

Host Performance as a Target of Manipulation by Parasites: A Meta-Analysis

Authors: McElroy, Eric J., and de Buron, I.

Source: Journal of Parasitology, 100(4) : 399-410

Published By: American Society of Parasitologists

URL: <https://doi.org/10.1645/13-488.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

HOST PERFORMANCE AS A TARGET OF MANIPULATION BY PARASITES: A META-ANALYSIS

Eric J. McElroy and I. de Buron

Department of Biology, College of Charleston, 58 Coming St., Charleston, South Carolina 29401. Correspondence should be sent to: deburoni@cofc.edu

ABSTRACT: The mechanisms underlying parasite-altered host behavior and fitness remain largely unanswered. The purpose of this review is to provide a perspective that has not been fully incorporated into the debate on how parasites manipulate their hosts. We argue that performance capacity is an important target of parasitic manipulation, and we aim to integrate the study of performance with that of parasitic manipulations of host behavior and fitness. We performed a meta-analysis from the published literature of 101 measures of the effect of parasites on host performance capacity to address the following questions. (1) Do parasites exert an important effect on host performance capacity? (2) Is that effect routinely to decrease or enhance performance capacity? And, (3) what factors explain variation in the effect sizes that have been quantified? Although negligible–small effect sizes were detected in 40/101 measures, host performance capacity was overall affected by parasitic infection, with a negative direction and medium–large magnitude in 58/101 measures and an increase in performance capacity in 3/101 measures. Host age, type of host performance, the host tissue infected by the parasite, and whether the study was experimental or based on natural infections each explained a significant amount of the variation in effect size. The significance of each factor is briefly discussed in light of the potential adaptive character of host manipulations by parasites.

Parasites are fascinating organisms, and the repulsion they trigger in many people typically changes into an intense attraction that is well exploited in popular culture including movie monsters, e.g., *Alien* and *Slither*, popular literature (Nagami, 2001; Zimmer, 2001; Coustau and Hertel, 2008), and science news (Welsh, 2012; Bennington-Castro, 2013) which vividly picture parasites as body snatchers and zombie-engineers. However, this spookiness subverts the subtleties and exquisiteness involved in parasitism, which makes it one of the most successful modes of life (Poulin and Morand, 2000; Combes, 2001). Our fascination is a mere reflection of the parasites' complexity, diversity, and key role in both population and ecosystem dynamics (Sukhdeo and Hernandez, 2005; Kuris et al., 2008; Thompson et al., 2013).

For years, people have observed that parasites could modify the phenotype of their hosts, and the term “manipulation” was coined to group all these modifications together whether they were behavioral, morphological, and/or ecological (Poulin and Thomas, 1999; Moore, 2002; Thomas et al., 2005; Moore, 2013). In an attempt to connect the dots and explain the ways parasites evolve to complete extraordinary life cycles, Combes (1991) coined the term ‘favorization.’ Although, the adaptive nature of host manipulation, in particular the case of trophic favorization, remains the object of debate and requires prudence (Poulin, 1995; Webster et al., 2000; Cézilly et al., 2010; Perrot-Minnot et al., 2012), the fact that such manipulations are extended phenotypes of the parasite's genes is well acknowledged (Combes, 2001; Beani, 2006; Poulin, 2010; Thomas et al., 2012). Not all parasites manipulate their hosts (Poulin, 2010), some do (Moore, 2002; Hughes et al., 2012), some ‘cheat’ (the ‘hitchhikers’ and the ‘lucky ones’) by taking advantage of manipulative co-infections (Thomas et al., 1998; Lafferty et al., 2000; Mouritsen, 2001; Leung and Poulin, 2007), and for numerous others we simply do not know where they stand in this mosaic of interactions. However, when manipulation occurs, the classic idea is that parasites negatively impact their hosts' fitness, e.g., decreased reproductive output, impeded mating, or reduced growth to the benefit of their own fitness (Robar et al., 2010). However, host manipulation by parasites is multidimensional and complex (Thomas et al., 2010;

Ponton et al., 2011; Cézilly et al., 2013), and parasites are now known to target suites of interrelated traits (Biron and Loxdale, 2013; Poulin, 2013). Thus, although there are numerous examples of apparently straightforward negative outcomes of manipulations for the host (e.g., Hurd, 2001; Barber et al., 2004; Shirakashi et al., 2008), the constant arms race and tradeoffs in host–parasite relationships, as well as the molecular “cross-talk” between hosts and parasites, may lead to more subtle and intriguing situations. For instance, a host's longevity and/or size may be increased (Hurd et al., 2001; Ziuganov, 2005; Hartikainen et al., 2013), and some parasites switch how they manipulate their host such that they can be both beneficial and detrimental to the same host at different times during their development in that host (Parker et al., 2008; Hammerschmidt et al., 2009; Dianne et al., 2011; Weinreich et al., 2013). Although the profound evolutionary implications of manipulative parasites are not yet fully understood (Thomas et al., 2005), host phenotype manipulation by parasites, in particular behavioral manipulation, is not uncommon and occurs in multiple host and parasite taxa (Moore, 2002, 2012; Hughes et al., 2012; Lafferty and Shaw, 2013). The ecological consequences of host manipulation are well appreciated, if not fully determined (Poulin and Thomas, 1999; Lafferty and Kuris, 2012), and as stated by Poulin and Levri (2012), “having manipulated hosts in an ecosystem is not unlike having 2 related host species present in a community, sharing many traits but differing sharply with respect to others.”

It is clear that parasites manipulate their hosts; however, *how* parasites manipulate their hosts at a mechanistic level, i.e., what is the target of the parasitic manipulation, remains a fundamental question and, as such, the physiological mechanisms underlying changes in host phenotype are the object of continuous research (Lefevre et al., 2009; Ludin et al., 2011; Biron and Loxdale, 2013; Hughes, 2013; Perrot-Minnot and Cézilly, 2013; van Houte et al., 2013; Pennisi, 2014). Despite major recent advances, in particular in studies of how brain-controlling/hijacking parasites alter host behavior (Prandovsky et al., 2011; Adamo, 2013; Flegr, 2013; Helluy, 2013), the mechanisms underlying parasite-altered host behavior and fitness remain largely unanswered for most parasites (Thomas et al., 2005; Hughes et al., 2012; Adamo and Webster, 2013; Hughes, 2013). The purpose of this review is to provide

DOI: 10.1645/13-488.1

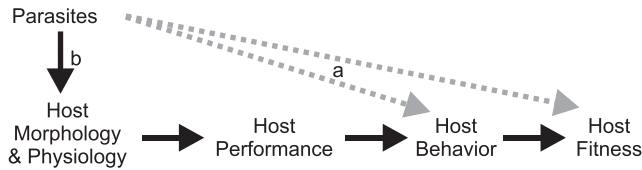


FIGURE 1. Theory predicts and data support the idea that variation in morphology/physiology predicts variation in performance capacity and that variation in performance capacity ultimately determines behavior and differential fitness between individuals (Arnold, 1983; Garland and Losos, 1994). (a) Dashed gray arrows showing the classic observation that parasites have an impact on host behavior or fitness. (b) The alternative hypothesis that parasites have a direct effect on host morphology and/or physiology, which then alters host performance, which then cascades into changes in host behavior and host fitness.

another perspective that has not yet been fully incorporated into the debate about the target of host manipulation by parasites.

