THE ROYAL SOCIETY

Manipulation of host behaviour by parasites: a weakening paradigm?

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New scientific paradigms often generate an early wave of enthusiasm among researchers and a barrage of studies seeking to validate or refute the newly proposed idea. All else being equal, the strength and direction of the empirical evidence being published should not change over time, allowing one to assess the generality of the paradigm based on the gradual accumulation of evidence. Here, I examine the relationship between the magnitude of published quantitative estimates of parasite-induced changes in host behaviour and year of publication from the time the adaptive host manipulation hypothesis was first proposed. Two independent data sets were used, both originally gathered for other purposes. First, across 137 comparisons between the behaviour of infected and uninfected hosts, the estimated relative influence of parasites correlated negatively with year of publication. This effect was contingent upon the transmission mode of the parasites studied. The negative relationship was very strong among studies of parasites which benefit from host manipulation (transmission to the next host occurs by predation on an infected intermediate host), i.e. among studies which were explicit tests of the adaptive manipulation hypothesis. There was no correlation with year of publication among studies on other types of parasites which do not seem to receive benefits from host manipulation. Second, among 14 estimates of the relative, parasite-mediated increase in transmission rate (i.e. increases in predation rates by definitive hosts on intermediate hosts), the estimated influence of parasites again correlated negatively with year of publication. These results have several possible explanations, but tend to suggest biases with regard to what results are published through time as accepted paradigms changed.

Keywords: adaptation; effect size; host manipulation; meta-analysis; publication bias

1. INTRODUCTION

Science is characterized by occasional breakthroughs resulting from new paradigms becoming widely accepted, because they provide simple and attractive explanations to widespread phenomena or to paradoxical results. Following a period of empirical research aimed at testing their validity, there is often a revolutionary shift from one popular paradigm to another. This pattern is so common in the history of science that it prompted Kuhn (1996) to describe it formally as the normal way in which scientific progress and revolutions are achieved. A consequence of this phenomenon is that researchers may show initial enthusiasm for a new paradigm and abandon it later as a new one comes along. This bandwagon effect could influence the type of research which is performed and, more importantly, the type of research which is published.

One well-known and important paradigm in the area of the evolutionary biology of host–parasite interactions has been the ability of parasites to manipulate the phenotype of their host to facilitate their own transmission (reviewed in Poulin 1998). Although the existence of the phenomenon had been suggested before (e.g. Wesenburg-Lund 1931), it was first thoroughly discussed and convincingly illustrated by Holmes & Bethel (1972). This paradigm has since generated much empirical research. In most systems studied, parasites appear to alter their host's behaviour or appearance in ways which increase parasite transmission, particularly in systems where the transmission of the parasite requires the predation of an intermediate host by a definitive host. The enthusiasm of parasitologists for the idea is understandable: not only did host manipulation by parasites offer an elegant, adaptive explanation for several intriguing observations, but also it placed parasites in the driver's seat of the coevolutionary relationship. It was not until the late 1980s and early 1990s that scientists took a closer, more critical look at the manipulation hypothesis and proposed alternative explanations, including non-adaptive ones. This period culminated in the publication of Moore & Gotelli's (1990) review and later in that of Poulin (1995). Subsequent theoretical analyses of the evolution of host manipulation were quick to point out that exceptions must exist and that many parasites with complex life cycles should not be manipulators (Poulin 1994*a*; Brown 1999). Did these papers mark the end of the paradigm or at least signal the weakening of its grasp on parasitological research? One possible way to answer this question might be to examine trends in the publication of quantitative results over the past 30 years in order to see whether support for the hypothesis has waned.

Here I use two independently derived data sets to test whether the magnitude of the reported changes in host behaviour induced by parasites and their measured effect on parasite transmission rates have changed over time. The null hypothesis here is that the magnitude of published effects has remained the same through time, as we would expect from unbiased research, such that the general validity of the manipulation hypothesis can be assessed using all accumulated results. However, this is not what I found. I discuss possible reasons for the correlations I observed between the published values for the above two parameters and the year in which they appeared in print. Whatever the underlying reason, though, the results presented offer a sobering message for all, suggesting that published results need to be

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considered with respect to their position within a paradigm cycle.

