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Animal behaviour

Do animals generally flush early and avoid the rush? A meta-analysis

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Optimal escape theory predicts that animals should balance the costs and benefits of flight. One cost of not fleeing is the ongoing cost of monitoring an approaching predator. We used a phylogenetic meta-analysis to test the general hypothesis that animals should initiate flight soon after they detect a predator—the ‘flush early and avoid the rush’ hypothesis. We found a large, significant overall relationship between the distance at which animals were approached or first detected a threat and the distance at which they fled. While these results are the first general test of the flush early and avoid the rush hypothesis, future work will be required to determine whether animals flush early to reduce ongoing attentional costs, or if they flush early as a form of risk reduction.

1. Introduction

Optimal escape theory predicts that individuals balance the costs and benefits of fleeing from predators [1–3]. Blumstein [4], recently, proposed one potential general rule in behavioural ecology which stated that animals should initiate flight soon after they detect a threat so as to reduce or to minimize ongoing attentional costs of monitoring the approaching predators. The flush early and avoid the rush hypothesis predicts that there should be a positive relationship between the predator’s starting distance (SD) or prey’s alert distance (AD) and flight initiation distance (FID). Previous support for the hypothesis came from testing the significance of correlations within a species, but these relationships are not always found [5,6]. Moreover, it is well known that statistical significance—on which such studies are based—is not synonymous with biological significance, and that there are some shortcomings of null hypothesis significance testing (e.g. lack of significance due low power; [7,8]). By contrast, estimating the effect size of a relationship gives us an estimate of the magnitude and direction of a phenomenon of interest and provides a better opportunity to understand the biological importance of a relationship [8].

Phylogenetic meta-analysis is a powerful effect size-based tool that overcomes many of the statistical limitations that may affect primary studies, beyond accounting for non-independence between species [8–10]. Hence, we conducted a phylogenetic meta-analysis to rigorously evaluate the flush early and avoid the rush hypothesis. We asked two broad questions. First, is there a uniform relationship between SD or AD and FID, and if so, what is its magnitude? Secondly, is there significant heterogeneity across taxa, and if so, what are the patterns?

2. Material and methods

(a) Data collection

To compile studies, we first searched the literature using Web of Science and Scopus for papers that cited [2] and retained those that tested the relationship between SD

Table 1. The combined effects of SD or AD on FID. Mean effect size (r), confidence interval of 95% (CI), number of species tested (spp.), total number of individuals tested (total N), degree of heterogeneity in effect size within the group (I^2), the number of studies reporting no effect to nullify the observed effect and rank correlation test to assess possible bias in publication (rank correlation).

group	r	CI	spp.	total N	I^2 (%)	fail-safe number	rank correlation (P)
birds	0.66	0.56–0.74	79	4456	96.6	39 941	0.888
mammals	0.70	0.48–0.84	7	676	98.4	746	0.764
lizards approached slowly	0.20	0.07–0.33	6	230	0	1	0.452
lizards approached rapidly	0.59	0.44–0.71	3	208	10.7	53	0.296

Table 2. Pairwise comparison (z and (p -value)) between mean effect sizes of different groups. Values in italic indicate statistical significance (i.e. $p < 0.008$).

	birds	mammals	lizards approached slowly
mammals	0.36 (0.720)		
lizards approached slowly	5.55 (<i>< 0.001</i>)	3.45 (<i>0.001</i>)	
lizards approached rapidly	0.87 (0.382)	0.89 (0.371)	3.74 (<i>< 0.001</i>)

(or the highly correlated AD) on FID. In sequence, we searched in the same database for studies published prior to 31 January 2012 using the terms 'SD', 'AD', 'FID', 'flight distance', 'escape distance', 'approach distance', 'flushing distance' and 'response distance'. From these papers, we included studies that had variation in the SD or in the AD (rather than trying to keep it constant across trials) such that its influences on FID could be inferred. From 295 surveyed studies, 25 met the criteria.

We identified five broad taxonomic groups that have been studied: birds, mammals, lizards, snakes and arthropods. Because of insufficient sample sizes ($n = 1$), we excluded snakes and arthropods from phylogenetic meta-analysis (but see the electronic supplementary material, S1). Speed of predator approach is positively associated with FID [11]. Most species were originally studied with a slow approach velocity (mean \pm s.e. = 34.06 ± 1.27 m min⁻¹, $n = 94$), but three (out of six) species of lizards were studied with a faster approach (126.5 ± 6.62 m min⁻¹, $n = 3$). Because of heterogeneity in approach speed, we divided lizards in two groups according to approach speed.

(b) Estimating effect sizes

We used the Pearson's product-moment correlation coefficient, r , as our measure of effect size.

The r -value gives the strength (0, no correlation; 1, completely correlated) and direction (positive or negative) of the relationship between species FID and SD or AD. When possible, we tabulated r directly. When not provided, we used formulae in Rosenthal [12] to calculate r . If the same species was tested by two independent studies, we estimated its r as the weighted mean [13]. For five species, both SD and AD metrics were measured. In these cases, we opted to use the AD because, despite their high correlation, SD is ultimately used as a proxy for AD [2]. Studies have shown that individuals approached from distances shorter than their optimal FID flee immediately, and this can inflate the overall relationship (because $r = 1$ in this zone) [5,6]. To avoid incorrectly overestimating the effect size in a given species because SD was within a zone of immediate flight, we calculated effect sizes from studies that excluded data where animals flushed as soon as the experimenter moved.

(c) Phylogenetic meta-analysis

We fitted a random-model phylogenetic meta-analysis; a meta-analytic framework that explicitly accounts for non-independence of taxa through the inclusion of a covariance matrix containing phylogenetic relatedness [10]. Phylogenetic information from taxa is provided in the electronic supplementary material, S1. For analysis, r -values were transformed to Fisher's z .

Just as in ordinary meta-analysis, the overall mean effect size was calculated as the weighted average r . Estimates were considered significant if their 95% confidence interval (CI) did not include zero [9]. We estimated I^2 as a measure of consistency across species [14]. I^2 represents the proportion of observed variation that is not random error (0%, all error; 100%, no error). As part of our heterogeneity analysis, we used cluster analysis to search for homogeneous groups. To estimate publication bias [15], we used the rank correlation test [16]. Also, we calculated the fail-safe number [17], which is a metric that documents the number of unpublished studies with no effect that would be needed to eliminate an observed effect. We compared groups using z -tests. Multiple comparisons were corrected with Bonferroni correction (accepting as significant $p < 0.008$).

By definition, an approached animal cannot initiate the flight from a distance longer than SD or AD. This constraint can potentially create a spurious relationship between the variables if the variance increases with the distance [18]. To test the robustness of our results, we conducted a sensitivity analysis [9], where we excluded the effect sizes potentially affected by this kind of mathematical artefact (details in the electronic supplementary material, S1). We conducted the analysis with the program PHYLOMET 1.3 [10].

3. Results

Our analysed dataset consisted of 95 species, from 23 studies, that were conducted on 5570 individuals (see the electronic supplementary material, S1). Birds and mammals approached slowly and lizards approached rapidly; all had large, positive and significant overall means (estimates ranged from 0.59 to 0.70; table 1). Pairwise comparison showed that they did not have significantly different effect sizes (table 2). Lizards

approached slowly had substantially and significantly smaller effect sizes than other groups (table 2), yet lizards approached slowly were quite homogeneous (table 1). Within other groups, there was some heterogeneity between species (table 1). An examination of dendrograms was not revealing; there was neither obvious taxonomic split nor did close relatives necessarily respond similarly (see the electronic supplementary material, S1).