We argue that whole-organism performance capacity is an important target of parasitic manipulation. Whole organism performance capacity is a physical quantity (e.g., distance, speed, frequency, time) that measures how well an organism *can* execute a given behavior or ecologically relevant task (Arnold, 1983; Garland and Losos, 1994; Irschick and Henningsen, 2009), e.g., how fast a fish can swim or how far a grasshopper can jump. Performance capacity has been intensely studied for the last several decades, and it is now widely accepted that performance capacity is a key trait (and maybe *the* key trait) that is targeted by selection (Arnold, 1983; Garland and Losos, 1994; Husak et al., 2006; Irschick and Le Galliard, 2008; Irschick et al., 2008). Performance is related to morphology, physiology, behavior, and fitness (Fig. 1). It is determined, i.e., constrained, by underlying morphological and physiological systems (Fig. 1). For example, the ability of a fish to swim rapidly is determined by its available muscle mass, muscle cell physiology, stored energy, and body/fin shape (Langerhans, 2009). In turn, performance constrains the behaviors in which the organism can engage (Garland and Losos, 1994). For example, a male lizard that cannot bite as hard is less likely to win fights and secure mates (Lappin and Husak, 2005). Thus, parasites that directly alter host morphology or physiology could influence host performance capacity because morphology and physiology constrains/predicts performance. Additionally, because performance constrains behavior and because behavior is a key predictor of fitness, parasites could exert their effect on host fitness and behavior via the filter of performance capacity (Fig. 1). We suggest that a hypothesis for how parasites impact host fitness is that parasites have a direct effect on host morphology and physiology and that this results in a change in performance capacity and then behavior and, ultimately, host fitness (Fig. 1).

Thinking of all of the ways that parasites induce changes in host morphology, physiology, and behavior quickly makes one wonder how often performance is impacted by parasites, especially given that so much research has shown performance as a key linkage between these traits. However, the literature of the effects of parasites on host performance capacity is limited to several examples, and no synthesis is yet available. Thus, the goal of this review paper is to use meta-analysis of the published literature on the effect of parasites on host performance capacity to address the following questions. Do parasites exert an important effect on host performance capacity? Is that effect

routinely to decrease or enhance performance capacity? And, what factors explain variation in the effect sizes that have thus far been quantified?

DATA COMPILATION FOR META-ANALYSIS

We compiled published studies of the effect of parasitism on performance capacity. We searched the following databases: Web of Science, Google Scholar, and Zoological Records using the following terms: parasit* and performan* and swim* or flight or run* or stamin* or locomot* or speed*, and various taxonomic terms, e.g., amphib*, fish*, insect*, etc., and we back-tracked the literature prior to 1980. We purposely decided against including studies on parasitoids because the use of the key word parasitoid* mostly yielded papers about the performance of the parasitoids themselves. We also purposely did not include any studies on performance when used in the sense of fitness, e.g., reproductive output or growth/weight gain. This search yielded 76 papers. Several studies recorded multiple types of performance capacity and multiple aspects of the same type of performance. In these cases, we kept each record of a type of performance, e.g., endurance vs. speed, but only 1 aspect of the same type of performance, e.g., if endurance was measured as time and distance, we only kept 1 measurement, chosen randomly. We only included studies that examined parasite presence/absence on performance; measures of the effect of parasite load or density on performance were not included in our meta-analysis (11 studies). We then calculated the effect size (Hedges' *g*) for the effect of parasite presence/absence on each performance measurement using a spreadsheet function following Gurevitch and Hedges (2001) or using the compute.es (Del Re, 2013) package in R v.3.0.1 (R Core Development Team, 2013). These different techniques were required, as published studies were heterogeneous in how they reported results, i.e., means, standard deviations, and samples sizes vs. *t*-test or *F*-test. Sixteen studies were not usable for the meta-analysis because they did not report enough statistical information to compute an effect size. After removing studies for the reasons stated above, the final dataset consisted of 49 studies (Table I) and 101 measures of effect size. In addition to the effect size, we recorded the following factors that were hypothesized to predict effect size from each study (Table II): (1) host taxon (to class, except Crustacea which is a subphylum), (2) host type (intermediate, definitive, paratenic), (3) host age (juvenile, adult, all ages, or none reported), (4) type of host activity (swimming, running, etc.), (5) type of host performance (speed, endurance, etc.), (6) parasite taxon (various taxonomic levels based on typical classification: digenean, acanthocephalan, etc.; see Table I), (7) type of parasite (endoparasite, mesoparasite, ectoparasite), (8) location of stage of parasite studied (external vs. internal), (9) specific location of parasite on/in the host (skin/gills, blood, viscera, etc.), (10) type of tissue the stage of the parasite studied infects or directly alters (epithelial, connective, etc.), (11) stage of the parasite when it infects the host (developed [adults, trophozoites, etc.] vs. developing [metacercariae, juveniles, etc.]), (12) parasite's type of life cycle (simple, complex, and other for non-defined life cycles such as fungus), (13) mode of transmission of the parasite at the stage it was studied (e.g., trophically via a predator or via a vector, or by direct contact), and (14) type of infection in study (experimental vs. natural).

TABLE I. References to studies used in the meta-analysis classified according to the type of performance tested in the original studies and host and parasite taxa.

Type of performance	Host taxon	Parasite taxon	References	
Acceleration	Insecta	Chelicerates	McLachlan et al., 2008	
		Teleost	Blake et al., 2006	
	Teleost	Cestodes	Blake et al., 2006	
		Digeneans	Umberger et al., 2013	
Distance	Amphibia	Nematodes	Goodman and Johnson, 2011	
		Digeneans	Chatfield et al., 2013	
Duration	Amphibia	Fungi	Pfennig and Tinsley, 2002	
		Monogeneans	Shirakashi et al., 2008	
Efficacy	Teleost	Monogeneans	Umberger et al., 2013	
		Nematodes	Goodman and Johnson, 2011	
Endurance	Amphibia	Digeneans	Kelehear et al., 2009; Marr et al., 2010	
		Nematodes	Kunz and Pung, 2004	
	Crustacea	Digeneans	Schiefer et al., 1977; Bradley and Altizer, 2005	
		Nematodes	Hockmeyer et al., 1975; Villacide and Corley, 2008	
	Insecta	Apicomplexans	Schwanz, 2006	
		Nematodes	Daniels, 1985	
	Mammalia	Digeneans	Schall et al., 1982; Schall, 1990; Clobert et al., 2000	
		Squamata	Chelicerates	Main and Bull, 2000
	Teleost	Amphibia	Amoebozoans	Powell et al., 2008
			Ciliophorans	Munderle et al., 2004
		Teleost	Crustaceans	Wagner et al., 2003; Östlund-Nilsson et al., 2005; Grutter et al., 2011; Binning et al., 2013
			Digeneans	Klein et al., 1969
			Kinetoplastids	Kumaraguru et al., 1995
			Molluscs	Taeubert and Geist, 2013
			Monogeneans	Shirakashi et al., 2008
			Myxozoans	Moles and Heifetz, 1998; Ryce et al., 2001; Wagner et al., 2005; DuBey et al., 2007; Fetherman et al., 2011
			Nematodes	Munderle et al., 2004; Palstra et al., 2007
			Opisthokonta	Kocan et al., 2006
	Frequency	Amphibia	Monogeneans	Pfennig and Tinsley, 2002
			Chelicerates	McLachlan et al., 2008
	Maneuvering	Insecta	Apicomplexans	Marden and Cobb, 2004
			Myxozoans	Wagner et al., 2005
Power	Teleost	Chelicerates	Goodman and Johnson, 2011	
		Nematodes	Goodman and Johnson, 2011; Pizzatto and Shine, 2011a, 2011b, 2012; Chatfield et al., 2013	
Repeat endurance	Amphibia	Acanthocephalans	Medoc and Bessel, 2008	
		Cestodes	Wedekind and Milinski, 1996	
Speed	Crustacea	Digeneans	Kunz and Pung, 2004	
		Apicomplexans	Schiefer et al., 1977; Bradley and Altizer, 2005	
	Insecta	Chelicerates	McLachlan et al., 2008	
		Kinetoplastids	Roberts, 1981	
	Nematodes	Nematodes	Villacide and Corley, 2008	
		Digeneans	Schwanz, 2006	
	Mammalia	Insects	Devevey et al., 2010	
		Squamata	Schall et al., 1982; Oppliger et al., 1996	
	Squamata	Chelicerates	Main and Bull, 2000; Ekner-Grzyb et al., 2013	
		Teleost	Cestodes	Barber et al., 2004; Blake et al., 2006
	Teleost	Crustaceans	Nendick et al., 2011	
		Digeneans	Blake et al., 2006; Santos et al., 2011	
	Teleost	Nematodes	Umberger et al., 2013	
		Teleosts	Brunnschweiler, 2006	

STATISTICAL ANALYSES

All analyses were done in R version 3.0.1 (R Core Development Team, 2013). We interpreted effect sizes according to Cohen (1988). We tested for bias in our data set using the function

regtest, constructing a funnel plot, and estimating 'missing' data using the trim and fill method in the R package metafor (Viechtbauer, 2010). Our goals were to (1) summarize general findings for effect sizes in the literature, and (2) test for the effect of each factor on effect sizes. To achieve these goals we used

TABLE II. Hypotheses for the impact of each factor studied on the change in host performance due to parasitism. A > denotes a larger negative effect size (i.e., more reduced performance due to parasite). Some hypotheses are based on findings or remarks of previous authors (see references) but do not systematically reflect their conclusions (i.e., more than one reference for a factor may indicate conflicting evidence).