2. METHODS

The first data set used here is that of Poulin (1994*b*), who compiled the results of studies published before 1993 on parasite-induced behavioural changes for a meta-analysis of the effects of host taxonomy, parasite taxonomy and mode of parasite transmission on the magnitude of the behavioural change. Poulin's (1994*b*) study included 114 comparisons between infected and uninfected hosts, obtained from 21 studies. All were on helminth parasites and focused on host behaviours which are not specifically related to reproduction, social interactions or foraging. To update the data set, a systematic survey was performed of all issues of the *Canadian Journal of Zoology*, *International Journal for Parasitology*, *Journal of Parasitology* and *Parasitology* published between 1993 and mid-1999. These are the four journals most likely to publish empirical results on host manipulation by parasites. While not providing a comprehensive survey of all recent literature, this approach should at least generate a representative sample of the latest results. Following Poulin's (1994*b*) criteria, I included results only if the following data were given or could be estimated accurately: the mean of some behavioural trait and its standard error or deviation and the sample size for both a group of infected hosts and an uninfected control group and with neither group exposed to a predator. The latter criterion ensured that the behaviour reported was spontaneous rather than elicited by some threat. When data had to be obtained from a graph, I used the average of three separate readings. Additional criteria were used to ensure some standardization of the data set. In particular, I included only measurements taken after the onset of parasite infectivity for the next host, where applicable; in addition, if the results were presented separately for different host sex or age classes, they were treated as separate comparisons (see Poulin (1994*b*) for further details). Applying these criteria meant that almost half of the studies found were excluded from the analysis, but there is no reason to believe that their inclusion would affect the outcome.

For each comparison, a measure of standardized effect size was computed as $J(\bar{X}_p - \bar{X}_u)/s$, where J is equal to $1-(3/4N-1)$ and serves as a correction for small sample sizes (Hedges & Olkin 1985). Other parameters are $\bar{X}_p$ and $\bar{X}_u$, respectively the means of the parasitized and unparasitized groups, s which is the pooled standard deviation of the two groups and N which is the total sample size. Since the magnitude of the behavioural change induced by parasites is of greater concern here than its direction, I used the absolute value of effect sizes rather than their actual signed value.

The comparisons were also classified using categorical variables, namely the host and parasite taxonomies, whether or not the parasite's transmission was achieved via predation of its current host by its next host (thus potentially influenced by parasite-induced changes in host behaviour) and the type of host behaviour measured. The latter classification consisted of two categories: (i) activity behaviours relating to a host's ability or willingness to move, its stamina or its velocity, and (ii) microhabitat choice, including measures of orientation, quantitative responses to external stimuli and actual microhabitat preferences.

The second data set consists of a list of 14 estimates of the relative increase in transmission to a definitive host by predation resulting from the manipulation of intermediate host phenotype by parasites. The list is taken unchanged from table 1 in Thomas *et al.* (1998). It was compiled to provide empirical validation for a theoretical model of the consequences of manipulation for parasite transmission and evolution. The list is exhaustive, as far as I know; no other comparable estimates have been published since. Each estimate of the increase in the transmission rate represents the difference between the proportion of parasitized intermediate hosts captured by a predator (definitive host) and that of unparasitized intermediate hosts in either field or laboratory experiments.

Table 1. *Numbers of the different types of behavioural comparisons between infected and uninfected hosts used in the analysis*

(Sources: (1) Moore (1983*a*), (2) Wilson & Edwards (1986), (3) Carmichael & Moore (1991), (4) Gotelli & Moore (1992), (5) Bethel & Holmes (1973), (6) Moore (1983*b*), (7) Brown & Thompson (1986), (8) Moore *et al.* (1994), (9) Daniels (1985), (10) Townson (1970), (11) Wülker (1985), (12) Rowland & Lindsay (1986), (13) Benton & Pritchard (1990), (14) Moore & Lasswell (1986), (15) Vance (1996), (16) McNair & Timmons (1977), (17) Rau (1983), (18) Hay & Aitken (1984), (19) Saumier *et al.* (1988), (20) Webster (1994), (21) Cox & Holland (1998), (22) Pearre (1979), (23) Lowenberger & Rau (1994), (24) Krause & Godin (1994), (25) Hurd & Fogo (1991), (26) Poulin *et al.* (1992), (27) Robb & Reid (1996), (28) Pasternak *et al.* (1995), (29) Wedekind & Milinski (1996) and (30) Giles (1983).)