With the exception of lizards approached slowly, all other groups had robust results to unpublished studies (table 1). Because effect size of lizards approached slowly differed just slightly from zero, publication of any null effect would change its effect to not different from zero. None of the taxa appeared to have publication biases (see table 1 and electronic supplementary material, S1). Finally, the sensitivity analysis showed that our results remained roughly the same after excluding effect sizes potentially estimated from a spurious relationship (see the electronic supplementary material, S1).

4. Discussion

Do animals flush early and avoid the rush? One recent study questioned the generality of the relationship by suggesting that there might be statistical problems associated with using SD as a proxy for AD [18]. However, another recent paper [19] provided a robust methodology that showed that previous conclusions using different methodologies were supported. Our meta-analysis attempted to control for some of these issues by eliminating data for individuals that flushed immediately, and permitted us to generally test the null hypothesis of no effect [6,19]. Additionally, we were careful to conduct a sensitivity analysis that excluded potential spurious relationships. The results of this additional analysis illustrate the robustness of our results. Indeed, this is the first study to explicitly evaluate and support the 'flush early and avoid the rush' hypothesis by demonstrating a large and positive relationship between SD (or AD) and FID. Moreover, nearly 60 per cent of the estimated effect sizes were large (i.e. $r > 0.5$; following Cohen [7]).

Overall, birds and mammals fled relatively soon when they detected a simulated predator (humans), despite this experimental scenario creating a low-potential risk because the person approached them slowly. By contrast, in lizards, speed of approach influenced the nature of the relationship. Therefore, in birds and mammals, but not lizards, the results

of the meta-analysis are consistent with Blumstein's [4] suggested mechanism of reducing ongoing monitoring costs.

The idea that there is a cost to ongoing monitoring is based on the fact that the ability to focus attention is a limited entity, and thus must be divided among various tasks [20]. For instance, we expect that foraging success will be reduced if attention to monitoring an approaching threat is required. Thus, a prediction from our meta-analysis is that if we were to exclude those taxa with naturally low-cost monitoring, individuals from other species will flee earlier if distracted by other stimuli while being approached (e.g. sounds, multiple threats, etc.). Future studies corroborating this prediction would be consistent with the mechanism based on ongoing monitoring costs.

Based on his work with lizards, Cooper [5] suggested that individuals with relatively low monitoring costs (e.g. sit-and-wait foragers) escaped solely because of the increased risk and not owing to the attentional costs of ongoing monitoring. One possible explanation is that as the duration of a predator's approach increases, prey may assess a greater risk. Furthermore, Cooper [5] developed a methodology that could be used (in some cases) to determine whether reduction of risk (rather than cost) is the factor influencing escape decisions. However, it is also possible that the observed relationship between FID and SD in lizards is the product of a biased sample of foraging mode or phylogenetic similarity (half of the species were phrynosomatid lizards; [6]), as well as of costs and benefits. Thus, we encourage future studies to test lizard species from other clades and with different foraging modes to clarify this issue.

Finally, our meta-analysis identified interspecific variation in flight responses within taxonomic groups, a finding that suggests that species might differentially assess increasing threats. Dendrograms and similar results between phylogenetic and ordinary meta-analysis (see the electronic supplementary material, S1) provide clues that the variation in responses between species was not accounted for by their phylogenetic relationship, suggesting a weak phylogenetic signal for this trait. Future studies that identify the traits or conditions explaining this variation would better help us understand the dynamics of risk assessment.

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References

1. Ydenberg RC, Dill LM. 1986 The economics of fleeing from predators. *Adv. Stud. Behav.* **16**, 229–247. (doi:10.1016/S0065-3454(08)60192-8)
2. Blumstein DT. 2003 Flight initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manag.* **67**, 852–857. (doi:10.2307/3802692)
3. Cooper WEJ, Frederick WG. 2007 Optimal flight initiation distance. *J. Theor. Biol.* **244**, 59–67. (doi:10.1016/j.jtbi.2006.07.011)
4. Blumstein DT. 2010 Flush early and avoid the rush: a general rule of antipredator behavior? *Behav. Ecol.* **21**, 440–442. (doi:10.1093/beheco/arq030)
5. Cooper WEJ. 2005 When and how do predator starting distances affect flight initiation distances? *Can. J. Zool.* **83**, 1045–1050. (doi:10.1139/Z05-104)
6. Cooper WEJ. 2008 Strong artifactual effect of starting distance on flight initiation distance in the actively foraging lizard *Aspidoscelis exsanguis*. *Herpetologica* **64**, 200–206. (doi:10.1655/07-081.1)
7. Cohen J. 1992 A power primer. *Psychol. Bull.* **112**, 155–159. (doi:10.1037/0033-2909.112.1.155)
8. Nakagawa S, Cuthill IC. 2007 Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev. Camb. Philos. Soc.* **82**, 591–605. (doi:10.1111/j.1469-185X.2007.00027.x)
9. Borenstein M, Hedges LV, Higgins JPT, Rothstein HR. 2009 *Introduction to meta-analysis*. Chichester, UK: John Wiley & Sons, Ltd.
10. Lajeunesse MJ. 2009 Meta-analysis and the comparative phylogenetic method. *Am. Nat.* **174**, 369–381. (doi:10.1086/603628)
11. Stankowich T, Blumstein DT. 2005 Fear in animals: a meta-analysis and review of risk assessment. *Proc. R. Soc. B* **272**, 2627–2634. (doi:10.1098/rspb.2005.3251)
12. Rosenthal R. 1991 *Meta-analytic procedures for social research*, 2nd edn. New York, NY: Russel Sage Foundation.

13. Cheung SF, Chan DK-S. 2004 Dependent effect sizes in meta-analysis: incorporating the degree of interdependence. *J. Appl. Psychol.* **89**, 780–791. (doi:10.1037/0021-9010.89.5.780)
14. Higgins JPT, Thompson SG, Deeks JJ, Altman DG. 2003 Measuring inconsistency in meta-analyses. *BMJ* **327**, 557–560. (doi:10.1136/bmj.327.7414.557)
15. Jennions MD, Møller AP. 2002 Relationships fade with time: a meta-analysis of temporal trends in publication in ecology and evolution. *Proc. R. Soc. Lond. B* **269**, 43–48. (doi:10.1098/rspb.2001.1832)
16. Begg CB, Mazumdar M. 1994 Operating characteristics of a rank correlation test for publication bias. *Biometrics* **50**, 1088–1101. (doi:10.2307/2533446)
17. Rosenthal R. 1979 The file drawer problem and tolerance for null results. *Psychol. Bull.* **86**, 638–641. (doi:10.1037/0033-2909.86.3.638)
18. Dumont F, Pasquretta C, Réale D, Bogliani G, Hardenberg A. 2012 Flight initiation distance and starting distance: biological effect or mathematical artefact? *Ethology* **118**, 1–12. (doi:10.1111/eth.12006)
19. Chamailé-Jammes S, Blumstein DT. 2012 A case for quantile regression in behavioral ecology: getting more out of flight initiation distance data. *Behav. Ecol. Sociobiol.* **66**, 985–992. (doi:10.1007/s00265-012-1354-z)
20. Dukas R. 2004 Causes and consequences of limited attention. *Brain Behav. Evol.* **63**, 197–210. (doi:10.1159/000076781)

Electronic Supplementary Material 1

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RESULTS FROM META-ANALYSIS

We identified 97 species effect sizes that we compiled from 25 different studies. From this, 87 effect sizes were estimated from relationship between flight initiation distance (FID) and starting distance (SD), and 10 from relationship between FID and alert distance (AD). A considerable amount of work has been conducted on birds; an observation reflected in the taxonomic distribution of effect size estimates: 82% birds, 7% mammals, 6% lizards approached slowly, 3% lizards approached rapidly, 1% snakes, and 1% arthropods (table S1). However, because insufficient sample sizes ($N = 1$), we excluded snakes and arthropods from analysis (table S1).

