

Sexual selection: when to expect trade-offs

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Empirical evidence is mixed for interspecific trade-offs in investment among sexually selected traits. One important reason may be the way resources are allocated among species. Consider a set of species that obtains the same fitness pay-off for investment in song or plumage. Simulations where resources were normally distributed among species revealed significant trade-offs between song and plumage ($\bar{x} \pm \text{s.d.}$ of $r = -0.54 \pm 0.06$). However, simulations where resources were distributed in a negative binomial fashion usually produced positive correlations ($r = 0.11 \pm 0.09$). Repeating simulations on three published studies that concomitantly quantified elaboration of song and plumage indicated that trade-offs are likely, although these analyses make assumptions that require further evaluation. Moreover, there are currently too few empirical distributions to make generalizations about the likelihood of interspecific trade-offs in sexually selected traits.

Keywords: bird song; plumage; resource allocation

1. INTRODUCTION

Life-history theory is predicated on trade-offs, defined here as negative correlations between investments in two demands. Organisms are faced with several competing demands, but it is impossible to maximally allocate resources to all demands, so organisms are assumed to trade benefits of investing in one demand against benefits of investing in another [1,2]. Thus, a negative relationship is expected between allocations to competing demands, such as song versus plumage [3]. However, are there ways in which positive associations between competing demands could occur (also see [4])? Here, I explore how relationships between competing demands are affected by the way resources are distributed among species (although resource allocations and intensities of selection differ in the time frames over which they change, the two variables exert the same influence on trade-offs).

Several studies [5–9] have tested for evidence of interspecific trade-offs in investment among sexually selected traits; results have been mixed. I argue that some of the ambiguity in these results may arise from differences in resource distributions in the systems under study. Although I focus on sexually selected traits, my findings have implications for the study of trade-offs in general.

2. METHODS AND RESULTS

Assume that (individuals within) species acquire the same reservoir of energetic resources, and fitness pay-offs are equivalent for investments in either song or plumage. Intensity of selection is equivalent for all species. Here, the trivial outcome is a perfect negative correlation ($r = -1.00$) between investment in the two traits. This is the expected trade-off that underpins evolutionary theory. However, a uniform distribution of resources among species is unrealistic.

Assume instead that resources are normally distributed among species. I assigned resources to 100 species using random normal deviates (table 1 and figure 1a); programs were written in SAS (Statistical Analysis System, Cary, NC, USA) and are available upon request. I multiplied resource allocation of each species by a random number between 0 and 1; this product was how much that species invested in plumage. The remaining resources were invested in song (table 1). Under these conditions, strong evidence for trade-offs emerged (figure 1b), and correlations between song and plumage were consistently and significantly negative in 1000 replicates (figure 1c).

As an alternative, assume that most species are allocated a small reservoir of resources, and a few are allocated a large reservoir (e.g. as is the case for interspecific patterns of extra-pair paternity, one correlate of the intensity of sexual selection [10], and for the distribution of wealth in many human societies). Distributions such as these, with most observations close to the origin, are referred to as negative binomial (table 1 and figure 1d). I created a negative binomial distribution by assigning 1 unit of resources to 50 species, 2 to 25, 3 to 13, 4 to 6, 5 to 3, 6 to 1, 7 to 1 and 8 to 1. To add variation to these allocations, I took a random number between 0 and 1, randomly assigned a negative or positive sign, and added this to the original resource allocations. Thus, resource allocations could be as low as 0 or as high as 9. Under these circumstances, instead of trade-offs, there was a tendency for positive correlations to emerge (figure 1e,f).