parasite taxon	host type	activity	microhabitat choice	sources
Acanthocephala	invertebrates	38	35	1–8
	vertebrates	2	1	9
Nematoda	invertebrates	12	8	10–15
	vertebrates	12	5	16–21
Digenea	invertebrates	—	11	22, 23
	vertebrates	—	1	24
Cestoda	invertebrates	7	4	5, 25–29
	vertebrates	—	1	30
total		71	66	—

3. RESULTS

(a) *Parasite-induced changes in host behaviour*

A further 23 comparisons from nine studies were added to the 114 comparisons derived from the 21 studies compiled by Poulin (1994*b*) following a search of more recent journals (table 1). There was a strong, negative relationship between the year of publication and the magnitude of the reported effect size across all 137 comparisons between the behaviour of infected and uninfected hosts (Spearman's rank correlation, $r_s = -0.319$ and $p = 0.0002$). This relationship was also apparent only across the 114 comparisons listed in Poulin (1994*b*) and compiled for a different purpose ($r_s = -0.349$ and $p = 0.0002$). The sample sizes used in the 137 comparisons did not correlate with the year of publication ($r_s = 0.113$ and $p = 0.1863$).

Perhaps the most striking feature of these results is that the relationship between effect size and the year of publication is contingent upon whether or not a parasite-induced modification of host behaviour can be adaptive

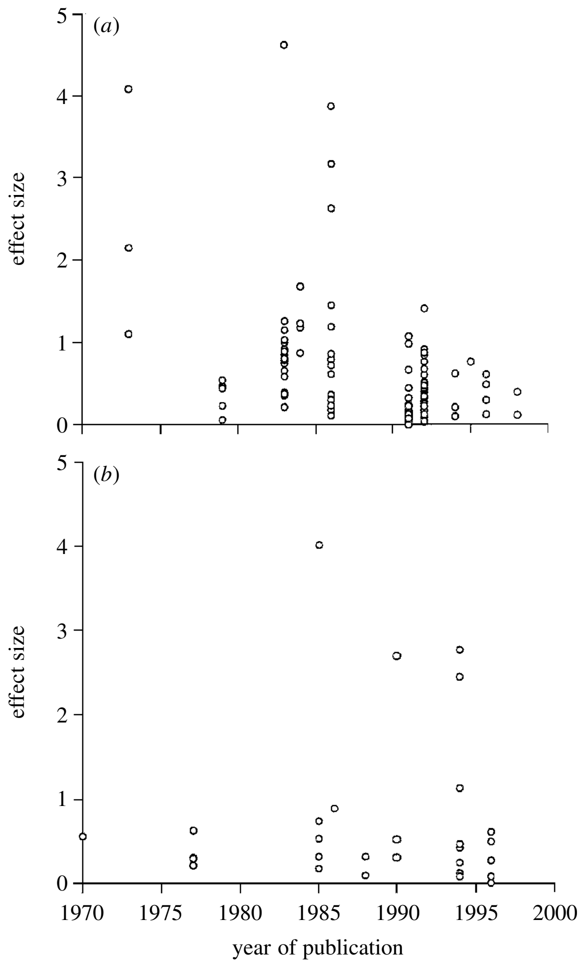

Figure 1. Effect size or the relative magnitude of the behavioural difference between infected and uninfected hosts as a function of the year of publication. The data are presented separately for (*a*) 107 comparisons involving parasites which are transmitted when their host is ingested by the next host in their life cycle, and (*b*) 30 comparisons involving parasites which obtain no obvious benefits by modifying the host behaviour.

for the parasite (figure 1). Among the 107 comparisons involving systems in which the parasite infects an intermediate host and is transmitted to its next or definitive host when the latter preys on the intermediate host, the negative correlation between effect size and the year of publication is very strong ($r_s = -0.385$ and $p = 0.0001$). Most of the large effect sizes among these comparisons were published in the 1970s or early 1980s. However, among the 30 comparisons involving systems with other modes of transmission and in which changes in host behaviour have no obvious adaptive value, the correlation disappears ($r_s = -0.158$ and $p = 0.3948$); among these comparisons, most large estimates were published after 1985.