With the exception of one lizard species (*Callisaurus draconoides*) that reported zero effect size, all relationship between SD or AD and FID were positive (table S1). Following Cohen's criteria [1], 3.1% of effect sizes were nearly zero (r from 0 to 0.09), 9.3% were low (r from 0.1 to 0.29), 27.8% were medium (r from 0.3 to 0.49), and 58.8% were large ($r > 0.5$).

Closely related species are more likely to have similar phenotypes than those more distantly related. The existence of a phylogenetic structure on animal responses makes observations not statistically independent. So, in our study we fitted a random-model phylogenetic meta-analysis; a framework that permits meta-analysis to explicitly account for any non-independence of taxa by including a covariance matrix that contains phylogenetic relatedness [2]. Random effects within groups are appropriate since we expect that some variation in FID depends on species, individual's sex and age, as well as methodological differences between studies [3]. For analysis, *r*-values were transformed to Fisher's *z*.

To reconstruct the phylogeny of birds to species of our dataset, we used the most recent avian phylogeny [4]. However, as it is not a consensus phylogeny, we randomly choose ten tree hypotheses from those available at the avian phylogeny website--<http://birdtree.org/>--and we ran the analysis with each tree. The inclusion of any phylogenetic hypotheses resulted in very similar results. Thus, we conservatively used those that yielded the least overall mean effect size (difference between results were in decimal scales). Composite phylogenies were also available for mammals [5], and lizards [6]. Phylogenies are shown in figure S1.

We used two metrics to indicate if “flush early” response has a phylogenetic signal. The first, Blomberg's *K*, is a descriptive metric that indicate the strength of phylogenetic signal in a trait [7]. As many others, it assumes underlying Brownian model of evolution, which more closely related species are more similar to each other [8,9]. *K*-values less than one (limited to zero) implies that relatives resemble each other less than expected under Brownian motion. In turn, the second metric is a Monte Carlo based test that make no assumption about model of evolution underling data. This test gives the probability of the observed variance of the phylogenetically independent contrasts (PIC; [8]) be obtained by random [7]. Importantly, low variance of PIC means that related species have similar values of a given trait [8]. Thus, *P*-values > 0.05 indicate that observed variance of PIC is not statistically significant (i.e. have

no evidence of phylogenetic signal). We used R package Picante 1.5 [10] to calculate both metrics. Due to inefficiency of the metrics to deal with so few species [7], mammals and lizards were not investigated. Both metrics indicated, respectively, a weak and no significant phylogenetic signal in “flush early” response in birds ($K = 0.29$; PIC $P = 0.174$).

However, similarity of results between a phylogenetic and ordinary meta-analysis (i.e. one that ignored phylogenetic structure) suggests that there is a limited phylogenetic signal on effect size estimated for mammals and lizards too. All z -tests comparing results of same groups had $P > 0.4$ (table S2, S3).

Birds and mammals were quite variable in the relationship between SD and FID (respectively, $I^2 = 96.6\%$ and 98.4%), whereas lizards approached rapidly had low variability ($I^2 = 10.7\%$), and lizards approached slowly were extremely homogeneous ($I^2 = 0\%$). An examination of the dendrograms from the cluster analysis was not revealing beyond showing that there were no obvious taxonomic clusters (figure S2).

A global effect size could not be calculated in the phylogenetic meta-analysis because some species appeared more than once (some lizards were included in the ‘fast lizard’ and ‘slow lizard’ groups), and such data structure is not permitted in the analysis [2]. However, the traditional meta-analysis permits us to estimate the global effect size of the relationship between FID and SD or AD (which also includes snakes and the arthropod that we previously excluded). Our results from this non-phylogenetic analysis suggest that the global effect is large.

There is a tendency for studies with small sample sizes but with large effect sizes to be more likely to be published than those with small effect sizes [3]. A significantly negative correlation between effect size and sample size indicates a publication bias [3]. However, the rank correlation test (based on Kendall’s tau; [11]) does not indicate a publication bias (table

S4). Likewise, the visual evaluation of funnel plot also does not indicate this kind of bias in the data (figure S3). From this we infer that our results should be somewhat generalizable.

NULL MODEL AND SENSITIVITY ANALYSIS

Logically, FID must be less than SD and AD (an animal can not flush or look at a person before a person starts walking towards it). Thus, when we plot all possible FIDs under a given range of SD or AD values, we typically obtain a shape that approximates a right triangle. This constraint has implications on traditional null hypothesis testing because it violates the homoscedasticity assumption of linear regression (because the variance increases with increases in SD or AD) [12]. Consequently, it is possible that there may be potentially spurious relationships between FID and SD or AD [12,13]. If so, some of the estimates of effect size that we compiled may not reflect a real biological effect and that, because better sampled studies are given greater weight, large effect sizes could inflate our estimates of average effects.

Two recent works proposed null models to test statistical significance of the FID-SD (or AD) correlation [12,13]. Importantly, one of these [13] showed that the relationship may indeed be real in several species. Unfortunately for a meta-analysis, both methods require large amounts of raw data for their calculation and we were unable to obtain such data for our study.

We propose an alternative method to eliminate the effect of potentially spurious results using a null model based on observed effect sizes. Our goal was to create a null model that more realistically reflected the data used to estimate the observed correlation between variables. To do so, we extracted from papers information about the mean and standard deviation of a species' FID, and the maximum starting distance (SD_{max}). For 11 species for

which data were missing, we inferred parameters using average values from its taxonomic group (see table S1).

The null model generated N random numbers ($N =$ species sample size) extracted from a uniform distribution to simulate SD ($SD \sim U(\text{FID mean}, \text{SD max})$) and N random numbers from a normal distribution to simulate FID ($\text{FID} \sim N(\text{FID mean}, \text{FID standard deviation})$). To truncate FID (so that $\text{FID} \leq \text{SD}$), we wrote an algorithm (in ESM 2) in which normally distributed numbers were generated until all points of FID fell within the constrained range. We then calculated the correlation coefficient (r) for these simulated numbers and repeated this 9999 times. From these simulation results, we calculated the probability that the observed r -values used as an effect size in meta-analysis were created by a spurious relationship by dividing the number of r -values \geq observed by the number of iterations. Overall, we generated a vector of P -values for effect sizes of species. P -values < 0.05 were considered significant (i.e. unlikely to have been yielded by a spurious relationship). The simulation routine was written in R [14].

Note that we explicitly used a species' mean FID as the lower limit to SD rather than minimum SD that was in a given data set. We did so to reduce the chance of simulating immediate flight (i.e. where $\text{SD} = \text{FID}$) caused by SD being below the optimum FID. Moreover, had we done so, it would have included unrealistic data since experimenters used a relatively standardized FID protocol [15] where observations of immediate flight were excluded. Thus, to be conservative we also excluded from meta-analysis correlations that explicitly included immediate flight data (e.g. [16,17]). Using the mean FID as the lower limit to SD also make our model more parsimonious by prevent the inclusion of additional parameters to control immediate flight (like λ used in [13]). We justify this because introducing λ (which must be estimated by simulation) adds complexity to our null model and

we felt that it did not, in this case, add value to our desire to understand the relationship between SD and FID.

