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The exploitation of sexual signals by predators: a meta-analysis

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Sexual signals are often central to reproduction, and their expression is thought to strike a balance between advertising to mates and avoiding detection by predatory eavesdroppers. Tests of the predicted predation costs have produced mixed results, however. Here we synthesized 187 effects from 78 experimental studies in a meta-analytic test of two questions; namely, whether predators, parasites and parasitoids express preferences for the sexual signals of prey, and whether sexual signals increase realized predation risk in the wild. We found that predators and parasitoids express strong and consistent preferences for signals in forced-choice contexts. We found a similarly strong overall increase in predation on sexual signallers in the wild, though here it was modality specific. Olfactory and acoustic signals increased the incidence of eavesdropping relative to visual signals, which experienced no greater risk than controls on average. Variation in outcome measures was universally high, suggesting that contexts in which sexual signalling may incur no cost, or even reduce the incidence of predation, are common. Our results reveal unexpected complexity in a central viability cost to sexual signalling, while also speaking to applied problems in invasion biology and pest management where signal exploitation holds promise for bio-inspired solutions.

1. Introduction

Sexual signals rank among the most elaborate and conspicuous innovations showcased by animals. Their ubiquity speaks to their importance in sexual reproduction where they advertise, among other things, the location [1], identity [2], availability [3] or quality [4] of prospective mates. These benefits are met by countervailing costs, however, with predation and parasitism standing among the most exhaustively studied [5–7]. Early work noted that the conspicuousness of sexual signals should also attract unwanted attention from predators, thereby establishing a fundamental trade-off [8,9]. This simple observation has since been borne out in a wealth of empirical tests [10–12], while more recent efforts have built on these foundations to highlight predation as a selective force in sexual systems more generally. In ecological terms, predation-induced shifts in signalling behaviour [13,14] and mate choice [15,16] are now well documented, while at evolutionary scales the need to balance between signalling to conspecifics and avoiding predators can culminate in genetic polymorphisms [17,18] and population divergence [19,20].

The interception of signals by unintended receivers is best known as 'eavesdropping' and is the route through which predation costs are imposed upon sexual signallers. Birds localize lizard prey using their colourful ornaments [21,22], flies attend the advertisement calls of frogs to extract a blood meal [23,24], and wasps use the sex pheromones of aphids as kairomones to identify hosts [25,26]. While the risk to sexual signallers is well articulated in general terms, questions remain as to whether and how such costs vary predictably across contexts. A signal's modality, in particular, may drive differential predation, with the expectation of modality-specific costs guided by knowledge of the structure of signals and **Table 1.** The fundamental properties of signals across five modalities which, in part, define the predicted magnitude of eavesdropping risk to signalling individuals. Adapted from [29].

property	visual	olfactory	acoustic	tactile
range	short/medium	medium/long	long	short
longevity	short	medium/long	short	short
transmission speed	fast	slow	fast	fast
specificity	medium	low	medium	high
complexity	low	high	high	medium
energetic cost	medium	low	high	low
localizability	high	low	medium/high	low
predicted risk	low	medium/high	medium/high	low

signalling environments [27,28]. A general prediction from signal detection theory is that modalities characterized by shorter ranges, faster transmission and/or reduced longevity—as typifies visual and vibratory signals—should comparatively reduce the risk to signallers, while the increased range and longevity of olfactory and auditory signals may lead to a heightened risk of predation, on balance (table 1). Coevolution between signallers, receivers and eavesdroppers will of course modify the balance of risk and reward in a given system (e.g. [27,30,31]), but the inherent properties of modalities set the foundation for, and ultimately constrain, such processes. Recent work on multimodal signalling has broached this question indirectly [32–34], but most studies (understandably) still take a narrower taxonomic and modality-specific focus (as noted in [7]).

While central to theory in sexual selection and communication, signal exploitation holds interest across fields which have often progressed in isolation. For example, predicting the likelihood of invasiveness by introduced species is a longstanding conservation goal [35]. The responses of native predators to invasive prey, or vice-versa, is key to such ends, for which knowledge of the use of prey cues—including sexual signals—is vital [36,37]. In more applied terms, the promotion of natural predators is a central tenet of integrated pest management [38] for which the sexual signals of prey have proven a source of commercially viable bioinspiration in trap and lure design. Much effort has been expended on extracting and synthesizing pest sex pheromones for use in attracting predators amid managed crops (reviewed in [39]), though with mixed success (e.g. [40-43]). Underlying these disparate programmes is a shared interest in the predation costs to signalling, but the fragmentation of knowledge has constrained opportunities for fruitful, reciprocal exchange.

Here we conducted the first quantitative synthesis of whether and to what extent sexual signals increase the risk of eavesdropping by predators and parasites. Our aim was to answer the following three related questions. (1) Do predators and parasites express preferences for organisms bearing sexual signals? (2) Do sexual signals increase the risk of predation and parasitism in the wild? (3) Are there biological or methodological moderators—such as signalling modality—which influence the magnitude of predator preferences or risks to signallers?