No.	Factor	Hypotheses	References
1	Host taxon	Vertebrate taxa > invertebrate taxa	Poulin, 1994; Lafferty and Shaw, 2013
2	Host type	Intermediate/paratenic > definitive	Perrot-Minnot and Cézilly, 2009
3	Host age	juvenile > adult	Herrel and Gibb, 2006
4	Host activity	No difference expected	
5	Host performance	No differences expected	
6	Parasite taxon	Nematodes and cestodes > acanthocephalans	Poulin, 1994; Lafferty and Shaw, 2013
7	Parasite type	Endoparasite > ectoparasite/mesoparasite	Lafferty and Shaw, 2013
8	General parasite location	Internal > external	Lafferty and Shaw, 2013
9	Specific parasite location	Skin/gills and soma and blood > viscera	Chubb et al., 2010; Lafferty and Shaw, 2013
10	Parasite tissue	Muscle, neural, connective > epithelial, body cavity	Chubb et al., 2010; Lafferty and Shaw, 2013
11	Parasite stage	Developing > developed	Hammerschmidt et al., 2009; Chubb et al., 2010
12	Parasite cycle	Complex > simple	Perrot-Minnot and Cézilly, 2009
13	Parasite transmission	Trophic > vector/dispersal/contact	Holmes and Zohar, 1990
14	Type of infection	Experimental > natural	

mixed-model meta-analysis in metafor (Viechtbauer, 2010), with Hedges' g as the response, studies weighted by the inverse of their variance, factors as fixed effects, and host phylogeny, parasite taxonomy (species nested in factor 6, see above), and study identification as random effects. Two of the 14 factors we tested were collinear with other factors (specific parasite location was collinear with the tissue infected by the parasite, and parasite stage was collinear with host type) which prevented model fitting. Thus, we removed the specific location of the parasite and host type before proceeding. We compiled a host phylogeny based on published studies (Lavrov et al., 2004; Steppan et al., 2004; Ishiwata et al., 2011; Weigmann et al., 2011; von Reumont et al., 2012; Wainwright et al., 2012; Near, Dornburg et al., 2013; Near, Eytan et al., 2013; Pyron et al., 2013) in Mesquite 2.75 (Maddison and Maddison, 2011). To account for multiple measurements per species we included a soft polytomy, with branches of zero length emanating from each species to the individuals within that species. This was necessary, as different measurements within each species corresponded to different levels of the factors studied. We then set all other branch lengths to 1 and then ultrametrized the tree. To compute the phylogenetic correlation matrix we used the branch length transformation (Pagel's lambda) that achieved the maximum likelihood fit using the function corPagel from the ape package (Paradis et al., 2004). Several of the factors had missing data or levels with only 1 or 2 observations; thus, we recoded these levels as 'other' within each factor prior to fitting the model. When a factor had a significant impact on effect size, we tested for differences across factor levels using pairwise t -tests whose P -values were corrected using the Benjamini-Hochberg method (Benjamini and Hochberg, 1995). We checked the residuals using Lilliefors normality test in the package nortest (Gross and Ligges, 2012) and they were normally distributed ($D = 0.081$, $P = 0.08$). Homogenous residual variance was tested using Fligner-Killeen tests, which revealed slight heteroskedasticity for parasite taxon (F-K median $\chi^2 = 18.5$, $df = 9$, $P = 0.03$) and parasite transmission (F-K median $\chi^2 = 9.1$, $df = 3$, $P = 0.03$). Although linear models are generally robust to slight violation of their assumptions, we interpret the results from these factors with caution.

MAGNITUDE AND DIRECTION OF EFFECT SIZE

Host performance capacity was generally reduced due to parasitism, with a negative direction and medium-large magnitude (mean effect size \pm 95% confidence interval = -0.666 ± 0.155 ; Fig. 2). The majority (57%, 58/101 measures) were medium-large negative effect sizes with a large decrease in performance (effect size ≤ -0.8) detected in 40 measures and a medium decrease ($-0.8 < \text{effect size} \leq -0.5$) detected in 18 measures (Fig. 2). Increases in performance capacity due to parasitism were rare (3%, 3/101 measures), with a large increase in performance (effect size ≥ 0.8) detected in 1 measure and a medium increase ($0.5 \leq \text{effect size} < 0.8$) detected in 2 measures (Fig. 2). These studies included an increase in swimming performance in a rodent, *Microtus arvalis* (see Devevey et al., 2010), an amphipod, *Gammarus roeseli* (see Medoc and Beisel, 2008), and in diving performance in a lizard, *Sphenomorphus quoyii* (see Daniels, 1985). Negligible-small effect sizes were detected in 40 studies (40%, 40/101 measures).

BIAS IN REPORTED EFFECT SIZES

Effect sizes were significantly related to their standard errors (Egger's regression test, $z = -3.8$, $P = 0.0001$), which indicates that reported effect sizes may be biased. The funnel plot and the trim and fill method revealed that there were 15 missing effect size measures all greater than 0 (Fig. 2). Seven of these missing effect sizes were greater than 0.8 (large effect size) and 2 others were greater than 0.5 (medium effect size). This analysis suggests that the reported effect sizes are biased because of a lack of published reports of medium-large magnitude increases in host performance due to parasitic infection.

FACTORS THAT EXPLAIN VARIATION IN EFFECT SIZE

Many of the factors tested did not explain variation in effect size (Table III; Fig. 3) including host taxon, host activity, parasite taxon, type of parasite, general location of parasite, stage when the parasite infects its host, the parasite's type of life cycle, and the way the parasite is transmitted. Host age, type of host performance, the type of tissue the stage of parasite studied