Ultimately, we conducted a sensitivity analysis [3] by re-analyzing our dataset when we excluded the potentially artifactual effect sizes.

Results and Discussion

From 95 species effect sizes included in the phylogenetic meta-analysis, 17 had P -values ≥ 0.05 (table S1). However, it is important to highlight that 10 of 17 not significant r_s were those that were nearly zero or were otherwise classified as small [1]. Remember that what motivated our developing of a null model was the concern about heterogeneous variance. Yet, even under a traditional null hypothesis test that meets all of the assumptions of linear regression, we would expect that values with a small r_s (and sample size similar to that observed) would have a $P > 0.05$ simply because of its small effect size [18]. Thus, perhaps we should not be that concerned about potentially spurious effects. The potentially artifactual effect sizes of the remaining seven species were medium in magnitude. Finally, there was no evidence that high effect sizes were spurious; a problem, that if present, could have an effect on our conclusions about overall magnitude.

In conclusion, even after conservatively excluding all effect sizes that might have come from a spurious relationship, our results remained roughly the same as in previous analysis with entire data (table S5, S6). In brief, our analyses show that the small numbers of potentially artifactual effect sizes were not sufficient to significantly change the inferences drawn from our phylogenetic meta-analysis results.

Table S1. Parameters of all species surveyed in meta-analysis to test the flush early and avoid the rush hypothesis. Species were grouped into birds (B), mammals (M), lizards approached slowly (LS), lizards approached rapidly (LF), snakes (S), and arthropods (A). SD (max), maximum starting distance used by experimenter to approach species; FID (mean), mean FID; and FID (StDev), FID standard deviation; N, sample size; r , correlation coefficient from relationship between predator's starting distance or alert distance, and flight initiation distance (FID) used as effect size; P (null), P -value yielded by a null model where FID is constrained to $FID \leq SD$ (see details in text). SD (max), FID (mean) and FID (StDev) values in bold indicates that were inferred from average values of its respective taxa group because such information is missing in source study. Effect sizes (r) in bold were estimated from relationship between FID and alert distance; the remainder effect sizes were all estimated from relationship between FID and starting distance. P -values in red indicates that effect size were significant under the null model (<0.05).

Group	Species	Family	SD (max)	FID (mean)	FID (StDev)	N	r	P (null)	Source
B	<i>Acanthiza pusilla</i>	Pardalotidae	20.0	4.3	3.4	29	0.538	0.0251	[15]
B	<i>Acanthorhynchus tenuirostris</i>	Meliphagidae	19.0	4.8	3.1	42	0.399	0.0946	[15]
B	<i>Acridotheres tristis</i>	Sturnidae	75.0	11.6	9.4	40	0.796	0.0001	[15]
B	<i>Alectura lathami</i>	Megapodiidae	95.0	12.0	13.0	27	0.639	0.0021	[15]
B	<i>Anas castanea</i>	Anatidae	158.0	46.0	21.4	57	0.82	0.0001	[15]
B	<i>Anas superciliosa</i>	Anatidae	162.0	38.9	29.0	50	0.869	0.0001	[15]
B	<i>Anthochaera chrysoptera</i>	Meliphagidae	35.0	6.2	3.5	40	0.365	0.0476	[15]

B	<i>Anthus novaeseelandiae</i>	Motacilidae	61.0	12.3	5.2	62	0.349	0.0270	[15]
B	<i>Ardea alba</i>	Ardeidae	208.1	47.4	36.3	34	0.564	0.0118	[19]
B	<i>Arenaria interpres</i>	Scolopacidae	46.0	14.4	6.5	47	0.212	0.4424	[15]
B	<i>Cacatua galerita</i>	Cacatuidae	91.0	13.6	11.8	43	0.741	0.0001	[15]
B	<i>Cacatua roseicapila</i>	Cacatuidae	42.6	9.9	6.3	50	0.916	0.0001	[20]
B	<i>Calidris mauri</i>	Scolopacidae	97.1	22.6	14.3	21	0.265	0.3730	[19]
B	<i>Calidris ruficollis</i>	Scolopacidae	62.0	16.4	8.7	62	0.553	0.0002	[15]
B	<i>Carpodacus mexicanus</i>	Fringillidae	30.0	18.6	12.0	48	0.636	0.0010	[21]
B	<i>Chenonetta jubata</i>	Anatidae	115.7	18.6	12.0	29	0.941	0.0001	[22]
B	<i>Cisticola exilis</i>	Sylviidae	25.0	5.2	3.1	38	0.711	0.0001	[15]
B	<i>Coracina novaehollandiae</i>	Campephagidae	100.0	19.8	14.5	26	0.806	0.0001	[15]
B	<i>Corvus coronoides</i>	Corvidae	165.0	25.6	22.6	70	0.839	0.0001	[15]
B	<i>Dacelo novaeguineae</i>	Halcyonidae	88.0	13.2	13.0	57	0.658	0.0001	[15]
B	<i>Egretta novaeholiandiae</i>	Ardeidae	191.0	30.8	20.2	56	0.37	0.0352	[15]
B	<i>Egretta thula</i>	Ardeidae	208.1	23.5	24.9	38	0.534	0.0062	[19]
B	<i>Elseyornis melanops</i>	Charadriidae	68.0	23.1	9.5	44	0.473	0.0218	[15]
B	<i>Eopsaltria australis</i>	Petroicidae	45.0	9.4	5.6	84	0.636	0.0001	[15]

B	<i>Eurystomus orientalis</i>	Coraciidae	137.0	21.9	24.1	32	0.838	0.0001	[15]
B	<i>Gallinula tenebrosa</i>	Rallidae	59.0	14.8	10.7	37	0.86	0.0001	[15]
B	<i>Gerygone mouki</i>	Pardalotidae	16.0	3.6	2.0	35	0.395	0.0492	[15]
B	<i>Grallina cyanoleuca</i>	Dicruridae	100.0	18.8	10.6	99	0.66	0.0001	[15]
B	<i>Gymnorhina tibicen</i>	Artamidae	142.8	18.6	12.0	28	0.928	0.0001	[22]
B	<i>Haematopus fuliginosus</i>	Haematopodidae	128.0	30.5	15.8	62	0.381	0.0323	[15]
B	<i>Haematopus longirostris</i>	Haematopodidae	329.0	37.9	17.7	48	0.342	0.0255	[15]
B	<i>Heteroscelus brevipes</i>	Scolopacidae	164.0	17.3	8.6	48	0.627	0.0001	[15]
B	<i>Heteromyias albispecularis</i>	Petroicidae	57.0	9.2	6.9	26	0.469	0.0435	[15]
B	<i>Himantopus himantopus</i>	Recurvirostridae	152.0	38.8	21.1	65	0.812	0.0001	[15]
B	<i>Himantopus mexicanus</i>	Recurvirostridae	155.9	30.0	17.6	70	0.393	0.0110	[19]
B	<i>Hirundo neoxena</i>	Hirundinidae	104.0	10.9	5.8	36	0.402	0.0199	[15]
B	<i>Larus delawarensis</i>	Laridae	95.6	28.0	19.0	14	0.441	0.2308	[19]
B	<i>Larus novaehollandiae</i>	Laridae	216.0	16.8	12.1	288	0.336	0.0001	[15]
B	<i>Lichenostomus chrysops</i>	Meliphagidae	22.0	4.7	4.1	31	0.689	0.0006	[15]
B	<i>Limosa lapponica</i>	Scolopacidae	227.0	22.1	14.8	196	0.468	0.0001	[15]
B	<i>Lonchura punctulata</i>	Passeridae	41.0	11.1	6.3	42	0.453	0.0333	[15]