2. Methods

(a) Systematic literature search

As our interest lay in identifying causal relationships, our broad aim was to retrieve experimental studies which manipulate the sexual signals of organisms, or models thereof, and quantify the outcome in terms of predation or parasitism. A preliminary search showed that the literature is dominated by two experimental paradigms which seek to answer closely related, but distinct, questions. One uses choice assays in which predators or parasites are presented with a forced binary decision between putative prey whose sexual signals have been manipulated by kind (i.e. entirely removed) or degree (e.g. [44-46]). The focal question such designs address is whether and to what extent eavesdroppers prefer organisms bearing sexual signals, and the resulting data are proportions from dichotomous choices. The other common approach manipulates the sexual signals of animals, or their signals in isolation, and exposes them to predation under natural or semi-natural conditions. Examples include the field deployment of clay or robotic models bearing colourful sexual ornaments [21,47], or sampling traps impregnated with isolated sex pheromones [48,49]. The question here being whether sexual signals increase the realized risk of eavesdropping, with the resulting data being quantitative measures of between-group differences in predation and/or parasitism. Given the conceptual and analytical differences between these approaches it is a distinction which we maintain throughout, and we refer to each as 'eavesdropper preference' and 'eavesdropping risk' assays, respectively, for convenience going forward. Note too that our focus is on sexual signals specifically, and so we excluded studies of other conspicuous signals like aposematic (warning) signals. See electronic supplementary material for further details on our systematic search and study screening.

(b) Data extraction and effect size calculation

For eavesdropper preference assays we used the logittransformed proportion, or log-odds [50], as the effect size describing the preference of eavesdroppers for organisms bearing sexual signals in binary choice assays. We back-converted all effects to raw proportions for reporting and display (below), and so values beyond 0.5 represent a greater number of choices for signalling individuals, and values less than 0.5 represent more choices for individuals with diminished or absent sexual signals (controls). For eavesdropping risk assays we estimated the standardized mean difference Hedges's g, and its variance [50], between treatment and control groups, with values above 0 therefore representing heightened predation on signalling individuals, and values below zero representing more attacks on control stimuli with reduced or no sexual signals [50]. In all cases these effects were estimated from raw or summary data presented in the main text or figures via the R package 'metaDigitise' v. 1.0.1 [51], or converted from available test statistics using the package 'compute.es' v. 0.2-5 [52].

We also recorded information from each study which we *a priori* hypothesized may moderate the strength of relationships between sexual signal expression and eavesdropper preferences

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or eavesdropping risk. This included signal modality, since differences in the active range, specificity, duration, localizability, exploitability and transmissibility may drive modality-specific costs to signalling (table 1). A general prediction being that modalities with reduced ranges, shorter durations, and/or brief transmission speed—as typifies visual and tactile signals should comparatively reduce the threat to signallers. As a corollary, the increased range, duration, and transmissibility of olfactory and auditory signals should lead to heightened risks to signallers on balance. We note, however, that such functional differences will be reduced and/or eliminated in eavesdropper preference assays owing to the close quarters, forced-choice experimental designs, among myriad other differences imposed by the artificiality of laboratory-based settings. And so these predictions are unlikely to hold.

We also classified the focal eavesdropping receiver in each study as either predators, parasites or parasitoids. Here we predicted stronger effects among parasitoids owing to typically higher rates of prey (and hence, sexual signal) specialization as compared to predators and parasites, which tend toward generalism. However, we recognize a suite of factors which broadly covary with these designations such as taxonomy (with parasitoid hosts largely limited to invertebrates [53]), feeding guild, and trophic level, which will serve to temper the strength of our prediction.

Finally we also classified the experimental manipulation of signals as either discrete or continuous. Discrete manipulations are those in which the signal was entirely absent in the control group (e.g. a non-broadcasting speaker, or an unscented stimulus), while continuous manipulations are those in which signal variation was graded between treatment and control groups (e.g. differential volume of mating calls or brightness of visual signals). This is an attempt to control for experimental differences in the magnitude of manipulations across diverse modalities and contexts, and also stands as a test of the consequences of ecologically salient differences in signal variability. Discrete manipulations approximate gross differences between signalling and non-signalling individuals, as is common between sexes or life-history stages, while continuous manipulations represent situations of between-signaller variation, as is typical among individuals competing for mates. Here we predicted that predation risk should be heightened among discretely manipulated stimuli owing to the increased conspicuousness and salience of signallers relative to controls.

(c) Statistical analyses

We constructed both multilevel meta-analytic and multilevel meta-regression models using the metafor package v. 3.0-2 [54] for R v. 4.0.1 [55]. To estimate an overall mean effect we ran intercept-only multilevel random-effects models, with studyand observation-level IDs included as random factors to control for the inclusion of multiple effects per study and to estimate residual variances, respectively. We also controlled for nonindependence arising from the inclusion of effects estimated from shared control groups by fitting the off-diagonal covariances in the sampling covariance matrix assuming a correlation of r = 0.5 [56]. Signaller taxon and study were broadly confounded in our dataset, which argues for the inclusion of either a study- level or phylogenetic random effect to account for the possibility of phylogenetic non-independence, but not both. We favour the former for simplicity as several studies were conducted above the level of species, and because between-study variances are more commonly modelled in meta-analyses [57].

To examine the effects of the three moderators described above—modality, eavesdropper, and manipulation—we constructed separate univariate multilevel random-effects models with the random effects structure as above. We examined the $Q_{\rm m}$ statistic, an omnibus test of model coefficients, to determine whether moderators significantly influenced the mean effect size, and estimated the amount of variance explained by the fixed factors in each meta-regression model via the marginal R^2 [58]. Where an omnibus test was significant we performed pairwise *post-hoc* Tukey contrasts for each moderator level with Holm's method to control the family-wise error rate [59], using the R package multcomp v. 1.4-17 [60]. To estimate the heterogeneity of effect sizes we use both I^2 , which we partitioned at the levels of study and observation ID [57], and we calculated 95% prediction intervals for meta-analytic means and all moderator levels [61]. In all models, we considered effect size estimates whose 95% confidence intervals did not overlap zero to be statistically significant.