Over the 30 years of research covered in this survey, the taxa of the parasites which were studied changed but in no particularly consistent way which could have provided an explanation for the above results (figure 2). The proportions of comparisons of either activity or microhabitat choice behaviours or involving either invertebrates or vertebrates have remained much more constant. In any event, the negative relationship between

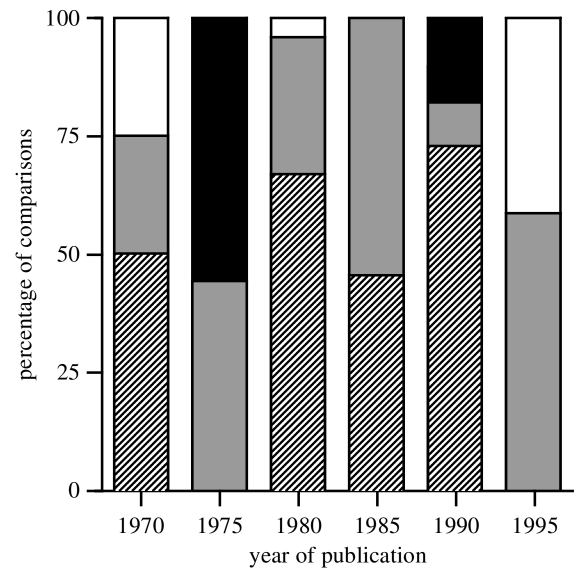

Figure 2. Proportions of behavioural comparisons between infected and uninfected hosts involving acanthocephalans (hatched), nematodes (shaded), cestodes (white) and digeneans (black) for each five-year period beginning with the year indicated below the columns.

effect size and the year of publication generally holds for any type of host behaviour and for almost all host and parasite taxa studied (table 2). The only exception is digenean parasites, for which there is no apparent trend.

Because most studies contributed more than one comparison to the data set, it may well be that there are problems of non-independence between comparisons. However, when repeating the analysis using a single value per study, i.e. the average effect size computed across all effect sizes reported in a study, the negative association between the year of publication and effect size still stands (30 studies, $r_s = -0.410$ and $p = 0.0273$) (see figure 3). Again, the overall correlation is only due to the studies involving parasites which can improve their transmission to their next predatory host by altering the host behaviour: among these 20 studies, the mean effect size and year of publication are clearly negatively correlated ($r_s = -0.543$ and $p = 0.018$). Among the ten studies of parasites whose transmission is not dependent on host predation, there is no significant correlation ($r_s = -0.226$ and $p = 0.4985$).

(b) *Parasite-mediated increases in the transmission rates*

Among the 14 estimates of increases in transmission to definitive hosts gathered by Thomas *et al.* (1998), the magnitude of the estimate correlates negatively with the year of publication ($r_s = -0.550$ and $p = 0.0475$). The scatter of data points shows a roughly triangular pattern (figure 4), suggesting that it is the lower bound and not the upper bound of the range of estimates which has decreased over time. Only two studies used systems in which the intermediate host is a vertebrate. Among the 12 other systems, where the intermediate host is an arthropod, the negative relationship between the estimated increase in the transmission rate and the year of publication is even stronger ($r_s = -0.747$ and $p = 0.0132$). The 14 studies focused on parasites including protozoans, digeneans,

Table 2. *Spearman's rank correlation coefficient between the year of publication and effect size for various subsets of behavioural comparisons between infected and uninfected hosts*

category subset	number of comparisons	correlation coefficient	p
type of behaviour			
activity	71	−0.217	0.0694
microhabitat choice	66	−0.392	0.0016
parasite taxonomy			
Acanthocephala	76	−0.373	0.0012
Nematoda	37	−0.367	0.0277
Digenea	12	0.220	0.4649
Cestoda	12	−0.794	0.0085
host taxonomy			
invertebrates	115	−0.279	0.0028
vertebrates	22	−0.394	0.0706

cestodes and acanthocephalans. It must be pointed out that five (and the first four) of the first six published estimates came from studies on acanthocephalans; only one of the latter eight studies involved acanthocephalan parasites.