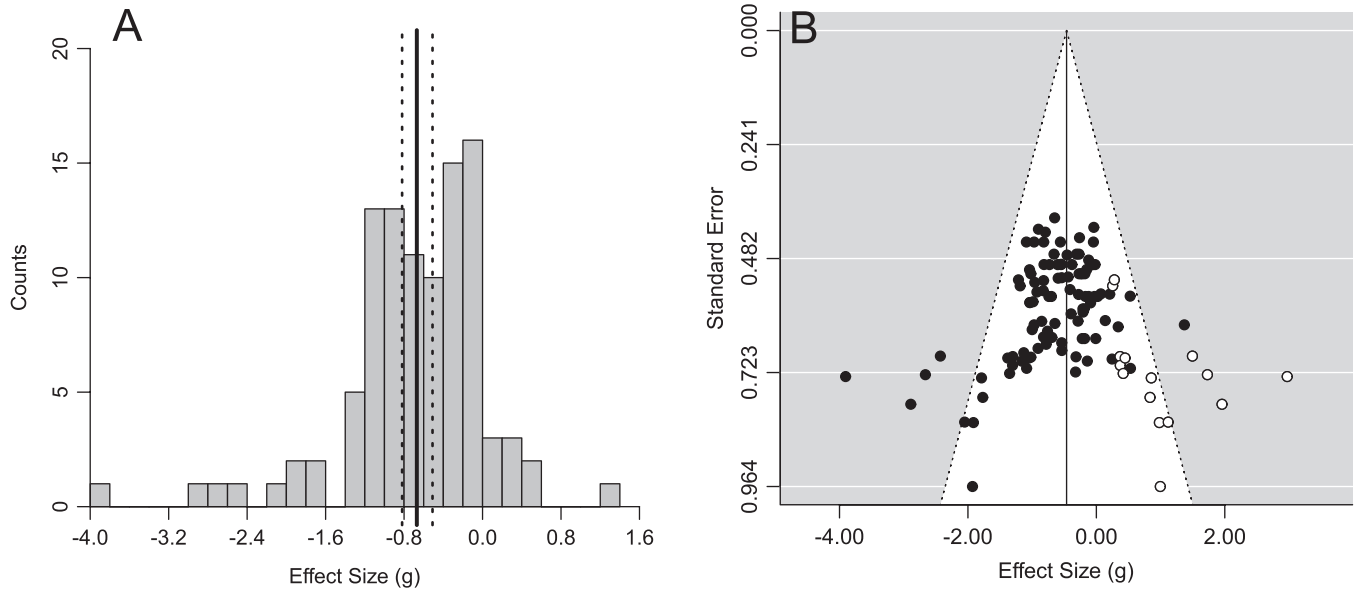


FIGURE 2. (A) Frequency histogram of effect sizes from published studies of the effect of parasitism on host performance capacity. Effects sizes less than 0 indicate a decrease in performance due to parasitism; values greater than 0 indicate an increase in performance due to parasitism. Solid vertical line is the mean effect size; dashed vertical lines are the 95% confidence intervals. (B) Funnel plot of effect sizes vs. standard error of the effect size. Dotted lines indicate the 95% pseudo-confidence intervals. Black dots are the measured effects from the literature. White dots are those estimated to be 'missing studies' based on the trim and fill method.

infects, and the type of infection in the study each explained a significant amount of the variation in effect size (Table III; Fig. 3). Studies that did not report host age or included all ages had significantly greater decreases in performance than did known adult or juvenile hosts ($P = 0.03$), and juvenile hosts had marginally greater decreases in performance than did adult hosts ($P = 0.09$). Endurance had marginally greater decreases in performance than did speed ($P = 0.09$), whereas all other host performance comparisons showed similar effect sizes ($P > 0.10$). Connective tissue had greater decreases in performance than did all 'other' tissues (which included studies with no data). Finally, experimental infections resulted in greater negative effects on host performance than did naturally occurring infections. Year of publication was not correlated with effect size ($r = -0.04$, $P = 0.69$). However, more-recent publications show greater variance in effect sizes than did the older studies (Fig. 4).

GENERAL PATTERNS IN HOW PARASITES INFLUENCE PERFORMANCE

The majority of studies analyzed show that the presence of parasites reduces host performance capacity and that the effect of parasites is most often in the medium–large category (Fig. 2). This result agrees with the general idea that parasites harm or live at the expense of their hosts, even if not grossly pathogenic, and that they impact their host at the individual, population, and ecosystem levels (see review by Combes, 2001). Additionally, via a recent meta-analysis, Robar et al. (2010) showed that parasitized individuals have an $\sim 2.6\times$ higher mortality than do non-parasitized individuals. Therefore, our result suggests that the mechanism by which parasites reduce host fitness and, thus, by which they can impact the host population, could often be due to the reduction of host performance capacity even though rarely studied, per se. For instance, parasitized animals show different

migratory patterns compared to uninfected ones (Sjöberg et al., 2009) or cannot reach, or are delayed in reaching, their spawning grounds (Palstra et al., 2007; Kocan et al., 2009) or breeding grounds (Møller et al., 2004; Lopez et al., 2013). Among these examples, only Palstra et al. (2007) and Kocan et al. (2009) demonstrate that a reduction in performance is what constrains the host's ability to engage in effective (swimming) behavior. Other reasons, often invoked by authors to explain an alteration of behavior that reduces infected hosts' fitness include poor body condition, increased metabolism, or depressed immune function (Yorinks and Atkinson, 2000; Madelaire et al., 2013) or changes in host morphology such as alteration of feathers (Marzal et al., 2013; Pap et al., 2013) or lateralization (Roche et al., 2013) due to parasitic infection. Here, we emphasize that these changes in physiology and morphology likely underpin changes in performance capacity, and yet most studies have not identified how performance changes and whether it constrains behavior.

Some parasite-induced behavioral alterations may benefit the host (see examples in Combes, 2001 and Moore, 2012). We found 3 cases of medium–large increases in host performance capacity due to parasitism (Fig. 2). Two of them involve acanthocephalans, many of which are known to manipulate their intermediate hosts (Poulin, 1995; Moore, 2002). Daniels (1985) reported increased diving time in a lizard due to infection by an acanthocephalan, and Medoc and Beisel (2008) reported increased swimming speed in an amphipod also infected by an acanthocephalan. In these 2 cases, it was reasoned by the authors that the increase in host performance capacity might make the host less likely to be eaten by the 'wrong' predators (birds for the skink, a benthic invertebrate for the amphipod) and more likely to be eaten by the definitive host (a snake for the skink and a bird for the amphipod). Thus, these may be examples of predation suppression (sensu Hammerschmidt et al., 2009), which is a

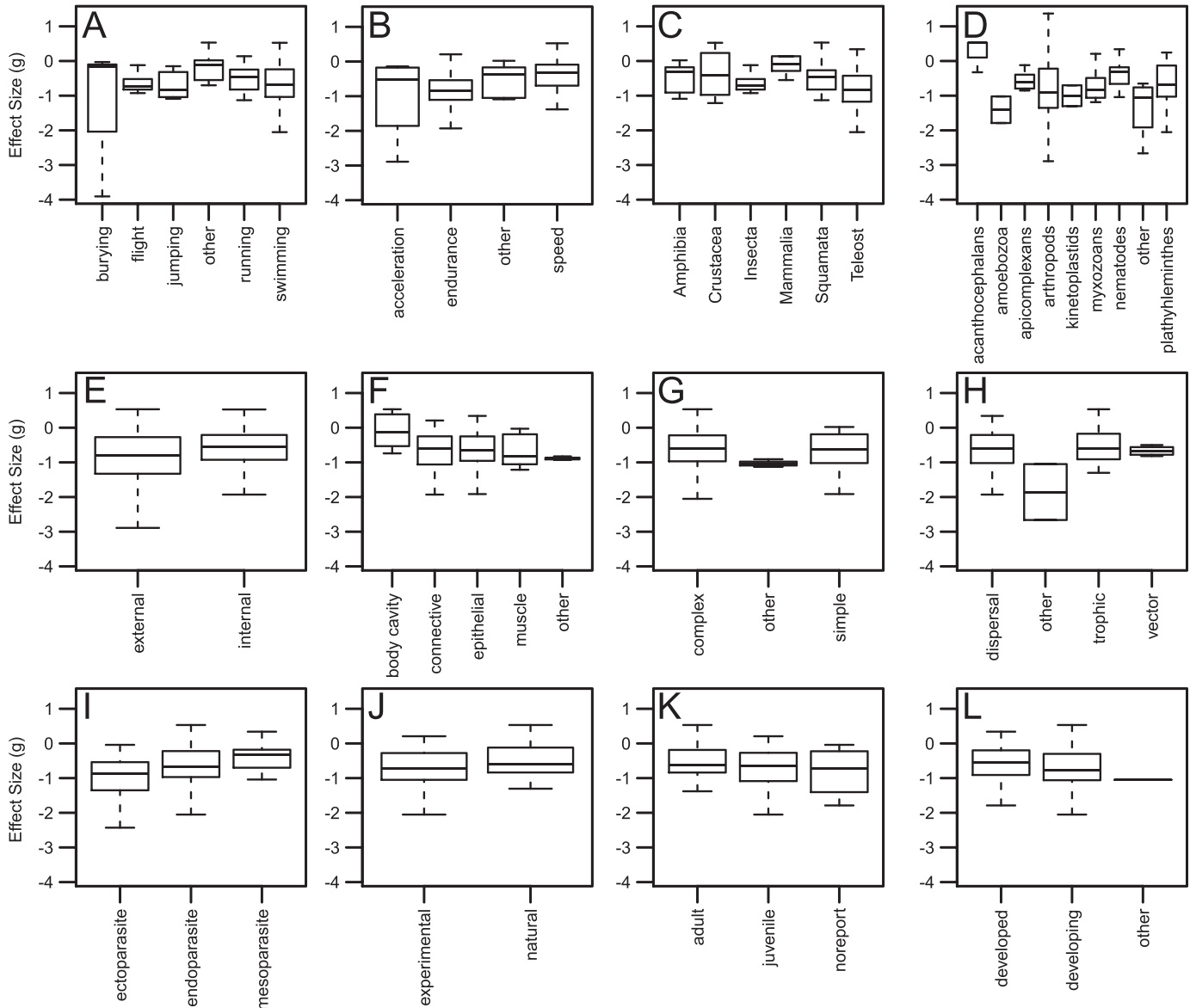


FIGURE 3. Effect sizes in change of host performance according to various factors. For each level, black bar is the median, box is the interquartile range, and whiskers are 1.5 times the interquartile range. (A) Host activity. (B) Host performance. (C) Host taxa. (D) Host age. (E) Location of the parasite on/in the host. (F) Type of tissue the parasite infects. (G) Parasite's type of life cycle (H) Parasite's mode of transmission. (I) Type of parasite. (J) Type of infection. (K) Host age. (L) Parasite's stage when it infects.