(d) Publication bias

We explored the possibility of small-study effects, including publication bias, via the visual inspection of funnel plots supported by Egger's regression [62] and trim-and-fill tests using the R_0 estimator [63]. In both cases we fitted study precision (the inverse of sampling variance) against meta-analytic residuals derived from our null models with the full random effects structure described above, to account for the multilevel structure of our data [57].

3. Results

(a) Eavesdropper preference

We obtained 72 effects from 29 studies examining eavesdropper preferences for sexual signalling individuals (or the sexual signals of individuals) in forced-choice assays [26,30, 43,45,46,64–85]. Some 23 species were represented among signallers across five classes, with studies involving insects (k =49) predominating over ray-finned fishes (k = 12), amphibians (k = 6), arachnids (k = 4), and mammals (k = 1). Predators (k =34) and parasitoids (k = 38) were approximately equally represented among eavesdroppers, with fish (k = 10) and mammals (k = 9) the most common predators and wasps (k = 34) the most common parasitoid. We found no studies involving parasites. Studies of olfactory signals predominated (k = 31), with vibratory, auditory, and visual signals near equally common (k = 13, 13, 15, respectively).

Overall, we identified a moderate to strong preference of eavesdroppers for individuals bearing sexual signals (mean proportion = 0.712, 95% CI = 0.657–0.762, k = 72; figure 1). This held irrespective of the signal's modality (figure 1; see electronic supplementary material, tables S1 and S2 for full numerical results henceforth), as predicted, and neither the signal receiver nor the nature of the experimental manipulation modulated this result (figure 2). That is, we found a clear preference for signalling individuals (or their signals alone) across all MLMR models (figures 1 and 2). There was strong heterogeneity both overall (I^2 = 0.645, 95% CI = 0.562–0.717) and among subgroups (table 1), and relatively wide prediction intervals affirmed the existence of considerable variation in outcome measures (figures 1 and 2).

In terms of publication bias, inspection of the funnel plot revealed a weak asymmetry in the distribution of effects, with an under-representation of lower-powered, negative outcomes (electronic supplementary material, figure S2). This was affirmed by a significant intercept in our Egger's test (est = -1.215, z = 6.012, p < 0.001). A trim-and-fill analysis suggested the possible absence of five effects, whose addition



Figure 1. Forest plots depicting the meta-analytic mean effect of sexual signalling on the preference of predators eavesdroppers (*a*) and the risk of predation eavesdropping (*b*), as well as the mean effects within each signalling modality as estimated via moderator analyses. For preference assays the displayed effects are proportions back-transformed from logits, while Hedges's g was used to summarize the results of predation risk assays. Points are scaled by the precision of each estimate, and solid lines denote 95% confidence intervals while broken lines indicate 95% prediction intervals. (Online version in colour.)

slightly reduced the estimated meta-analytic mean (mean proportion = 0.642, 95% CI = 0.597–0.702, k = 72). The relative subtlety of both the asymmetry and adjusted estimate suggest that any underlying publication bias is exerting only a weak effect, however.

(b) Eavesdropping risk

We collated 115 effects from 49 studies which quantified the eavesdropping risk to sexual signalling individuals [10,12,21, 23-25,40-43,47-49,86-120]. Approximately 58 species were used as signallers, with insects (k = 55), reptiles (k = 21), and amphibians (k = 20) the best represented groups. A minority of studies drew on 'generic' representations of signals or signallers above the species level, and most manipulated model rather than live animals, thereby negating any effects of signaller behaviour (see discussion). The responses of predators (k =66) were more often the focus than parasitoids (k = 40), and those involving parasites (k = 9) were uncommon. The available effects were unequally distributed across signalling modalities. Olfactory signals were again the most common (k = 57), followed by visual (k = 30) and auditory (k = 28), and we found no suitable effects from studies of vibratory signalling in the wild.

We found a strong positive mean effect overall, suggesting heightened eavesdropping risk for individuals bearing sexual signals (mean g = 0.958, 95% CI = 0.652–1.264, k = 115;

figure 1). Here, unlike among eavesdropper preference assays, the effects varied by modality (figure 1). Consistent with our predictions, both olfactory and auditory signals increased eavesdropping risk to a greater extent than visual signals, and were strong and positive on-average (electronic supplementary material, table S2). We found no evidence for an effect of visual sexual signalling on the risk of predation, however, with the confidence interval from our MLMR including zero (figure 1). Indeed, the prediction interval for the visual modality was nearly symmetrical about the value of zero, suggesting that conspicuous visual sexual signals are almost as likely to decrease as increase the risk of eavesdropping by predators in the wild. Effects were strong and positive across eavesdropper types, though our prediction of significantly heightened risk from parasitoids, as compared to predators and parasites, was not supported (figure 2). The direction of the difference in mean effects between eavesdroppers was in the predicted direction, though the small sample of effects from parasites (k = 9) is limiting. The estimated mean effect was also positive across both types of experimental manipulation, though only weakly so among studies that induced continuous, graded variation in signal expression (figure 2). Counter to predictions, we found no difference in average effects between discrete and graded signal manipulations. Heterogeneity was high across all measures (table 2; $I^2 = 0.865$, 95% CI = 0.835–0.889), and prediction intervals wide and reaching beyond zero in all MLMR models



Figure 2. Forest plots denoting moderators of effect size estimates from studies of predator eavesdropper preferences for, or predation eavesdropping risk to, individuals bearing sexual signals. The effects are proportions back-transformed from logits for preference assays, and Hedges's *g* for predation risk assays. 'Eavesdropper' describes the guild of the unintended receiver(s), while 'manipulation' describes the magnitude of the difference in sexual signal expression between treatment and control group. Discrete manipulation represent cases of presence/absence between group, while continuous manipulations are those which introduce graded variation between treatments and controls. Points are scaled by the precision of each estimate, and solid lines denote 95% confidence intervals while broken lines indicate 95% prediction intervals. (Online version in colour.)