B	<i>Malurus cyaneus</i>	Maluridae	31.0	6.4	3.5	95	0.548	0.0001	[15]
B	<i>Malurus lamberti</i>	Maluridae	29.0	4.3	3.4	39	0.632	0.0003	[15]
B	<i>Manorina melanocephala</i>	Meliphagidae	154.0	4.6	4.4	40	0.13	0.2871	[15]
B	<i>Manorina melanophrys</i>	Meliphagidae	38.0	4.0	3.2	47	0.551	0.0004	[15]
B	<i>Meliphaga lewinii</i>	Meliphagidae	70.0	7.6	6.5	45	0.702	0.0001	[15]
B	<i>Neochmia temporalis</i>	Passeridae	46.0	7.1	5.3	68	0.55	0.0002	[15]
B	<i>Numenius madagascariensis</i>	Scolopacidae	240.0	65.5	41.6	69	0.681	0.0001	[15]
B	<i>Ocyphaps lophotes</i>	Columbidae	56.0	12.6	9.3	31	0.657	0.0011	[15]
B	<i>Oriolus sagittatus</i>	Oriolidae	52.0	10.2	6.8	35	0.78	0.0001	[15]
B	<i>Pelecanus conspicilatus</i>	Pelecanidae	300.0	32.6	25.4	66	0.761	0.0001	[15]
B	<i>Phalacrocorax carbo</i>	Phalacrocoracidae	115.0	32.3	20.6	36	0.78	0.0001	[15]
B	<i>Phalacrocorax melanoleucos</i>	Phalacrocoracidae	162.0	19.7	14.3	67	0.524	0.0001	[15]
B	<i>Phalacrocorax sulcirostris</i>	Phalacrocoracidae	155.0	22.9	15.5	37	0.548	0.0018	[15]
B	<i>Phalacrocorax varius</i>	Phalacrocoracidae	132.0	31.2	18.0	27	0.411	0.0963	[15]
B	<i>Philemon corniculatus</i>	Meliphagidae	41.0	10.0	5.9	64	0.495	0.0023	[15]
B	<i>Phylidonyris novaehollandidae</i>	Meliphagidae	46.0	7.1	4.6	50	0.512	0.0011	[15]
B	<i>Platycercus elegans</i>	Psittacidae	56.0	18.6	12.0	41	0.702	0.0003	[23]

B	<i>Platycercus eximius</i>	Psittacidae	49.0	10.4	6.6	27	0.425	0.0876	[15]
B	<i>Pluvialis squatarola</i>	Charadriidae	159.6	58.0	24.4	42	0.477	0.0241	[19]
B	<i>Porphyrio porphyrio</i>	Rallidae	186.0	34.5	21.8	68	0.711	0.0001	[15]
B	<i>Psophodes olivaceus</i>	Cinclosomatidae	29.0	5.8	3.3	55	0.497	0.0015	[15]
B	<i>Ptilonorhynchus violaceus</i>	Ptilonorhynchidae	27.0	9.1	5.4	28	0.657	0.0035	[15]
B	<i>Rhipidura fuliginosa</i>	Dicruridae	34.0	6.2	4.4	44	0.589	0.0001	[15]
B	<i>Rhipidura leucophrys</i>	Dicruridae	82.0	11.5	9.8	54	0.86	0.0001	[15]
B	<i>Sericornis citreogularis</i>	Pardalotidae	33.0	5.6	4.5	49	0.663	0.0001	[15]
B	<i>Sericornis frontalis</i>	Pardalotidae	21.0	4.1	2.5	43	0.617	0.0001	[15]
B	<i>Sterna bergii</i>	Laridae	178.0	17.3	10.7	68	0.071	0.5268	[15]
B	<i>Strepera graculina</i>	Artamidae	86.0	14.8	14.5	93	0.687	0.0001	[15,24]
B	<i>Streptopelia chinensis</i>	Columbidae	62.0	12.7	9.0	52	0.482	0.0085	[15]
B	<i>Struthio camelus</i>	Struthionidae	100.4	18.6	12.0	129	0.942	0.0001	[25]
B	<i>Sturnus vulgaris</i>	Sturnidae	60.0	14.0	9.3	30	0.514	0.0260	[15]
B	<i>Threskiornis molucca</i>	Threskiornithidae	224.0	32.8	20.4	75	0.452	0.0006	[15]
B	<i>Tringa melanoleuca</i>	Scolopacidae	112.5	36.0	7.3	10	0.352	0.2326	[19]
B	<i>Turdus merula</i>	Turdidae	100.4	18.6	12.0	194	0.468	0.0001	[26]

B	<i>Turdus migratorius</i>	Turdidae	35.0	18.6	12.0	160	0.342	0.2060	[27]
B	<i>Vanellus miles</i>	Charadriidae	211.0	46.8	30.5	60	0.622	0.0001	[15]
B	<i>Zoothera lunulata</i>	Muscicapidae	34.0	8.9	3.1	31	0.161	0.4320	[15]
B	<i>Zosterops lateralis</i>	Zosteropidae	31.0	5.5	3.9	36	0.646	0.0004	[15]
M	<i>Aepycerus melampus</i>	Bovidae	412.0	86.6	44.6	170	0.823	0.0001	[28]
M	<i>Macropus giganteus</i>	Macropodidae	215.3	86.6	44.6	34	0.936	0.0001	[22]
M	<i>Marmota flaviventris</i>	Sciuridae	370.5	82.2	44.4	76	0.811	0.0001	[29,30]
M	<i>Octodon degus</i>	Octodontidae	60.0	25.0	1.0	139	0.51	0.0001	[31]
M	<i>Odocoileus hemionus columbianus</i>	Cervidae	290.0	86.6	44.6	78	0.689	0.0001	[32]
M	<i>Rangifer tarandus tarandus</i>	Cervidae	1500.0	227.5	132.0	91	0.34	0.0123	[33,34]
M	<i>Sciurus carolinensis</i>	Sciuridae	36.0	11.8	0.8	88	0.25	0.0204	[35]
LS	<i>Aspidoscelis exsanguis</i>	Teiidae	19.0	4.7	4.1	18	0.136	0.7480	[17]
LS	<i>Callisaurus draconoides</i>	Phrynosomatidae	11.9	3.8	1.7	20	0	0.8177	[36]
LS	<i>Leiocephalus carinatus</i>	Leiocephalidae	40.0	3.9	0.9	38	0.064	0.4172	[37]
LS	<i>Podarcis lilfordi</i>	Lacertidae	17.9	2.8	0.5	100	0.2	0.0474	[38]
LS	<i>Sceloporus virgatus</i>	Phrynosomatidae	19.2	1.7	0.9	21	0.046	0.5185	[16]
LS	<i>Urosaurus ornatus</i>	Phrynosomatidae	19.2	1.3	0.7	33	0.22	0.1608	[16]

LF	<i>Callisaurus draconoides</i>	Phrynosomatidae	11.9	5.6	4.5	19	0.389	0.3600	[36]
LF	<i>Podarcis lilfordi</i>	Lacertidae	17.9	2.6	0.5	134	0.65	0.0001	[38]
LF	<i>Sceloporus virgatus</i>	Phrynosomatidae	16.4	2.6	0.9	55	0.51	0.0004	[16]
S	<i>Nerodia sipedon</i>	Colubridae	15.0	3.9	1.2	95	0.57	0.0001	[39]
A	<i>Phidippus princeps</i>	Salticidae	30.1	20.0	12.3	56	0.275	0.3334	[40]*

*Effect size estimated from results of experiment 1 (no autotomized individuals).