However, what are empirical distributions of resources among species? Resources may generally be viewed as being normally distributed among individuals within populations, but interspecific patterns may be quite different. Although there are many empirical data for interspecific distributions of investment in single sexually selected traits, there are far fewer data for concomitant investment in pairs of traits. Following the same protocols as above, I simulated possible investment allocations based on the empirical distributions of combined (using principal components analysis (PCA)) investments in song and plumage from three studies that had significant samples (more than 25 species) of bird species. Variables (terms defined in original papers) that were linear combinations of other variables were not included. For Shutler & Weatherhead [9], a PCA was run on song variables (pitch, repertoire, minimum frequency and maximum frequency). Scores from PC1 were combined with percentage sexual dimorphism in plumage in a second PCA to create scores of total investment. Data for plumage in [5] were published in [11]; there

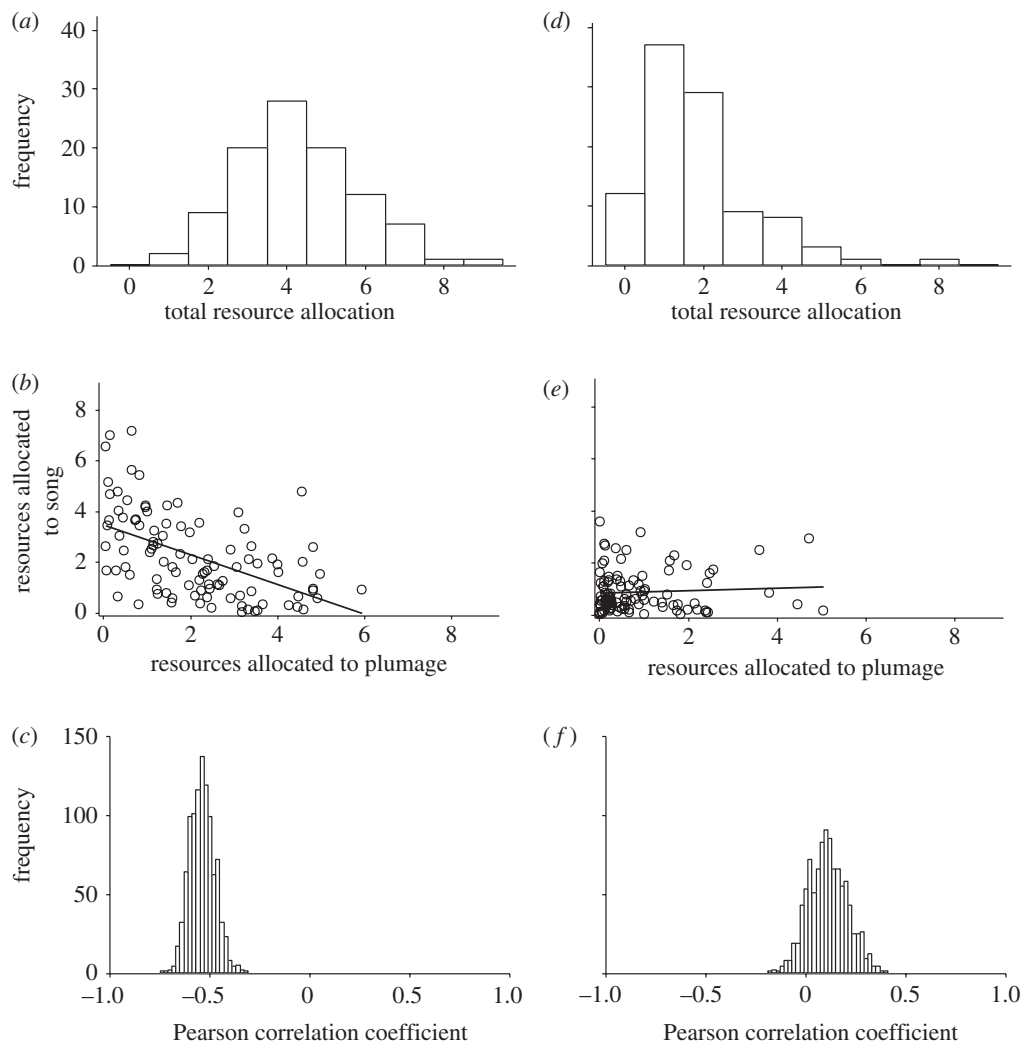


Figure 1. (a) Resources ($\bar{x} = 4.5 \pm 1.5$ s.d. arb. units) were allocated normally among 100 species. (b) If species randomly divided their resources between song and plumage, a trade-off emerged (sample plot). (c) In 1000 replicates of (b), \bar{x} of r was -0.54 ± 0.06 (all $p < 0.001$). (d) Resources were allocated following a negative binomial distribution among 100 species. (e) If species randomly divided their resources between song and plumage, there was often a positive correlation between the two traits (sample plot). (f) In 1000 replicates of (e), \bar{x} of r was 0.11 ± 0.09 ($p < 0.05$ in 17% of replicates).