Table 2. The results of meta-regression models examining moderators of effect sizes among eavesdropper preference and eavesdropping risk assays. Significance was determined via Q_m test for all fixed effects, marginal R^2 is the amount of variance explained by each fixed factor, and l^2 is an estimate of effect size heterogeneity. Each factor was tested using a separate multi-level mixed-effects model with a single fixed factor and two random factors (study ID and observation ID), while controlling for non-independence arising from shared controls within studies.

Context	moderator	d.f	Q _m	р	R ²	l ²
eavesdropper preference	modality	4	44.248	<0.001	0.076	0.832
	eavesdropper	2	49.590	<0.001	0.052	0.806
	manipulation	2	46.694	<0.001	0.008	0.816
eavesdropping risk	modality	3	61.454	<0.001	0.161	0.927
	eavesdropper	3	45.141	<0.001	0.073	0.935
	manipulation	2	36.750	<0.001	0.013	0.940

(electronic supplementary material, table S2), revealing strong variability in outcomes.

Here too inspection of the funnel plot revealed some evidence of asymmetry, with apparent missing effects in the lower left (electronic supplementary material, figure S2). This was supported by Egger's regression (est = -0.926, z = 5.277, p < 0.001), and our trim-and-fill analysis suggested up to 17 unreported effects. Adjusting to explore the influence of these 'missing' effects reduced the meta-analytic mean (mean g = 0.759, 95% CI = 0.436-1.082, k = 115), though again the difference was relatively minor and the overall estimated effect remained moderate to strong. This suggests a weak influence of any publication bias, though we acknowledge its possible existence and inflationary influence on model estimates when interpreting our results.

4. Discussion

Signalling to potential mates is often central to reproduction, though it brings with it the risk of eavesdropping by predators. Here we examined this predicted cost of sexual signalling in a meta-analysis of experimental studies. We found evidence for strong preferences for sexual signals by predators and parasites in a forced-choice context, which held irrespective of the signalling modality, the type of eavesdropper, or the nature of the experimental manipulation (figures 1 and 2). Under more natural conditions we found a similarly moderate to strong average effect, suggesting a heightened risk to signallers in the wild. This varied in a modality-specific manner as predicted (table 1), with the greatest costs borne by olfactory and auditory signals (figure 1). Curiously, however, the incidence of predation on visual signallers was not only reduced relative to other modalities, but was on average indistinguishable from nonsignalling controls. Further, we found substantial variation in outcomes across all modalities and contexts (electronic supplementary material, table S2), which suggests that circumstances under which signals incur no costs, or even reduce the burden of eavesdropping, should be common. The persistence of high heterogeneity across all models, however, also emphasizes the role of unmeasured differences in methodology and ecology between studies in shaping the distribution of effects. Contrary to our expectations, we found no statistical difference in average effects based on the type of eavesdropper or the nature of the experimental manipulations, though in both cases the weak estimated differences were in the predicted direction.

The clear preference for signallers (or their signals in isolation) expressed by eavesdroppers is unsurprising (figure 2), for two reasons. One is the salience of signals relative to controls. Selection, in general terms, favours increased conspicuousness in signals as a consequence of both the need for detectability amid environmental noise [27] and concurrent sexual selection favouring elaboration via runaway or indicator processes, or the exploitation of sensory biases [121]. All else being equal, this heightened salience of signals over controls will naturally attract the interest of viewers. The other reason is the perception of stimulus identity or category. Predators and parasites rely on informative cues such as the colours, calls and odours which characterize sexual signals—as a guide to potential prey [12,21]. The preference for signals is therefore interpretable as a preference for likely prey, given that most studies focus on interactions between signallers and their known, ecologically relevant eavesdroppers (e.g. [43,74,83]). The absence of modality-, manipulation- and predator-specific variation in the average strength of preferences (figures 1 and 2) is similarly unsurprising under a forced-choice experimental paradigm since most of the functional differences between signals (table 1) are negated in a laboratory setting. This also emphasizes the need for caution when extrapolating laboratory-based results to realized predation in the wild, where the effects of signal ecology are rendered apparent (electronic supplementary material, table S2).

The moderate to strong increase in eavesdropping risk we identified is consistent with the results from preference assays, though the concordance largely ends there. Of particular significance is the modality-specific nature of costs, with olfactory and auditory signals attracting heightened risk relative to visual signals (figure 2). This accords with signalling theory which, in general terms, describes how differences in the propagation of signals through natural environments underlies differential predation risk [29,122] (table 1). The on-average absence, and sometimes reduction, of risk associated with visual sexual signals is curious, but affirms recent work showing that predators impose no cost when their exposure to prey signals is infrequent, owing to neophobia and/or dietary conservatism [47]. Such effects are both widespread and common among predators [123], which therefore stands as a general working hypothesis for the modality-specific differences in outcomes seen in the current evidence base (figure 1). We also briefly note that this result touches on the 'paradox of aposematism' inasmuch as it suggests that, contrary to expectation, conspicuous but undefended prey may simply bear no additional predation cost in the wild (figure 1), thereby allowing the subsequent evolution of defences [124].