general phenomenon where parasites enhance the abilities of their host to protect it until transmission is optimal. While examples of predation suppression with respect to host behavior and host fitness are amassing (Koella et al., 2002; Hammerschmidt et al., 2009), examples of changes in performance capacity are, however, generally lacking (Chubb et al., 2010), with the caveat that some studies indeed measure performance but under the confusing term of 'activity' (see below). The third example of performance enhancement is for fleas infesting adult female voles (Devevey et al., 2010) and for which a performance increase is difficult to interpret in the light of either manipulation to favor parasite transmission or a beneficial value to the host, particularly because such performance enhancement is not observed in male voles or in either sex of voles infected as juveniles. For all 3 of these

examples, we again emphasize the need for exploration of the mechanism linking parasite to performance, i.e., morphology and physiology (Fig. 1).

Every meta-analysis must confront publication bias, which can skew results and interpretations. That most published studies show a medium-large negative effect size suggests that the literature may be biased towards studies reporting 'significant' results in the expected direction, i.e., parasites reducing host performance. This notion was confirmed by a significant linear trend in the funnel plot and by the trim-and-fill method that suggests that studies with medium-large positive effect sizes representing increases in host performance capacity due to parasitism were 'missing' from our data set (Fig. 2B). This suggests either that studies that have demonstrated increases in

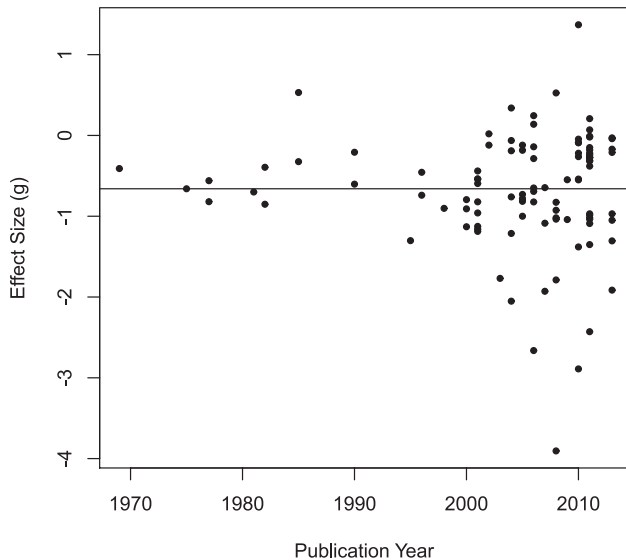


FIGURE 4. Bivariate plot of effect size vs. year of publication. Solid line is the mean effect size (-0.66).

host performance capacity due to parasites have not been published or that, on the contrary, cases of parasites increasing host performance capacity are indeed rare. The former explanation is not unreasonable given the difficulty in shifting paradigms (see also Poulin [2000] for additional arguments about publication bias). However, the fact that variance in effect sizes is increasing with publication year, and that new studies are rapidly accumulating (39 of the 101 measures were collected since 2010 [Fig. 4]), suggests that performance enhancement by parasites is on the cusp of being more broadly recognized. Also encouraging is that 35% of the published studies show no, or negligible, size effect, suggesting that non-significant results are regularly reported and that the potential lack of such reports is not a source of bias.

Another issue is that we chose not to use the term ‘behavior’ in our search criteria, whereas parasitologists appear to often treat the terms “behavior,” “activity,” and “performance” similarly. Consequently, although parasitologists have been heavily invested in testing how parasites change host behavior, there are undoubtedly studies where ‘behavior’ was reportedly tested but ‘performance’ was actually measured, and these studies may have been missed by our search criteria. To address the scope of this issue, we reviewed all papers cited in a meta-analysis of parasite-induced changes in host behavior which explicitly included activity (Poulin, 1994). Of the 21 studies examined, 3 clearly measured performance (Townson, 1970; Benton and Pritchard, 1990; Carmichael and Moore, 1991), although none of these 3 papers actually called the measurement ‘performance.’ Therefore, it is important to emphasize the definitions of performance and behavior within the classic framework of the ecomorphological or performance paradigm. Performance is defined as the capacity for an organism to do an ecologically relevant task or execute a behavior (Arnold, 1983; Garland and Losos, 1994). In other words, performance defines what an organism *can do* and behavior is what an organism actually *does* (Reilly and Wainwright, 1994). It would be most useful for these definitions

and this framework to be fully incorporated into the study of behavioral manipulations by parasites to help differentiate change in behavior from performance and change in the underlying mechanisms of performance.

PARASITE-RELATED FACTORS THAT EXPLAIN VARIATION IN EFFECT SIZE

We examined 8 factors related to parasite biology that could be expected to influence the magnitude of change in host performance due to parasitism (Table II). Among these factors, only the tissue that the parasite infects (or directly alters) explained a significant amount of the variation in effect sizes (Table III). Post hoc tests differentiated connective tissue from all others as being the habitat of parasites showing larger effect size on their host performance (Table III; Fig. 3). Although Lafferty and Shaw (2013) also found that site of infection often defined the parasites’ capacities to manipulate their hosts, they noted that, in contradiction to our findings, manipulative parasites more commonly inhabited the central nervous system, the body cavity, or the muscles of their hosts. However and significantly, measurements included in our results also took into account the tissues altered by the parasites, most of which altered blood either by living in it (Schall, 1990; Oppliger et al., 1996) or feeding on it (Main and Bull, 2000; Devevey et al., 2010; Ekner-Grzyb et al., 2013). Because parasites are well recognized to affect both their host metabolism and immune function, which can be considered physiological targets for some manipulative parasites, these results support our hypothesis that by having a direct effect on host physiology, parasites induce a change in their performance capacity. It is also possible that infections by *Myxobolus* spp., which were reported as inducing skeletal deformities (Ryce et al., 2001; DuBey et al. 2007; Fetherman et al., 2011) and that we thus tagged as altering the connective tissue, may have biased our findings because these parasites also likely affect the hosts’ muscular and nervous systems. However, such a complication is inherent to studying parasitism and will require an extremely large data set to be overcome.

Although previous meta-analyses suggested that acanthocephalans are less likely to influence host activity than are other helminths (Poulin, 1994; Lafferty and Shaw, 2013), and that trophic transmission has a smaller effect on host activity than do other modes of transmission (Poulin, 1994), we found little statistical support for either of these (Table III). However, it should be noted that 2 of the 3 studies of acanthocephalans had increased host performance (see above) and, thus, there could be a difference due to infection by this parasite taxon that is known to be almost entirely comprised of manipulators. In fact, overall we found that very few aspects of the parasite’s biology explained variation in effect size, even though there are valid hypotheses for why these factors should explain changes in performance (Table II). Additionally, several of these factors explain parasite-induced host mortality (Robar et al., 2010). The reason for the lack of significant factors in the present study is unclear. One issue that slices across many factors is wildly uneven sampling in factor levels and factor levels with uneven taxa sampling, e.g., all acanthocephalans have complex life cycles. In addition, parasite–host interactions are typically specialized, and it may be the specialized nature of these interactions that prevents these

TABLE III. Results of the mixed model meta-analysis for the impact of each factor on variation in effect size. Post hoc groupings were determined by *t*-tests corrected for multiple comparisons using the Benjamini-Hochberg method (Benjamini and Hochberg, 1995); only significant differences between levels within a factor are reported (A > denotes a larger negative effect size). Comparisons not listed are not significantly different.