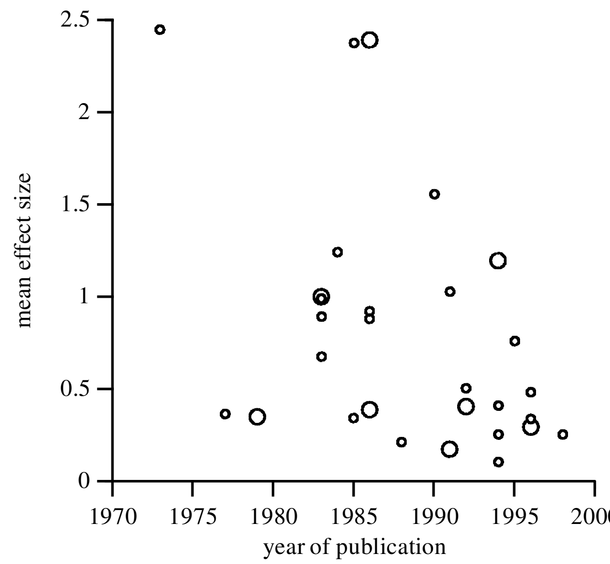

Figure 3. Mean effect size of published studies, computed from the separate effect sizes of parasitism on host behaviour reported in each of 30 studies, as a function of the year of publication. Larger symbols represent studies which contributed five or more effect size estimates to the analysis.

4. DISCUSSION

Scientific research and its publication follows trends and fashions like other aspects of human culture. Kuhn (1996) found a recurrent pattern in the history of science, in which widely accepted paradigms are almost inevitably replaced by others in an endless cycle which still allows for progress. These paradigm shifts can happen in a matter of just a few years, because of the initial enthusiasm of scientists for new ideas. However, what may also happen is that this enthusiasm can act to bias the type of results which are published. This is well illustrated by two recent examples from evolutionary biology. Alatalo *et al.* (1997) found that published estimates of the heritability of secondary sexual traits from parents to offspring increased significantly in the late 1980s, immediately following the publication of theoretical models of sexual selection showing that a high heritability was to be expected. In a similar vein, Simmons *et al.* (1999) reported that the proportion of studies supporting a role for fluctuating asymmetry in sexual selection showed a marked chronological decline through the 1990s, coinciding with an increase in the number of criticisms published against the measurement and importance of fluctuating asymmetry. The results I present here show a resemblance to those of Simmons *et al.* (1999): at a time when alternative explanations were proposed for the manipulation of host phenotype by parasites, published estimates of the force of this phenomenon and of its impact on parasite transmission became increasingly smaller. The existence of the phenomenon is not in doubt; it is the magnitude of its effects which requires a reassessment. This does not represent a true paradigm shift, but a possible case of increasing experimental rigour, coupled with a growing interest in exceptions to the general pattern, a greater willingness to investigate increasingly subtle manipulation effects and a broadening of the taxonomic scope of investigations.

The scatter of points observed here (figures 1*a*, 3 and 4) suggests that the smallest published effect size estimates have tended to become lower over time, with the number of studies published per year increasing. An explanation could be that researchers hesitate to submit reports presenting non-significant effect sizes in the early stages of a scientific revolution, but become more willing once the paradigm is well established. Similarly, the reluctance on the part of reviewers and editors to accept non-significant results could weaken over time. This may in part explain the results concerning the decreasing effect sizes in behavioural comparisons between infected and uninfected hosts. However, this cannot explain the observed pattern in figure 4. All the estimates of increases in the parasite transmission rates listed by Thomas *et al.* (1998) and analysed here were statistically significant, even the weaker ones published most recently. (Urdal *et al.* (1995) reported non-significant results, but Wedekind & Milinski (1996) reanalysed their results using a more appropriate test and found that the increased predation rate was statistically significant.) The most likely explanation for the decrease over time of these estimates is that more investigators began looking at parasites other than acanthocephalans after the mid-1980s. The ability to manipulate host phenotype seems to be an ancestral, well-developed character in acanthocephalans (Moore 1984); other parasites may not be as efficient in their efforts to manipulate host behaviour.