It should be remembered that most studies in our sample necessarily discounted the influence of behaviour by both signallers and predators. In that sense our estimates can be understood as representing the baseline risk of predation absent any adaptations for actively enhancing and/or subverting the privacy of communication. Such innovations are well documented (e.g. [125,126]). Predicting their form and occurrence, however, is an enduring challenge for which knowledge of the signal features that drive differential risk offers some guide (table 1). Visual signallers should seek to minimize their localizability, for example, through the coupling of highly directional signals with precision displays, as seen among iridescent insects (e.g. [127,128]). While auditory signallers may temper the reach of calls by shifting frequencies, or even modalities (from higher- to lower-risk; figure 1), under threat of predation, as seen among forest-dwelling katydids [129-131]. Fully appraising such possibilities demands deeper knowledge of the structure and diversity of sensory environments, signals, and receivers, which remain valuable avenues for future work [132].

Our findings also reach into applied domains, as reflected in the breadth of fields captured in our evidence survey (electronic supplementary material, table S1). Predicting and responding to biotic invasions is a pressing conservation challenge, for one, with recent work emphasizing the importance of cue recognition in mediating interactions between invasive and native species [36,37]. That visual signals attract minimal cost (figure 1), for example, suggests conspicuous

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ornaments will present little impediment to introduced species becoming invasive. This is consistent with general evidence for neophobia among predators, as well as the importance of search-image formation in guiding visual foragers [123]. By contrast, the heightened risk associated with olfactory signals is laid bare in work showing the rapid exploitation of such information by invasive predators (e.g. [36]). This dynamic also presents opportunities, however, with recent studies deliberately familiarising invasive predators with unrewarding odours and, in doing so, improving outcomes for vulnerable prey [133,134].

Similar efforts to 'weaponize' eavesdropping are ongoing in pest management, where the encouragement of natural predators is central to contemporary control methods [38]. The strong effects associated with parasitoids and parasites (albeit with a very limited sample of the latter; figure 2), and the heightened influence of olfactory and auditory signals over visual (figure 1), suggest them as profitable targets for future strategies. This aligns with a substantial body of work centered on developing artificial, bio-inspired kairomones from the sex pheromones of key pests such as aphids and moths [39,135]. The substantial variation in effects we found however, as captured in wide prediction intervals, suggests artificial lures may benefit from redundancy across modalities for improved efficacy (given the unreliability of any single modality, on average; electronic supplementary material, table S2), and supports more general calls for multimodal solutions to control problems [136].

The study of sexual communication has driven general advances in theory and its application [121,135]. That signals capture the interest of eavesdroppers and increase the risk of

predation, but in a variable and modality-specific manner, anchors our understanding of a central cost to sexual communication, and sex more generally [8,121]. Much remains to be learned, however. Signalling in vibratory and electric modalities is sorely understudied in all respects and warrants further general attention. As does the extent to which plasticity, including behaviour, can dynamically balance the demands of signalling with the foundational costs of predation described here. Multimodal systems present promising, albeit underused, sources for progress on all fronts, including open problems of signal evolution amid sustained eavesdropping (e.g. [137]). These are exciting areas for progress on questions of broad significance.

Data Accessibility. All data and code necessary to reproduce our analyses are publicly available via GitHub (https://github.com/EaSElab-18/ ms_metarisk) and are persistently archived via Zenodo at https:// doi.org/10.5281/zenodo.6534204 [138].

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analysis, methodology, visualization, writing—original draft, writing—review and editing; T.L.: conceptualization, data curation, validation, writing—review and editing; K.D.L.U.: conceptualization, data curation, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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The exploitation of sexual signals by predators: a meta-analysis Supplementary material

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Supplementary methods

$Systematic\ literature\ search$

We sought to gather an extensive, representative sample of evidence in two ways. For one, we systematically searched the scientific literature via two bibliographic databases — Web of Science, and Scopus and two thesis databases — Open Access Theses and Dissertations, and Proquest Theses and Dissertations — on June 29 2021. We designed our search terms to favour sensitivity over specificity given the breadth of empirical contexts (both fundamental and applied) in which our focal questions have been tested. Following refinement and sensitivity testing against a pre-selected set of 20 articles (with a 90% retrieval rate for each database taken as a heuristic threshold), we ultimately used the search string: ("sex*" OR "social" OR "courtship" OR "conspicuous*" OR "mate" OR "mating") AND ("signal*" OR "ornament" OR "communicat*" OR "cue" OR "display" OR "pheromone" OR "kairomone" OR "call" OR "vocali" OR "song" OR "olfact*") AND ("predat*" OR "risk*" OR "eavesdrop*" OR "attack" OR "exploit*" OR "parisit*" OR "locali*" OR "trap*") NOT (human OR people OR adolescen* OR child* OR media OR aposemat* OR warn^{*} OR phylo^{*} OR plastic^{*}). In the Web of Science we searched the entire Core Collection, and refined the results by the subject areas of Zoology, Ecology, Behavioural Sciences, Entomology, Evolutionary Biology, and Biology, which yielded 5622 results. In Scopus we refined by the topics of Agricultural and Biological Sciences, and Environmental Sciences, which ultimately returned 4866 results. Secondary to our database search, we performed forward (cited-by) and backward (citing) searches of the reviews of Zuk & Kolluru [1], Kotiaho [2], Magnhagen [3], and Hughes et al. [4].

