | 0.356 | -0.403 | 0.687 |
| | Body condition | -2.060 | 0.039 | 0.283 | 0.777 | 1.540 | 0.124 |
| | Immune or antioxidant capacity | 0.075 | 0.941 | 1.046 | 0.295 | 1.213 | 0.225 |
| | Parasite resistance | -0.851 | 0.395 | -0.301 | 0.763 | 0.407 | 0.684 |
| | Survival | -1.981 | 0.048 | -1.983 | 0.047 | -0.750 | 0.453 |
| Body size | – | 0.936 | 0.349 | 1.241 | 0.215 | 0.812 | 0.417 |
| Aggression or social dominance | – | -0.710 | 0.478 | -0.257 | 0.797 | 0.515 | 0.606 |
| Traits related to sperm competition | – | – | – | – | – | -2.076 | 0.038 |
| Age | – | -0.862 | 0.388 | -0.701 | 0.484 | -0.276 | 0.782 |

**Table S5.**

Marginal $R^2$ (i.e. variation of data explained by fixed factors) and conditional $R^2$ (i.e. variation of data explained by random and fixed factors) of meta-analytical models on the relationship between putative sexual signal conspicuousness and different variables, with sub variable, sex, and trait type as fixed factors.

| **Variable** | **Marginal $R^2$** | **Conditional $R^2$** |
|---|---|---|
| Attractiveness | 0.023 | 0.387 |
| Benefits to sexual signal bearers or to their mates | 0.041 | 0.400 |
| Individual condition | 0.049 | 0.395 |
| Body size | 0.012 | 0.617 |
| Aggression or social dominance | 0.019 | 0.742 |
| Traits related to sperm competition | 0.033 | 0.571 |
| Age | 0.005 | 0.537 |

**Table S6.**

Results of meta-analytical models on the relationship between putative sexual signal conspicuousness and different variables, with the square root of the inverse of effective sample size (SIESS) and publication year of empirical sources as moderators. Positive estimates for SIESS indicate publication bias and negative estimates for publication year indicate time-lag publication bias (shaded rows highlight these cases when statistically significant).

| Variable | Term | Estimate | SE | z-value | p-value | 95% CI |
|---|---|---|---|---|---|---|
| **Attractiveness** | Intercept | 0.356 | 0.045 | 7.835 | <0.001 | 0.267 to 0.442 |
| | SIESS | 0.056 | 0.028 | 1.948 | 0.051 | -0.001 to 0.111 |
| | Time-lag | -0.054 | 0.028 | -1.937 | 0.053 | -0.109 to 0.000 |
| **Benefits to sexual signal bearers or to their mates** | Intercept | 0.170 | 0.016 | 10.85 | <0.001 | 0.140 to 0.201 |
| | SIESS | 0.033 | 0.010 | 3.444 | 0.001 | 0.014 to 0.052 |
| | Time-lag | -0.052 | 0.012 | -4.262 | <0.001 | -0.077 to -0.028 |
| **Individual condition** | Intercept | 0.187 | 0.027 | 6.910 | <0.001 | 0.134 to 0.240 |
| | SIESS | 0.048 | 0.010 | 5.015 | <0.001 | 0.029 to 0.066 |
| | Time-lag | 0.001 | 0.011 | 0.060 | 0.953 | -0.021 to 0.023 |
| **Body size** | Intercept | 0.231 | 0.046 | 5.067 | <0.001 | 0.142 to 0.321 |
| | SIESS | 0.016 | 0.018 | 0.894 | 0.372 | -0.020 to 0.052 |
| | Time-lag | -0.029 | 0.024 | -1.200 | 0.230 | -0.076 to 0.018 |
| **Aggression or social dominance** | Intercept | 0.244 | 0.073 | 3.326 | 0.001 | 0.100 to 0.388 |
| | SIESS | 0.063 | 0.036 | 1.752 | 0.080 | -0.007 to 0.134 |
| | Time-lag | -0.115 | 0.047 | -2.465 | 0.014 | -0.207 to -0.024 |
| **Traits related to sperm competition** | Intercept | 0.111 | 0.036 | 3.117 | 0.002 | 0.041 to 0.181 |
| | SIESS | -0.082 | 0.034 | -2.416 | 0.016 | -0.149 to -0.016 |
| | Time-lag | -0.059 | 0.040 | -1.455 | 0.146 | -0.138 to 0.020 |
| **Age** | Intercept | 0.211 | 0.070 | 3.017 | 0.003 | 0.074 to 0.349 |
| | SIESS | 0.012 | 0.023 | 0.542 | 0.588 | -0.032 to 0.056 |
| | Time-lag | -0.038 | 0.030 | -1.245 | 0.213 | -0.098 to 0.022 |

**Table S7.**

Association between the relationship between putative sexual signal conspicuousness and attractiveness (Zr-attractiveness) and the relationship between putative sexual signal conspicuousness and other variables (benefits: Zr-benefits, individual condition: Zr-condition, body size: Zr-size, aggression or social dominance: Zr-dominance, traits related to sperm competition: Zr-sperm, and age: Zr-age), depending on two approaches (across- and within-studies) and two distinct models (uni- and bivariate). *N* indicates the number of effect sizes used in each approach. Shaded rows highlight estimates whose 95% confidence interval does not overlap zero.'

| Variable | Approach | *N* | Model | Estimate | 95% CI |
|---|---|---|---|---|---|
| **Benefits to sexual signal bearers or to their mates** | Across-studies | 66 | Univariate | 0.283 | 0.136 to 0.429 |
| | | | Bivariate | 0.739 | 0.359 to 0.985 |
| | Within-studies | 68 | Univariate | 0.246 | 0.102 to 0.390 |
| | | | Bivariate | 0.636 | 0.272 to 0.941 |
| **Individual condition** | Across-studies | 64 | Univariate | 0.218 | 0.053 to 0.383 |
| | | | Bivariate | 0.466 | -0.078 to 0.922 |
| | Within-studies | 32 | Univariate | 0.330 | 0.085 to 0.574 |
| | | | Bivariate | 0.505 | -0.056 to 0.944 |
| **Body size** | Across-studies | 59 | Univariate | 0.135 | -0.077 to 0.347 |
| | | | Bivariate | 0.167 | -0.309 to 0.639 |
| | Within-studies | 47 | Univariate | 0.003 | -0.225 to 0.231 |
| | | | Bivariate | -0.013 | -0.663 to 0.667 |
| **Aggression or social dominance** | Across-studies | 24 | Univariate | 0.275 | -0.102 to 0.653 |
| | | | Bivariate | 0.197 | -0.551 to 0.796 |
| | Within-studies | 15 | Univariate | 0.199 | -0.167 to 0.565 |
| | | | Bivariate | 0.057 | -0.649 to 0.702 |
| **Traits related to sperm competition** | Across-studies | 13 | Univariate | 0.494 | -0.126 to 1.114 |
| | | | Bivariate | 0.286 | -0.820 to 0.970 |
| | Within-studies | 1 | Univariate | - | - |
| | | | Bivariate | - | - |
| **Age** | Across-studies | 39 | Univariate | -0.076 | -0.481 to 0.328 |
| | | | Bivariate | 0.001 | -0.664 to 0.719 |
| | Within-studies | 30 | Univariate | -0.086 | -0.523 to 0.351 |
| | | | Bivariate | 0.118 | -0.772 to 0.923 |