No.	Factor	Q_m	P	df	Post hoc comparisons
1	Host taxon	6.6	0.26	5	
2	Host type*				
3	Host age	8.5	0.01	2	No report > juvenile/adult ($P = 0.03$), juvenile > adult ($P = 0.09$)
4	Host activity	5.0	0.41	5	
5	Host performance	8.6	0.04	3	Endurance > speed ($P = 0.09$)
6	Parasite taxon	11.3	0.19	8	
7	Parasite type	2.9	0.24	2	
8	General parasite location	0.1	0.96	1	
9	Specific parasite location†				
10	Tissue altered	10.3	0.04	4	Connective > others ($P = 0.04$)
11	Parasite stage	1.4	0.49	2	
12	Parasite cycle	1.1	0.59	2	
13	Parasite transmission	0.8	0.86	3	
14	Type of infection	5.0	0.03	1	Experimental > natural

* Collinear with factor 11.

† Collinear with factor 10.

simplistic factors from explaining variation in how parasites influence host performance capacity.

HOST-RELATED FACTORS THAT EXPLAIN VARIATION IN EFFECT SIZE

Host age explained a significant amount of variation in effect size, and post hoc testing provided marginal support for the hypothesis that parasites should have a greater effect on juveniles when compared to adults (Tables II, III). Juveniles in general are thought to be under strong selection for performance capacity because they often must compete with adults, which have greater absolute abilities because of their larger size (Herrel and Gibb, 2006). This leads to performance compensation in juveniles (Herrel and Gibb, 2006) and to a juvenile's greater use of its physiological maximum performance capacity, particularly in nature (Irschick, 2000). That is, if a parasite infects a juvenile and adult of the same species, one would expect a greater effect on the juvenile because its morphological and physiological systems are already working near their maximum physical capacity and, thus, any alteration induced by a parasite would come at a relative greater performance cost to the juvenile. We identified 3 cases where the juvenile and adult data are available for the same host, infected by the same parasite, and involved in the same type of performance, i.e., *Anguilla anguilla* infected by *Anguillicoloides crassus* (see Munderle et al., 2004; Palstra et al., 2007), *Tiliqua rugosa* infected by *Aponomma hydrosauri* (see Main and Bull, 2000), and *Gasterosteus aculeatus* infected by *Schistocephalus solidus* (see Barber et al., 2004; Blake et al., 2006). The effect size for juveniles was more negative in 2 of these 3 examples and very large in *G. aculeatus*, suggesting that the pattern seen across studies is mirrored in this subset. Future studies that explicitly examine how parasites influence performance across both host and parasite ontogenies would be useful.

We did not expect the type of performance to explain variation in effect size, and yet we found that endurance was more affected than speed (Table III; Fig. 3). Endurance is dependent upon the

host's metabolic capacity, and several studies have demonstrated altered host metabolism due to parasitism (Robar et al., 2011), which can result in a reduction in endurance (Binning et al., 2013).

Finally, experimental infections had larger negative effect sizes than did natural infections (Table III; Fig. 3), suggesting (not surprisingly) that experimental approaches are more powerful. Yet, these experimental approaches are done by investigating the effect of a single parasite species and often with both the host and parasite raised for some time under laboratory conditions. Although this approach is scientifically sound and powerful for detecting causal relationships, it ignores the fact that most hosts are infected by several species of parasites, and the interaction between these parasites can be as important as the isolated effect of each species. Future experimental approaches that examine how multiple infections impact host performance capacity (Ferguson et al., 2012) under more-realistic conditions (mesocosms, field experiments) would likely yield a better understanding of how much parasites influence host performance capacity in nature.

THE EFFECT OF STUDY YEAR

Publication year was not correlated with effect size (Fig. 4). This finding is different from a previous meta-analysis of the effect of parasite on host behavior which showed that effect sizes were negatively related to publication year. This suggests that the publication history of parasites' impact on host performance capacity has not been unduly influenced by biases due to trends or prior expectations, as is apparent in the literature on parasites' effects on host behavior (Poulin, 2000). Although there is no trend, the amount of variation in reported effect sizes has increased with publication year. This may be due to the accumulation of studies that have examined a greater diversity of host-parasite interactions, which could be expected to result in more variable effect sizes. As noted above, the increase in variation with time may suggest that more positive effect sizes will

soon be discovered, as after ~2000 there are many more reports of effect sizes greater than 0.

CONCLUSION AND PROSPECTUS

Parasites exert important impacts on host performance capacity. In some cases the mechanistic underpinnings of changes in host performance, i.e., alteration of morphology or/and physiology (Fig. 1), are well understood; for example, a non-functional swimbladder in eels infected by nematodes (Palstra et al., 2007), a reduction in tracheal gas exchange in honey bees by mites (Harrison et al., 2001), or deformities of rainbow trout due to infection by myxozoans (Fetherman et al., 2011). However, in most cases they are not, and some possible mechanism can only be hypothesized (Goater et al., 1993; Bradley and Altizer, 2005). Although the mechanistic link between parasites and performance may be difficult to separate from other factors affecting host behavior, it nevertheless could involve a broad range of factors from simple morphological alterations to more-complex hormonal/biochemical changes in the host (Lafferty and Shaw, 2013). Importantly, parasites may impact host evolution via performance alteration. As such, an integrative understanding of parasites, host morphology/physiology, and host performance would greatly refine our understanding of how parasites alter host fitness and whether or not such an impact may have an adaptive value not only for the parasite but for the host as well (Harrison et al., 2001; Ebert, 2005).

ACKNOWLEDGMENTS

We thank 2 anonymous reviewers whose comments improved the manuscript and the Department of Biology at the College of Charleston for funding.