Study selection and screening

Guided by the PICOS framework [5], we included studies which experimentally tested the consequences of the presence/absence or magnitude of expression of an animal's sexual signal for predation or parasitism. We included studies of live animals, as well as those which examined only the signals themselves (e.g. isolated sex pheromones or broadcast mating calls set amidst traps). In terms of experimental designs, for eavesdropper preference assays we included studies which presented predators with a simultaneous choice of manipulated signals or signallers, while eavesdropping risk experiments must have employed manipulative assays in which treatment and control stimuli were continuously exposed under natural or semi-natural conditions. All included studies could have considered signals in any modality—namely acoustic, visual, olfactory, and vibratory—and must have directly manipulated the presence or absence of a signal or its magnitude. We also required that they report discrete measures of the intensity of predation or parasitism, or proxies thereof, such as the number of predatory attacks on model organisms or the number of parasites caught in traps, as borne by the signaller itself or related parties in a mating context (such as prospective mates or offspring, though these were rare). Experimental treatments could have involved the manipulation of either 'natural' signals (e.g. the presence/absence of a previously recorded call, or dulling of colour patch on a wild-collected animal), or synthetic ones (as in artificial models of visually ornamented animals, or the chemical synthesis of natural sex-pheromone blends).

We excluded studies which did not meet the above criteria, such as those which did not directly manipulate the expression of a sexual signal, which lacked a suitable comparator (a signal-absent or lessconspicuous treatment; also described below), or which recorded outcomes not directly interpretable or interchangeable as discrete measures of 'choice' in eavesdropper preference assays (such as time spent near a stimulus), or predation or parasitism intensity in eavesdropping risk assays (such as localisability). These criteria also necessarily excluded review articles, commentaries, and purely theoretical or modelling-based analyses (see table S1 for full inclusion/exclusion list).

Given the resulting volume of literature from our search (n = 6342 studies following duplicate removal: Fig S1), we screened for relevance in three stages: title only, title and abstract, and full text. At each stage we included all studies which could not be unambiguously excluded with reference to the above-detailed inclusion/exclusion criteria. From an initial pool of 6342 unique articles we retained 347 following title screening, and 160 following title and abstract screening, with 29 eavesdropper preference studies and 49 eavesdropping risk studies ultimately appropriate for synthesis following full-text evaluation (Fig. S1).

Following the initial full text processing and data extraction from eavesdropping risk experiments, we secondarily excluded all effect sizes which were estimated from contrasts in which either the treatment or comparator groups recorded zero events. That is, outcomes in which either the treatment and/or control groups recorded no attacks (or equivalent) by predators. This was initially motivated by the observation of excessive records of zero among control groups, and consequent extreme outliers in the resulting effect sizes estimate (Fig. S2). Indeed, among the 101 effects ultimately excluded (from an initial pool of 216), the records of zero events were entirely confined to comparator groups. We therefore excluded these for two reasons. The first is biological implausibility, as they suggest the complete absence of predation on nonsignalling individuals which is ecologically unlikely. The second is that the inclusion of such effects violates the distributional assumptions of our meta-analytic models using Hedge's g, and gives rise to extreme outliers and biased meta-analytic estimates (since all were confined to control groups) as a consequence of calculating differences against comparators with zero means and standard deviations. This process ultimately saw the exclusion of 14 additional studies (Table S1), resulting in the total included effects and studies reported below.

Supplementary figures and tables



Figure 1: PRISMA diagram depicting the systematic search and screening outcomes for empirical studies examining the predation cost of sexual signals.



Figure 2: The distribution of effects from predation-risk assays before (left) and after (right) the removal of outcome measures which were calculated from contrasts in which one group recorded zero events. Among the 101 effects excluded, the records of zero events were entirely confined to control groups, and we excluded them of the grounds of biological implausibility (i.e. the implication of no baseline predation; see main test) and statistical invalidity.



Figure 3: Funnel plots of study precision against conditional residuals from multi-level meta-analyic null models, for both predator preference (left) and predation risk (right) data. Both reveal slight asymmetry and hence the possibility of publication bias, as supported by Egger's regression and trim-and-fill analyses, though the adjusted estimates are only slightly reduced (see main text).

Table S1: Studies included in the final meta-analyses examining predator preferences for sexual signals and/or the predation risk of sexual signalling. Also noted are studies which were excluded at the full-text screening stage, along with the associated reason.

Author	Year	Signaller taxon	Predator taxon	Modality	Exclusion reason
Ahmadi & Poorjavad	2018	insecta	hymenoptera	olfactory	
Amdekar & Thaker	2019	reptilia	aves	visual	
Arakaki et al.	1996	insecta	hymenoptera	olfactory	
Arakaki et al.	2011	insecta	hymenoptera	olfactory	
Baird	2009	reptilia	aves	visual	
Benelli et al.	2014	insecta	hymenoptera	olfactory	
Bernal & de Silva	2015	amphibia	diptera	auditory	
Bernal et. al.	2006	amphibia	diptera	auditory	
Biagolini-Jr & Perrella	2020	aves	aves	visual	
Boo et al.	2004	insects	neuroptera	olfactory	
Bulbert et al.	2015	arachnida	arachnida	visual	
Cade	1975	insecta	diptera	auditory	
Cain et al.	2019	aves	aves	visual	
Caldart et al.	2016	amphibia	diptera	auditory	
Clark et al.	2016	arachnida	reptilia	visual	
Cushing	1985	mammalia	mammalia	olfactory	
Ellingson	1994	reptilia	aves	visual	
Fowler-Finn & Hebets	2011	arachnida	arachnida	visual	
Franco et al.	2011	insecta	hymenoptera	olfactory	
Fugere et al.	2015	amphibia	mammalia	auditory	
Gabrys et. al.	1997	insecta	hymenoptera	olfactory	
Geipel et al.	2020	insecta	mammalia	vibratory	
Glinwood et al.	1998	insecta	hymenoptera	olfactory	
Glinwood et al.	1999	insecta	hymenoptera	olfactory	
Glinwood et al.	2010	insecta	hymenoptera	olfactory	
Godin & McDonough	2003	actinopterygii	actinopterygii	visual	
Gotmark	1994	aves	aves	visual	
Hardie et al.	1991	insecta	hymenoptera	olfactory	