Table 1. Mechanics of simulations to determine how investment in song and plumage will be related, with some simulated data to illustrate. For the normal distribution, the proportion of resources invested in song (column 4) is the product of columns (1) and (3), and the proportion of resources invested in plumage (column 5) is column (4) subtracted from column (1). For the negative binomial distribution, the proportion of resources invested in song (column 4) is the sum of columns (1) and (2) multiplied by column (3), and the proportion of resources invested in plumage (column 5) is column (4) subtracted from column (1). When resources are distributed normally, for these data, r between song and plumage = -0.12 , whereas when resources have a negative binomial distribution, for these data, $r = +0.54$.

	(1) resources allocated	(2) random adjustment	(3) random number	(4) resources invested in song	(5) resources invested in plumage
normal distribution					
a	1.0		0.3	0.30	0.70
b	3.5		0.8	2.80	0.70
c	4.5		0.2	0.90	3.60
d	5.5		0.9	4.95	0.55
e	8.0		0.7	5.60	2.40
negative binomial distribution					
a	1	-0.1	0.6	0.54	0.36
b	1	+0.2	0.9	1.08	0.12
c	1	-0.4	0.4	0.24	0.36
d	2	-0.2	0.5	0.90	0.90
e	3	+0.0	0.4	1.20	1.80

were three species for which there were two sets of song data from different populations, but only a single set of plumage data in [11]: *Carduelis flammea*, *Carpodacus erythrinus* and *Loxia pytyopsittacus*. I assumed that plumage data for the two populations were equivalent. A first PCA was run on song variables (highest frequency, lowest frequency, note length, inter-note interval, number of notes, song length), a second PCA was run on plumage variables (carotenoid- and melanin-based dichromatism), and PC1 scores from the plumage and song PCAs were entered in a third PCA to create scores of total investment. Finally, for Ornelas *et al.* [8], a first PCA included song variables 77–94 (from their supplementary material, table S5). A second PCA included the plumage variables sexual dimorphism, plumage colour-dimorphism, proportion of male plumage that was carotenoid-based and proportion of male plumage that was melanin-based. PC1 scores from these two PCAs were combined as for Badyaev *et al.* [5].

In two instances, distributions of combined measures of investment in song and plumage were somewhere between a normal and negative binomial (figure 2*a,b*), and in the third instance, an outlier produced an unusual distribution (figure 2*c*). I added 3 to PC scores in simulations so all species received positive allocations. For Shutler & Weatherhead [9], correlations between song and plumage from 1000 iterations (as described above) averaged -0.44 ± 0.07 (range -0.60 to -0.20); equivalent values for Badyaev *et al.* [5] were -0.50 ± 0.07 (range -0.64 to -0.17), and for Ornelas *et al.* [8] were -0.50 ± 0.09 (range -0.69 to ± 0.12).

3. DISCUSSION

My analyses show how resource distributions profoundly influence whether investments in sexually selected traits will be traded off or positively related (also see [12,13]). Within populations or species, one might expect resources to be normally distributed, and thus for trade-offs to be clear. However, among species, negative binomial distributions may be more common, leading to positive associations instead of trade-offs. Two empirical studies reanalysed here that tested for trade-offs [8,9] found limited evidence of them, whereas Badyaev *et al.* [5] found more substantive evidence, but these different outcomes did not correspond to easily perceived differences in the distributions of investments (figure 2). Reasons for the different conclusions largely stem from the use of PCA rather than univariate analyses that were used in the original papers. Moreover, intentions of the former and current studies also differ. In any case, data from additional studies would probably reveal a broader range of likely outcomes, and should preferably measure the same traits for each taxon.