LITERATURE CITED

- ADAMO, S. A. 2013. Parasites: Evolution's neurobiologists. *Journal of Experimental Biology* **216**: 3–10.
- , AND J. P. WEBSTER. 2013. Neural parasitology: How parasites manipulate host behaviour. *Journal of Experimental Biology* **216**: 1–2.
- ARNOLD, S. J. 1983. Morphology, performance and fitness. *American Zoologist* **32**: 347–361.
- BARBER, I., P. WALKER, AND P. A. SVENSSON. 2004. Behavioural responses to simulated avian predation in female three-spined sticklebacks: The effect of experimental *Schistocephalus solidus* infection. *Behaviour* **141**: 1425–1440.
- BEANI, L. 2006. Crazy wasps: When parasites manipulate the *Polistes* phenotype. *Annales Zoologici Fenni* **43**: 564–574.
- BENJAMINI, Y., AND Y. HOCHBERG. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* **57**: 289–300.
- BENNINGTON-CASTRO, J. 2013. 12 real parasites that control the lives of their hosts. <http://io9.com/12-real-parasites-that-control-the-lives-of-their-hosts-461313366>. Accessed 6 March 2014.
- BENTON, M. J., AND G. PRITCHARD. 1990. Mayfly locomotory responses to endoparasitic infection and predator presence: The effects on predator encounter rate. *Freshwater Biology* **23**: 363–371.
- BINNING, S. A., D. G. ROCHE, AND C. LAYTON. 2013. Ectoparasites increase swimming costs in a coral reef fish. *Biology Letters* **9**: 20120927.
- BIRON, D. G., AND H. D. LOXDALE. 2013. Host-parasite molecular cross-talk during the manipulative process of a host by its parasite. *Journal of Experimental Biology* **216**: 148–160.
- BLAKE, R. W., P. Y. L. KWOK, AND K. H. S. CHAN. 2006. Effects of two parasites, *Schistocephalus solidus* (Cestoda) and *Bunodera* spp. (Trematoda), on the escape fast-start performance of three-spined sticklebacks. *Journal of Fish Biology* **69**: 345–355.
- BOYCE, N. P. 1978. Effects of *Eubothrium salvelini* (Cestoda: Pseudophylloidea) on the growth and vitality of sockeye salmon, *Oncorhynchus nerka*. *Canadian Journal of Zoology* **57**: 597–602.
- BRADLEY, C. A., AND S. ALTIZER. 2005. Parasites hinder monarch butterfly flight: Implications for disease spread in migratory hosts. *Ecology Letters* **8**: 290–300.
- BRUNNSCHWEILER, J. M. 2006. Sharksucker–shark interaction in two carcharhinid species. *Marine Ecology* **27**: 89–94.
- CARMICHAEL, L. M., AND J. MOORE. 1991. A comparison of behavioral alterations in the brown cockroach, *Periplaneta brunnea*, and the American cockroach, *Periplaneta americana*, infected with the acanthocephalan, *Moniliformis moniliformis*. *Journal of Parasitology* **77**: 931–936.
- CÉZILLY, F., A. FAVRAT, AND M. J. PERROT-MINNOT. 2013. Multidimensionality in parasite-induced phenotypic alterations: Ultimate versus proximate aspects. *Journal of Experimental Biology* **216**: 27–35.
- , F. THOMAS, V. MÉDOC, AND M.-J. PERROT-MINNOT. 2010. Host manipulation by parasites with complex life-cycles: Adaptive or not? *Trends in Parasitology* **26**: 311–317.
- CHATFIELD, M. W. H., L. A. BRANNELLY, M. J. ROBAK, L. FREEBORN, S. P. LAILVAUX, AND C. L. RICHARDS-ZAWACKI. 2013. Fitness consequences of infection by *Batrachochytrium dendrobatidis* in northern leopard frogs (*Lithobates pipiens*). *EcoHealth* **10**: 90–98.
- CHUBB, J. C., M. A. BALL, AND G. A. PARKER. 2010. Living in intermediate hosts: Evolutionary adaptations in larval helminthes. *Trends in Parasitology* **26**: 93–102.
- CLOBERT, J., A. OPLIGER, G. SORCI, B. ERNANDE, J. G. SWALLOW, AND T. GARLAND JR. 2000. Trade-offs in phenotypic traits: Endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Functional Ecology* **14**: 675–684.
- COHEN, J. 1988. *Statistical power analysis for the behavioral sciences*, 2nd ed. Lawrence Erlbaum Associates Publishers, Mahwah, New Jersey, 567 p.
- COMBES, C. 1991. Ethological aspects of parasite transmission. *American Naturalist* **138**: 866–880.
- . 2001. *Parasitism: The ecology and evolution of intimate interactions*. University of Chicago Press, Chicago, Illinois, 728 p.
- COUSTAU, C., AND O. HERTEL. 2008. *La malédiction du cloporte*. Tallandier, Paris, France, 186 p.
- DANIELS, C. B. 1985. The effect of infection by a parasitic worm on swimming and diving in the water skink, *Sphenomorphus quoyii*. *Journal of Herpetology* **19**: 160–162.
- DEL RE, A. C. 2013. *Compute.es: Compute Effect Sizes*. R package version 0.2-2. Available at: <http://cran.r-project.org/web/packages/compute.es>. Accessed 6 March 2014.
- DEVEVEY, G., P. BIZE, S. FOURNIER, E. PERSON, AND P. CHRISTE. 2010. Testing the predictive adaptive response in a host-parasite system. *Functional Ecology* **24**: 178–185.
- DIANNE, L., M. PERROT-MINNOT, A. BAUER, M. GALLIARD, E. LEGER, AND T. RIGAUD. 2011. Protection first then facilitation: A manipulative parasite modulates the vulnerability to predation of its intermediate host according to its own developmental stage. *Evolution* **65**: 2692–2698.
- DUBÉY, R. J., C. A. CALDWELL, AND W. R. GOULD. 2007. Relative susceptibility and effects on performance of Rio Grande cutthroat trout and rainbow trout challenged with *Myxobolus cerebralis*. *Transactions of the American Fisheries Society* **136**: 1406–1414.
- EBERT, D. 2005. Host adaptations against the costs of parasitism. In *Ecology, epidemiology, and evolution of parasitism in Daphnia* [Internet]. National Center for Biotechnology Information (U.S.), Bethesda, Maryland, Chapter 6. Available at: <http://www.ncbi.nlm.nih.gov/books/NBK2046/>. Accessed 27 May 2014.
- EKNER-GRZYB, A., Z. SAJKOWSKA, K. DUDEK, M. GAWAIEK, P. SKÓRKA, AND P. TRYJANOWSKI. 2013. Locomotor performance of sand lizards (*Lacerta agilis*): Effects of predatory pressure and parasite load. *Acta Ethologica* **16**: 173–179.
- FERGUSON, J. A., J. ROMER, J. C. SIFNEOS, L. MADSEN, C. B. SCHRECK, M. GLYNN, AND M. L. KENT. 2012. Impacts of multispecies parasitism on juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon. *Aquaculture* **362–363**: 184–192.
- FETHERMAN, E. R., D. L. WINKELMAN, G. J. SCHISLER, AND C. A. MYRICK. 2011. The effects of *Myxobolus cerebralis* on the physiological