Hardie et al.	1994	insecta	hymenoptera	olfactory
Harris & Todd	1980	insecta	diptera	olfactory
Hendrichs et al.	1994	insecta	hymenoptera	olfactory
Holt & Johnson	2009	actinopterygii	actinopterygii	auditory
Hughes et al.	2010	reptilia	mammalia	olfactory
Huigens et al.	2010	insecta	hymenoptera	olfactory
Huigens et al.	2011	insecta	hymenoptera	olfactory
Johnson & Candolin	2017	actinopterygii	actinopterygii	visual
Koczor et al.	2010	insecta	neuroptera	olfactory
Koivula & Korpimaki	2003	mammalia	multiple	olfactory
Laumann et al.	2007	insecta	hymenoptera	vibratory
Laumann et al.	2011	insecta	hymenoptera	vibratory
Legett et al.	2021	insecta	diptera	auditory
Lehmann & Heller	1998	insecta	diptera	auditory
Lindstrom et al.	2006	insecta	aves	auditory
Lloyd & Wing	1983	insecta	coleoptera	visual
Marshall et al.	2015	reptilia	aves	visual
Martin & Wagner	2010	insecta	diptera	auditory
Mendel	1995	insecta	hemiptera	olfactory
Mendel et. al.	2004	insecta	anthocoridae	olfactory
Merritt et al.	1993	insecta	hymenoptera	olfactory
Meuche et al.	2016	reptilia	diptera	auditory
Mitchell & Mau	1971	insecta	diptera	olfactory
Modarressie et al.	2013	actinopterygii	actinopterygii	visual
Moodie	1972	actinopterygii	actinopterygii	visual
Moyaho et al.	2004	actinopterygii	reptilia	visual
Muller, P; Robert, D	2002	insecta	diptera	auditory
Nakashima et al.	2016	insecta	hymenoptera	olfactory
Olsson et al.	1993	reptilia	aves	visual
Ord et al.	2021	reptilia	aves	visual
Pestana et al.	2020	aves	aves	visual
Pocklington & Dill	1995	actinopterygii	actinopterygii	visual

Ponce-Wainer & del Castillo	2008	insecta	hymenoptera	auditory	
Powell et al.	1993	insecta	hymenoptera	olfactory	
Pruden & Uetz	2004	arachnida	arachnida	visual	
Rivera et al.	2017	insecta	multiple	olfactory	
Ruiz-Rodriguez et al.	2012	aves	aves	visual	
Ryan et al.	1982	amphibia	mammalia	auditory	
Saavedra & Amo	2018	insecta	aves	olfactory	
Sakaguchi & Gray	2011	insecta	aves	olfactory	
Svensson et al.	2003	insecta	coleoptera	olfactory	
Stuart-Fox et al.	2002	reptilia	aves	visual	
Swierk et al.	2010	reptilia	aves	visual	
Toma et al.	2005	amphibia	diptera	aural	
Toma et al.	2019	amphibia	diptera	aural	
Tuttle & Ryan	1981	amphibia	mammalia	aural	
Tuttle & Ryan	1982	amphibia	mammalia	aural	
Vazquez et al.	2015	reptilia	aves	visual	
Woods et al.	2007	insecta	diptera	visual	
Xue et al.	2018	insecta	coleoptera	olfactory	
Ylonen et al.	2003	insecta	mammalia	olfactory	
Zhang et al.	2016	mammalia	felis	olfactory	
Aihara et al.	2016				Unsuitable treatment
Aldrich et al.	2007				Insufficient data
Ambrozio-Assis et al.	2018				Unsuitable comparator
Arakaki et al.	1997				Zero record in control group
Arif et al.	2021				Unsuitable outcome
Bailey & Haythornthwaite	1988				Unsuitable treatment
Beckers & Wagner Jr	2012				Insufficient sample size
Bell	1979				Insufficient sample size
Boo & Yang	2000				Unsuitable outcome, design
Borkent & Belton	2006				Unsuitable comparator
Branco et al.	2006				Zero record in control group
Branco et al.	2011				Zero record in control group

Buchler & Childs	1981	Unsuitable comparator, outcome
Cade	1981	Unsuitable comparator
Cade et al.	1996	Unsuitable comparator
Camp et al.	2018	Zero record in control group
Charles et al.	2015	Unsuitable comparator
Clark et al.	2018	Unsuitable comparator, outcome
Cummings et al.	2002	Unsuitable outcome
Dias et al.	2010	Unsuitable treatment
Dixon & Payne	1980	Unsuitable outcome
Dougherty et al.	2002	Unsuitable treatment
Ei-Sayed et al.	2009	Unsuitable design
Endler	1980	Insufficient data
Farris et al.	2008	Unsuitable comparator
Fowler	1987	Irretrivable
Fowler & Garcia	1987	Unsuitable treatment
Glinwood et al.	1999	Unsuitable comparator
Gomes et al.	2017	Zero record in control group
Grafe et al.	2008	Unsuitable design
Grant et al.	2015	Unsuitable comparator
Gray et al.	2007	Unsuitable comparator
Halfwerk et al.	2014	Unsuitable outcome
Hobel et al.	2014	Unsuitable comparator
Hodges & Dobson	1998	Unsuitable outcome
Hoefler et al.	2008	Unsuitable design
Hughes & Banks	2011	Unsuitable comparator, design
Hunt & Allen	1988	Zero record in control group
Husak et al.	2006	Unsuitable comparator
Koczor	2015	Nonsexual signal
Koedam et al.	2011	Unsuitable design
Kotiaho et al.	1998	Unsuitable design
Landolt & Zhang	2016	Unsuitable comparator
Legett et al.	2019	Unsuitable treatment