The observed decrease in the effect sizes of parasites on host behaviour over the three decades since Holmes & Bethel (1972) published their famous paper may have a more troubling explanation. The decrease is only apparent among studies that were specific tests of the adaptive manipulation hypothesis; it does not exist among studies that were simply examining the effects of parasites on host behaviour in terms of mere pathology or other consequences for the host. This may indicate that a

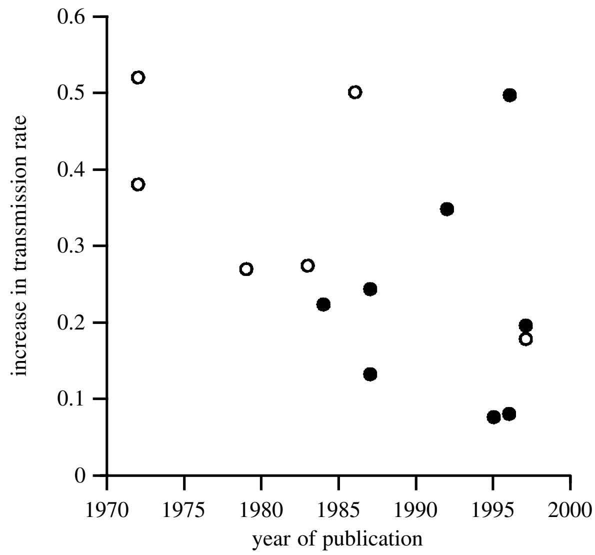

Figure 4. Estimates of the relative increase in the rate of parasite transmission resulting from behavioural changes in the host as a function of the year of publication (all data from table 1 in Thomas *et al*. (1998)). Studies on systems involving acanthocephalans are indicated by open symbols; the other studies were on other parasite taxa.

publication bias exists only in hypothesis-driven research in this area, in which predicted results may be anticipated, and not among more descriptive studies. This observation may explain one of the key results of Poulin's (1994*b*) meta-analysis, which showed that, overall and ignoring the year of publication, parasites which do not appear to benefit from changes in host behaviour had the greatest impact on host behaviour. If not because of a publication bias, why would published support for the adaptive manipulation hypothesis weaken over the years, while that for non-adaptive effects in other systems remain the same? It may well be that behavioural changes in the acanthocephalan–arthropod models used by early investigators (e.g. Hindsbo 1972; Holmes & Bethel 1972; Bethel & Holmes 1973) were so pronounced that further explorations of other systems were bound to generate weaker effects. On the one hand, these systems were ideal for illustrating the phenomenon but, on the other hand, they may have been an unfortunate choice for a first demonstration because they are difficult to match. Perhaps spectacular effects were necessary at first for the manipulation phenomenon to be recognized. If this is indeed the case, then the decrease in effect sizes over time was maybe unavoidable and the null hypothesis that the magnitude of published effects remains the same through time is not appropriate.

It is also worth mentioning that parasites certainly do not manipulate all characteristics of their host. Systematic investigations of the effects of parasitism on all host behaviours are bound to turn up some weak or non-existing associations even in systems where the parasite is a good manipulator of certain traits. However, one would expect that tests of the manipulation hypothesis would have become more refined over time and less likely to focus on irrelevant behaviours.

Another explanation, which is not mutually exclusive of the ones above, is the bias mentioned earlier regarding the publication of weak or non-significant results. When a fashionable hypothesis has gained acceptance but requires empirical support, it is easy to publish supporting evidence. Only when criticism mounts and alternative scenarios are proposed does it become possible to publish counter-examples. The paper by Moore & Gotelli (1990) may have been a turning point. There is no evidence that the research done in the past ten years is of a higher quality than that performed previously. The only measure of research quality available for the studies surveyed here is sample size and that has not changed significantly over the years. What may have happened instead is a shift in the parasitological community's view of adaptive manipulation, including a greater recognition of exceptions and alternative explanations and a greater willingness to publish less supportive results.

The sobering conclusion is that it may be impossible to perform any quantitative assessment of the extent or generality of phenomena such as host manipulation by parasites. The enthusiasm these phenomena generate may bias the published evidence, driving it in certain preferred directions. Immediately after the acceptance of a new paradigm, it may be the direction of the results rather than the quality of the research which determines whether a paper gets published; as time goes by the bias weakens, allowing a wider range of results to be published. The generalizations which can be made will change over time as the enthusiasm wanes and a more balanced set of results become available. Using the more up-to-date data set gathered for this analysis, I found that some of the results of my earlier meta-analysis (Poulin 1994*b*) have weakened; at the present rate they will be changed in a few years! This situation is not restricted to the study of host manipulation by parasites. With the studies by Alatalo *et al.* (1997) and Simmons *et al.* (1999), the present study is the third example of publication bias in the recent literature. Other fashionable research areas may suffer from the same shifts in paradigms and enthusiasm and the same publication trends.

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