Figure S1. Phylogenies of taxa included in phylogenetic meta-analysis. A, birds; B, mammals; and C, lizards.

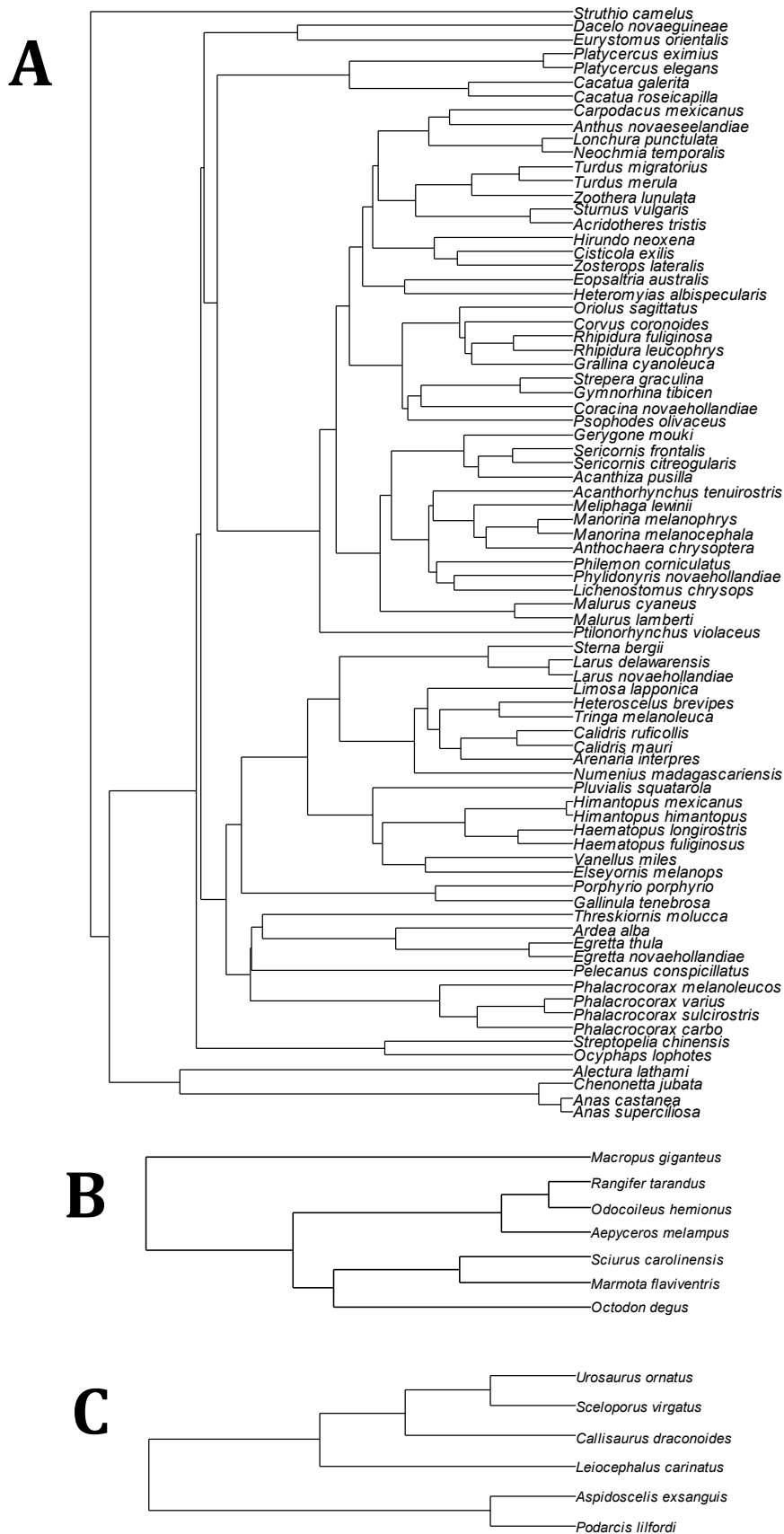


Table S2. The combined effects of starting distance or alert distance on flight initiation distance under ordinary meta-analysis. Mean effect size (r), confidence interval of 95% (CI), number of species tested (spp.), total of individuals tested (total N), degree of heterogeneity in effect size within the group (I^2), the number of studies reporting no effect to nullify the observed effect, and rank correlation test to assess possible bias in publication (rank correlation).

group	r	CI	spp.	total N	I^2 (%)	fail-safe number	rank correlation (P)
global effect	0.60	0.55 - 0.64	97	5721	87.0	58,152	0.810
birds	0.62	0.56 - 0.67	79	4456	85.8	39,941	0.888
mammals	0.69	0.48 - 0.83	7	676	94.3	746	0.764
lizards approached slowly	0.15	0.01 - 0.28	6	230	0.0	1	0.452
lizards approached rapidly	0.58	0.43 - 0.69	3	208	34.3	53	0.296

Table S3. Pair-wise comparison (z and (P -value)) between mean effect sizes of groups estimated under ordinary meta-analysis. Bold cells indicate statistical significance (i.e. $P < 0.008$).

	birds	mammals	lizards approached slowly
mammals	0.42 (0.676)		
lizards approached slowly	5.84 (< 0.001)	2.99 (0.003)	
lizards approached rapidly	0.39 (0.698)	0.58 (0.559)	3.55 (< 0.001)

Table S4. Results of the rank correlations to test for publication bias.

group	Kendall's tau	P^*
birds	-0.011	0.888
mammals	0.095	0.764
lizards approached slowly	-0.276	0.452
lizards approached rapidly	-0.667	0.296

**two-tailed.*

Figure S2. Dendrograms of each group to explore possible patterns explaining the observed heterogeneity. A, birds; B, mammals; C, lizards approached slowly; D, lizards approached rapidly. Species with same colors means that it belongs to the same family.