Lehmann et al.	2001	Unsuitable outcome
Losel et al.	1996	Zero record in control group
Mangold	1978	Insufficient data
Millar et al.	1996	Unsuitable comparator
Mougeot & Bretagnolle	2000	Unsuitable outcome
Muller & Robert	2001	Unsuitable outcome
Noldus et al.	1991a	Unsuitable outcome
Noldus et al.	1991b	Unsuitable outcome
Page & Ryan	2008	Zero record in control group
Raghuram et al.	2015	Unsuitable outcome, design
Rhebergen et al.	2015	Insufficient data
Rice	1969	Unsuitable design, outcome
Roberts et al.	2007	Insufficient data
Rodrigo et al.	2013	Unsuitable outcome
Rosenthal et al.	2001	Unsuitable comparator, design
Sakaluk & Belwood	1984	Unsuitable treatment, outcome
Scholler & Prozell	2002	Zero record in control group
Soper et al.	1976	Insufficient data
Sternlicht	1973	Unsuitable comparator
Stucky	2016	Unsuitable treatment
Suckling et al.	2002	Insufficient data
Tillman et al.	2010	Zero record in control group
Tinghitella et al.	2021	Unsuitable design
Tsueda, H	2014	Unsuitable comparator
Tuttle et al.	1981	Unsuitable comparator
Tuttle et al.	1985	Unsuitable outcome, design
Viitala et al.	1995	Unsuitable outcome
Virant-Doberlet et al.	2011	Zero record in control group
Virgo et al.	2019	Unsuitable comparator
Wagner & Basolo	2007	Insufficient data, sample size
Wagner jr	1996	Unsuitable comparator
Walker	1964	Zero record in control group

Walker	1986	Zero record in control group
Walker	1993	Unsuitable treatment
Wei et al.	2008	Unsuitable design
Wing	1988	Unsuitable comparator
Xu et al.	2014	Zero record in control group
Zhang & Aldrich	2004	Unsuitable design

Table S2: Full results from our multi-level meta-analytic and meta-regression models, which synthesise outcomes from experimental studies examining both predator preferences for sexual signalling organisms, or the predation risk to signallers in the wild. 'Modality' refers to the modality of the signal, 'eavesdropper' is the guild of the focal unintended receiver, and 'manipulation' refers to the experimental manipulation of the signal (be it the discrete presence/absence of a signal between treatment and control groups, or continuous, graded variation between the two).

	Est.	Lower CI	Upper CI	Lower PI	Upper PI	n
Eavesdropper preference						
Null						
intercept-only	0.712	0.656	0.762	0.416	0.896	72
Modality						
auditory	0.707	0.553	0.824	0.354	0.913	13
olfactory	0.765	0.672	0.838	0.444	0.929	31
visual	0.669	0.556	0.765	0.331	0.892	15
vibratory	0.702	0.512	0.841	0.333	0.918	13
Eavesdropper						
parasitoid	0.676	0.586	0.755	0.372	0.881	38
predator	0.736	0.666	0.796	0.445	0.906	34
Manipulation						
continuous	0.692	0.576	0.788	0.371	0.895	17
discrete	0.720	0.655	0.778	0.418	0.902	55
Eavesdropping risk						
Null						
intercept-only	0.958	0.652	1.264	-1.355	3.271	115
Modality						
auditory	1.316	0.726	1.906	-0.881	3.514	28
olfactory	1.328	0.921	1.735	-0.806	3.462	57
visual	0.260	-0.213	0.733	-1.909	2.430	30
Eavesdropper						
parasite	1.526	0.554	2.498	-0.911	3.962	9
parasitoid	1.291	0.759	1.823	-1.006	3.588	40
predator	0.703	0.322	1.084	-1.564	2.971	66
Manipulation						
continuous	0.688	0.032	1.344	-1.728	3.103	25
discrete	1.016	0.664	1.367	-1.356	3.387	90

Table S3: The full results of post-hoc tests of moderator levels in our multi-level meta-regression models. 'Modality' refers to the modality of the signal, 'eavesdropper' is the guild of the focal unintended receiver, and 'manipulation' refers to the experimental manipulation of the signal (be it the discrete presence/absence of a signal between treatment and control groups, or continuous, graded variation between the two).

	Est.	s.e.	Z	р
Eavesdropper preference				
Modality				
olfactory - auditory	0.278	0.414	0.720	0.887
vibratory - auditory	-0.024	0.534	-0.044	1.000
visual - auditory	-0.175	0.418	-0.419	0.975
vibratory - olfactory	-0.321	0.474	-0.677	0.904
visual - olfactory	-0.473	0.340	-1.393	0.497
visual - vibratory	-0.152	0.478	-0.318	0.989
Eavesdropper				
predator - parasite	0.286	0.262	1.089	0.276
Manipulation				
discrete - continuous	0.137	0.300	0.453	0.650
Eavesdropping risk				
Modality				
olfactory - auditory	0.014	0.363	0.040	0.999
visual - auditory	-1.05	0.382	-2.760	0.015
visual - olfactory	-1.07	0.316	-3.375	0.002
Eavesdropper				
predator - parasite	-0.235	0.565	-0.415	0.907
parasitoid – parasite	-0.235	0.564	-0.415	0.907
predator - parasitoid	-0.588	0.334	-1.760	0.176
Manipulation				
discrete - continuous	0.335	0.368	0.910	0.363

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