There are several considerations that affect whether trade-offs will be detected (see [14] and [15] for discussion of additional issues including phylogeny). For example, timing of investment in traits may differ, so that species investing heavily in plumage before the breeding season may have time to recover before they start paying the energetic costs of singing.

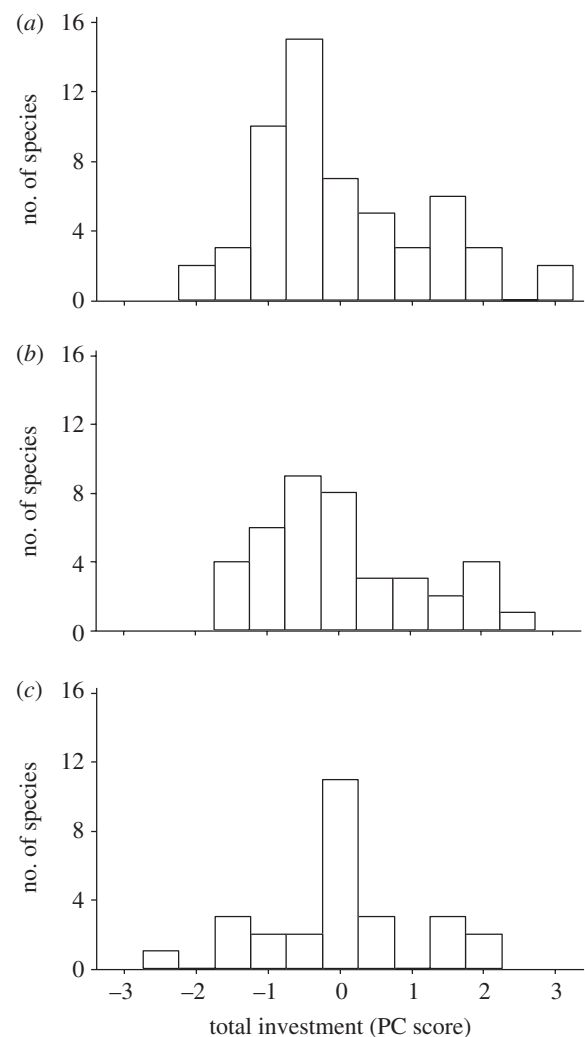


Figure 2. Empirical distributions of investment in sexually selected traits among species. (a) Distribution in investment in wood-warblers (data from [9]). (b) As for (a), distribution in investment for seven song traits for finches (data from [5]). (c) As for (a), distribution in investment for five plumage and 17 song traits for trogons (data from supplementary material tables in [8]).

This may reduce the strength of trade-offs within populations, but may be less of a factor in interspecific comparisons. Second, energetic investment in plumage may be more costly in other ways, such as predation risk, than it may be for song. However, my PCAs weighted all song and all plumage traits equally, and then song and plumage equally, but some traits will be more important to inter- or intraspecific competition. Thus, trade-offs may only exist for specific pairs of traits. Because these traits are likely to differ among species, there will also be differences in where trade-offs occur.

Several issues inherent in assessing costs and benefits of traits will be difficult to resolve. For example, as is the case with many interspecific studies, one assumption is that the same aspects of a trait have the same costs and benefits for each species. To illustrate, females of one species may pay more attention to the duration of trills, whereas in another species frequency range within a trill may be more important. Quantifying both the costs and benefits of the diverse

aspects of plumage and song will be exceedingly complex, particularly at an interspecific level.

Even armed with clear predictions about what to expect in studies of trade-offs, factors such as sample size and selection on other traits may produce results that are at odds with expectations, as indicated by the distribution of correlation coefficients in my simulations. Based on the distribution of correlation coefficients, such unexpected results may be less likely when resources are distributed normally than when they are distributed in a negative binomial fashion. Regardless, further empirical data are needed to assess whether trade-offs occur among sexually selected traits, and among traits in general [14]. The approach taken here suggests a starting point for further analysis.

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