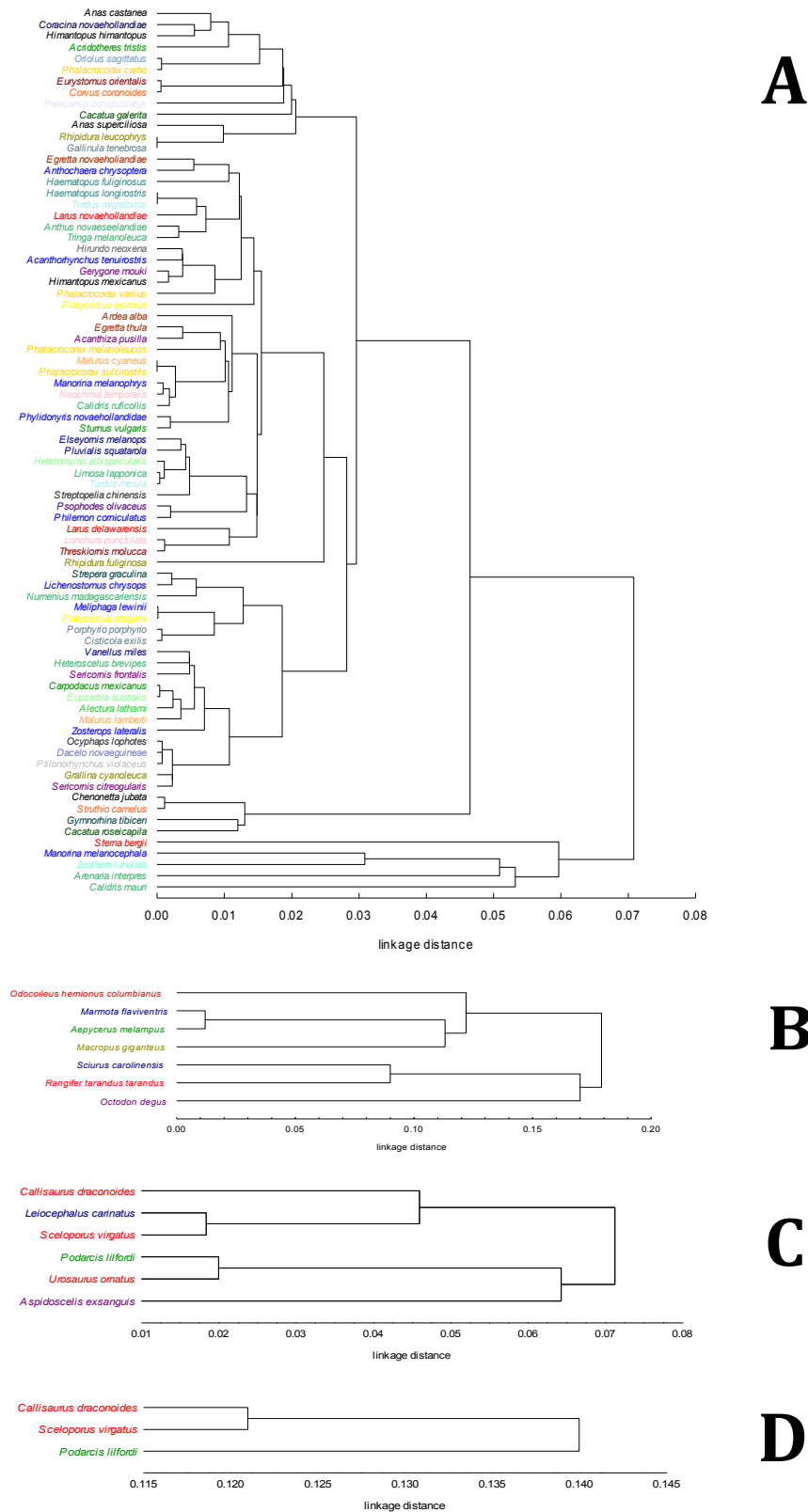


Figure S3. Funnel plot of each group to assess publication bias. Effect sizes are reported as Fisher's z , and sample sizes are reported as standard errors to improve the display of data. Note that standard error axis is inverted, which means that sample size increases as we move from bottom to top of axis. If there were an obvious bias, it would be seen by relatively more points in the right side than the left side in the bottom half of the funnel plots (i.e. more species with large than small effect size in studies with low sample sizes).

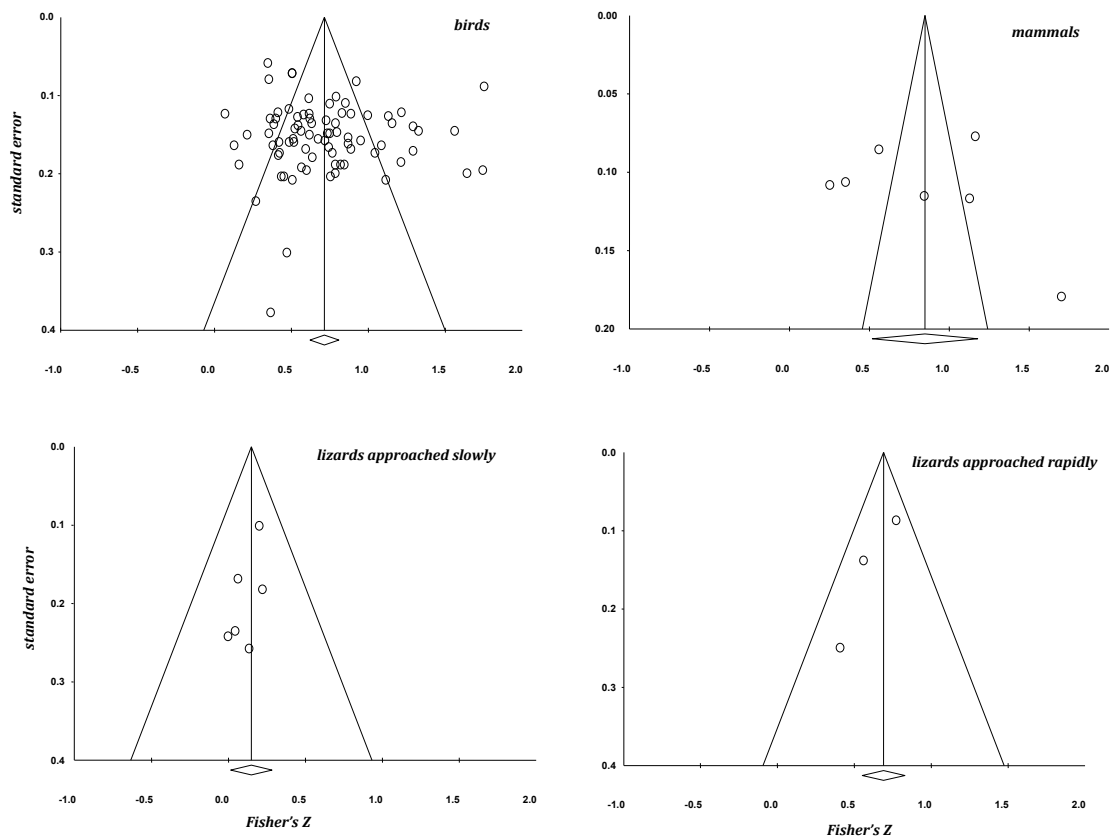


Table S5. Results of phylogenetic meta-analysis about effects of starting distance or alert distance on flight initiation distance after exclude potentially artifactual effect sizes. Mean effect size (r), confidence interval of 95% (CI), number of species tested (spp.), total of individuals tested (total N), degree of heterogeneity in effect size within the group (I^2), the number of studies reporting no effect to nullify the observed effect, and rank correlation test to assess possible publication bias (rank correlation).

group	r	CI	spp.	total N	I^2 (%)	fail-safe number	rank correlation (P)
birds	0.67	0.57 - 0.75	73	4176	96.6	37,145	0.434
mammals	0.70	0.48 - 0.84	7	676	98.4	746	0.764
lizards approached slowly	0.20	0.07 - 0.33	6	230	0.0	1	0.452
lizards approached rapidly	0.60	0.46 - 0.71	2	189	39.76	42	1.000*

*logically, P -value is 1 because remained only two points to estimate the rank correlation.

Table S6. Pair-wise comparison (z and (P -value)) between mean effect sizes of groups analyzed by phylogenetic meta-analysis after exclude potentially artifactual effect sizes. Bold cells indicate statistical significance (i.e. $P < 0.008$).

	birds	mammals	lizards approached slowly
mammals	0.28 (0.780)		
lizards approached slowly	5.59 (< 0.001)	3.45 (0.001)	
lizards approached rapidly	0.86 (0.388)	0.82 (0.413)	3.90 (< 0.001)

SUPPLEMENTARY REFERENCES

- 1 Cohen, J. 1992 A power primer. *Psychol. Bull.* **112**, 155–159.
- 2 Lajeunesse, M. J. 2009 Meta-analysis and the comparative phylogenetic method. *The Am. Nat.* **174**, 369–381. (doi:10.1086/603628)
- 3 Borenstein, M., Hedges, L. V., Higgins, J. P. T. & Rothstein, H. R. 2009 *Introduction to Meta-Analysis*. Chichester, UK: John Wiley & Sons, Ltd. (doi:10.1002/9780470743386)
- 4 Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
- 5 Bininda-Emonds, O. R. P. et al. 2007 The delayed rise of present-day mammals. *Nature* **446**, 507–12. (doi:10.1038/nature05634)
- 6 Blankers, T., Townsend, T. M., Pepe, K., Reeder, T. W. & Wiens, J. J. 2012 Contrasting global-scale evolutionary radiations: phylogeny, diversification, and morphological evolution in the major clades of iguanian lizards. *Biol. J. Linn. Soc.* **108**, 127–143.
- 7 Blomberg, S. P., Garland, T. & Ives, A. R. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.
- 8 Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- 9 Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
- 10 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P. & Webb, C. O. 2010 Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464.
- 11 Begg, C. B. & Mazumdar, M. 1994 Operating characteristics of a rank correlation test for publication bias. *Biometrics* **50**, 1088–1101.
- 12 Dumont, F., Pasquaretta, C., Réale, D., Bogliani, G. & Hardenberg, A. 2012 Flight initiation distance and starting distance: biological effect or mathematical artefact? *Ethology* **118**, 1–12. (doi:10.1111/eth.12006)
- 13 Chamaillé-Jammes, S. & Blumstein, D. T. 2012 A case for quantile regression in behavioral ecology: getting more out of flight initiation distance data. *Behav. Ecol. Sociobiol.* **66**, 985–992. (doi:10.1007/s00265-012-1354-z)
- 14 R Development Core Team, R. 2011 R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*. Vienna, Austria. (doi:10.1007/978-3-540-74686-7)

- 15 Blumstein, D. T. 2003 Flight initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.* **67**, 852–857.
- 16 Cooper, W. E. J. 2005 When and how do predator starting distances affect flight initiation distances? *Can. J. Zool.* **83**, 1045–1050. (doi:10.1139/Z05-104)
- 17 Cooper, W. E. J. 2008 Strong artifactual effect of starting distance on flight initiation distance in the actively foraging lizard *Aspidoscelis exsanguis*. *Herpetologica* **64**, 200–206.
- 18 Nakagawa, S. & Cuthill, I. C. 2007 Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev. Camb. Philos. Soc.* **82**, 591–605. (doi:10.1111/j.1469-185X.2007.00027.x)
- 19 Ikuta, L. A. & Blumstein, D. T. 2003 Do fences protect birds from human disturbance? *Biol. Conserv.* **112**, 447–452. (doi:10.1016/S0006-3207(02)00324-5)
- 20 Cárdenas, Y. L., Shen, B., Zung, L. & Blumstein, D. T. 2005 Evaluating temporal and spatial margins of safety in galahs. *Anim. Behav.* **70**, 1395–1399. (doi:10.1016/j.anbehav.2005.03.022)
- 21 Valcarcel, A. & Fernández-Juricic, E. 2009 Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? *Behav. Ecol. Sociobiol.* **63**, 673–685. (doi:10.1007/s00265-008-0701-6)
- 22 Gulbransen, D., Segrist, T., Del Castillo, P. & Blumstein, D. T. 2006 The fixed slope rule: an inter-specific study. *Ethology* **112**, 1056–1061. (doi:10.1111/j.1439-0310.2006.01265.x)
- 23 Boyer, J. S., Hass, L. L., Lurie, M. H. & Blumstein, D. T. 2006 Effect of visibility on time allocation and escape decisions in crimson rosellas. *Aust. J. Zool.* **54**, 363–367. (doi:10.1071/ZO05080)
- 24 Geist, C., Liao, J., Libby, S. & Blumstein, D. T. 2005 Does intruder group size and orientation affect flight initiation distance in birds? *Anim. Biodiv. Conserv.* **28**, 69–73.
- 25 Magige, F. J., Holmern, T., Stokke, S., Mlingwa, C. & Røskoft, E. 2009 Does illegal hunting affect density and behaviour of African grassland birds? A case study on ostrich (*Struthio camelus*). *Biodiv. Conserv.* **18**, 1361–1373. (doi:10.1007/s10531-008-9481-6)
- 26 Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J. & Regis, Y. 2009 Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.* **20**, 371–377. (doi:10.1093/beheco/arn151)
- 27 Eason, P. K., Sherman, P. T., Rankin, O. & Coleman, B. 2006 Factors affecting flight initiation distance in American robins. *J. Wildl. Manage.* **70**, 1796–1800.

- 28 Setsaas, T. H., Holmern, T., Mwakalebe, G., Stokke, S. & Røskoft, E. 2007 How does human exploitation affect impala populations in protected and partially protected areas? – A case study from the Serengeti Ecosystem, Tanzania. *Biol. Conserv.* **136**, 563–570. (doi:10.1016/j.biocon.2007.01.001)
- 29 Blumstein, D. T. et al. 2004 Locomotor ability and wariness in yellow-bellied marmots. *Ethology* **110**, 615–634.
- 30 Runyan, A. M. & Blumstein, D. T. 2004 Do individual differences influence flight initiation distance? *J. Wildl. Manage.* **68**, 1124–1129.
- 31 Lagos, P. A., Meier, A., Tolhuysen, L. O., Castro, R. A., Bozinovic, F. & Ebensperger, L. A. 2009 Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. *Can. J. Zool.* **87**, 1016–1023. (doi:10.1139/Z09-089)
- 32 Stankowich, T. & Coss, R. G. 2006 Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behav. Ecol.* **17**, 246–254. (doi:10.1093/beheco/arj020)
- 33 Reimers, E., Miller, F. L., Eftestøl, S., Colman, J. E. & Dahle, B. 2006 Flight by feral reindeer *Rangifer tarandus tarandus* in response to a directly approaching human on foot or on skis. *Wildl. Biol.* **12**, 403–413.
- 34 Reimers, E., Røed, K. H., Flaget, Ø. & Lurås, E. 2010 Habituation responses in wild reindeer exposed to recreational activities. *Rangifer* **30**, 45–60.
- 35 Engelhardt, S. C. & Weladji, R. B. 2011 Effects of levels of human exposure on flight initiation distance and distance to refuge in foraging eastern gray squirrels (*Sciurus carolinensis*). *Can. J. Zool.* **89**, 823–830. (doi:10.1139/Z11-054)
- 36 Cooper, W. E. J. 2010 Pursuit deterrence varies with predation risks affecting escape behaviour in the lizard *Callisaurus draconoides*. *Anim. Behav.* **80**, 249–256. (doi:10.1016/j.anbehav.2010.04.025)
- 37 Cooper, W. E. J. 2007 Escape and its relationship to pursuit-deterrent signalling in the Cuban curly-tailed lizard *Leiocephalus carinatus*. *Herpetologica* **63**, 144–150.
- 38 Cooper, W. E. J., Hawlena, D. & Pérez-Mellado, V. 2009 Interactive effect of starting distance and approach speed on escape behavior challenges theory. *Behav. Ecol.* **20**, 542–546. (doi:10.1093/beheco/arp029)
- 39 Cooper, W. E. J., Attum, O. & Kingsbury, B. 2008 Escape behaviors and flight initiation distance in the common water snake *Nerodia sipedon*. *J. Herpetol.* **42**, 493–500.
- 40 Stankowich, T. 2009 When predators become prey: flight decisions in jumping spiders. *Behav. Ecol.* **20**, 318–327. (doi:10.1093/beheco/arp004)