- performance of whirling disease resistant and susceptible strains of rainbow trout. *Journal of Aquatic Animal Health* **23**: 169–177.
- FLEGR, J. 2013. How and why *Toxoplasma* makes us crazy. *Trends in Parasitology* **29**: 156–163.
- GARLAND, T. G., AND J. B. LOSOS. 1994. Ecological morphology of locomotor performance in squamate reptiles. In *Ecological morphology: Integrative organismal biology*, P. C. Wainwright and S. M. Reilly (eds.). University of Chicago Press, Chicago, Illinois, p. 240–302.
- GOATER, C. P., R. D. SEMLITSCH, AND M. V. BERNASCONI. 1993. Effects of body size and parasite infection on the locomotory performance of juvenile toads, *Bufo bufo*. *Oikos* **66**: 129–136.
- GOODMAN, B. A., AND P. T. J. JOHNSON. 2011. Disease and the extended phenotype: Parasites control host performance and survival through induced changes in body plan. *PLoS ONE* **6**: e20193.
- GROSS, J., AND U. LIGGES. 2012. *Nortest*: Tests for normality. R package version 1.0–2. Available at: <http://CRAN.R-project.org/package=nortest>. Accessed 6 March 2014.
- GRUTTER, A. S., A. J. CREAN, L. M. CURTIS, A. M. KURIS, R. R. WARNER, AND M. I. MCCORMICK. 2011. Indirect effects of an ectoparasite reduce successful establishment of a damselfish at settlement. *Functional Ecology* **25**: 586–594.
- GUREVITCH, J., AND L. V. HEDGES. 2001. Meta-analysis: Combining the results of independent experiments. In *Design and analysis of ecological experiments*, S. M. Scheiner and J. Gurevitch (eds.). Oxford University Press, Oxford, U.K., p. 347–370.
- HAMMERSCHMIDT, K., K. KOCK, M. MILINSKI, J. C. CHUBB, AND G. A. PARKER. 2009. When to go: Optimization of host switching in parasites with complex life cycles. *Evolution* **63**: 1976–1986.
- HARRISON, J. F., S. CAMAZINE, J. H. MARDEN, S. D. KIRKTON, A. ROZO, AND X. YANG. 2001. Mite not make it home: Tracheal mites reduce the safety margin for oxygen delivery of flying honeybees. **204**: 805–814.
- HARTIKAINEN, H., I. FONTES, AND B. OKAMURA. 2013. Parasitism and phenotypic change in colonial hosts. *Parasitology* **140**: 1403–1412.
- HELLUY, S. 2013. Parasite-induced alterations of sensorimotor pathways in gammarids: Collateral damage of neuroinflammation? *Journal of Experimental Biology* **216**: 67–77.
- HERREL, A., AND A. C. GIBB. 2006. Ontogeny of performance in vertebrates. *Physiological and Biochemical Zoology* **79**: 1–6.
- HOCKMEYER, W. T., B. A. SCHIEFER, B. C. REDINGTON, AND B. E. F. ELDRIDGE. 1975. *Brugia pahangi*: Effects upon the flight capability of *Aedes aegypti*. *Experimental Parasitology* **38**: 1–5.
- HOLMES, J. C., AND S. ZOHAR. 1990. Pathology and host behavior. In *Parasitism and host behavior*, C. J. Barnard and J. M. Behnke (eds.). Taylor and Francis, London, U.K., p. 34–63.
- HUGHES, D. 2013. Pathways to understanding the extended phenotype of parasites in their hosts. *Journal of Experimental Biology* **216**: 142–147.
- , J. BRODEUR, AND F. THOMAS. 2012. Host manipulation by parasites. Oxford University Press, Oxford, U.K., 224 p.
- HURD, H. 2001. Host fecundity reduction: A strategy for damage limitation? *Trends in Parasitology* **17**: 363–368.
- , E. WARR, AND A. POLWART. 2001. A parasite that increases host life span. *Proceedings of the Royal Society B: Biological Sciences* **268**: 1749–1753.
- HUSAK, J. R., S. F. FOX, M. B. LOVERN, AND R. A. VAN DEN BUSSCHE. 2006. Faster lizards sire more offspring: Sexual selection on whole-animal performance. *Evolution* **60**: 2122–2130.
- IRSCHICK, D. J. 2000. Effects of behaviour and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. *Functional Ecology* **14**: 438–444.
- , AND J. P. HENNINGSSEN. 2009. Functional morphology: Muscles, elastic mechanisms, and animal performance. In *Princeton guide to ecology*, S. Levin (ed.). Princeton University Press, Princeton, New Jersey, p. 27–37.
- , AND J. LE GALLIARD. 2008. Studying the evolution of whole-organism performance capacity: Sex, selection, and haiku—An introduction. *Evolutionary Ecology Research* **10**: 155–156.
- , J. J. MEYERS, J. F. HUSAK, AND J. LE GALLIARD. 2008. How does selection operate on whole-organism performance capacities? A review and synthesis. *Evolutionary Ecology Research* **10**: 177–196.
- ISHIWATA, K., G. SASAKI, J. OGAWA, T. MIYATA, AND Z. SU. 2011. Phylogenetic relationships among insect orders based on three nuclear protein-coding gene sequences. *Molecular Phylogenetics and Evolution* **58**: 169–180.
- KELEHEAR, C., J. K. WEBB, AND R. SHINE. 2009. *Rhabdias pseudosphaerocephala* infection in *Bufo marinus*: Lung nematodes reduce viability of metamorph cane toads. *Parasitology* **136**: 919–927.
- KLEIN, W. D., O. W. OLSEN, AND D. C. BOWDEN. 1969. Effects of intestinal fluke, *Crepidostomum farionis*, on rainbow trout, *Salmo gairdnerii*. *Transactions of the American Fisheries Society* **98**: 1–6.
- KOCAN, R., P. HERSHBERGER, G. SANDERS, AND J. WINTON. 2009. Effects of temperature on disease progression and swimming stamina in *Ichthyophonus*-infected rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Diseases* **32**: 835–843.
- , S. LAPATRA, J. GREGG, J. WINTON, AND P. HERSHBERGER. 2006. *Ichthyophonus*-induced cardiac damage: A mechanism for reduced swimming stamina in salmonids. *Journal of Fish Diseases* **29**: 521–527.
- KOELLA, J. C., L. RIEU, AND R. E. L. PAUL. 2002. Stage-specific manipulation of a mosquito's host-seeking behavior by the malaria parasite *Plasmodium gallinaceum*. *Behavioral Ecology* **13**: 816–820.
- KUMARAGURU, A. K., E. W. H. BEAMISH, AND P. T. K. WOO. 1995. Impact of a pathogenic haemoflagellate, *Cryptobia salmositica* Katz, on the metabolism and swimming performance of rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Diseases* **18**: 297–305.
- KUNZ, A. K., AND O. J. PUNG. 2004. Effects of *Microphallus turgidus* (Trematoda: Microphallidae) on the predation, behavior, and swimming stamina of the grass shrimp *Palaemonetes pugio*. *Journal of Parasitology* **90**: 441–445.
- KURIS, A. M., R. F. HECHINGER, J. C. SHAW, K. L. WHITNEY, L. AGUIRRE-MACEDO, C. A. BOCH, A. P. DOBSON, E. J. DUNHAM, B. L. FREDENSBORG, T. C. HUSPENI ET AL. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* **454**: 515–518.
- LAFFERTY, K. D., AND A. M. KURIS. 2012. Ecological consequences of manipulative parasites. In *Host manipulation by parasites*, D. P. Hughes, J. Brodeur, and F. Thomas (eds.). Oxford University Press, Oxford, U.K., p. 140–154.
- , AND J. C. SHAW. 2013. Comparing mechanisms of host manipulation across host and parasite taxa. *Journal of Experimental Biology* **216**: 56–66.
- , F. THOMAS, AND R. POULIN. 2000. Evolution of host phenotype manipulation by parasites and its consequences. In *Evolutionary biology of host–parasite relationships: Theory meets reality*, R. Poulin, and S. Morand (eds.). Elsevier, Amsterdam, The Netherlands, p. 117–127.
- LANGERHANS, R. B. 2009. Morphology, performance, fitness: Functional insight into a post-Pleistocene radiation of mosquito fish. *Biology Letters* **5**: 488–491.
- LAPPIN, A. K., AND J. F. HUSAK. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizards (*Crotaphytus collaris*). *American Naturalist* **166**: 426–436.
- LAVROV, D. V., W. M. BROWN, AND J. L. BOORE. 2004. Phylogenetic position of the Pentastomida and (pan) crustacean relationships. *Proceedings of the Royal Society B: Biological Sciences* **271**: 537–544.
- LEFEVRE, T., S. A. ADAMO, D. C. BIRON, D. MISSE, D. HUGHES, AND F. THOMAS. 2009. Invasion of the body snatchers: The diversity and evolution of manipulative strategies in host-parasite interactions. *Advances in Parasitology* **68**: 45–83.
- LEUNG, T. L. F., AND R. POULIN. 2007. Interactions between parasites of the cockle *Austrovenus stutchburyi*: Hitch-hikers, resident-cleaners, and habitat-facilitators. *Parasitology* **134**: 247–255.
- LOPEZ, G., J. MUNOZ, R. SORIGUER, AND J. FIGUEROA. 2013. Increased endoparasite infection in late-arriving individuals of a trans-Saharan passerine migrant bird. *PLoS ONE* **8**: e61236.
- LUDIN, P., D. NILSSON, AND P. MASER. 2011. Genome-wide identification of molecular mimicry candidates in parasites. *PLoS ONE* **6**: e17546.
- MADDISON, W. P., AND D. R. MADDISON. 2011. Mesquite: A modular system for evolutionary analysis. Version 2.75. Available at: <http://mesquiteproject.org>. Accessed 6 March 2014.

- MADELAIRE, C. B., R. J. DA SILVA, AND F. R. GOMES. 2013. Calling behavior and parasite intensity in treefrogs, *Hypsiboas prasinus*. *Journal of Herpetology* **47**: 450–455.
- MAIN, A. R., AND C. M. L. BULL. 2000. The impact of tick parasites on the behavior of the lizard *Tiliqua rugosa*. *Oecologia* **122**: 574–581.
- MARDEN, J. H., AND J. R. COBB. 2004. Territorial and mating success of dragonflies that vary in muscle power output and presence of gregarine gut parasites. *Animal Behaviour* **68**: 657–665.
- MARR, S. R., S. A. JOHNSON, A. H. HARA, AND M. E. MCGARRITY. 2010. Preliminary evaluation of the potential of the helminth parasite *Rhabdias elegans* as a biological control agent for invasive Puerto Rican coquí (*Eleutherodactylus coqui*) in Hawaii. *Biological Control* **54**: 69–74.
- MARZAL, A., M. REVIRIEGO, I. G. HERMOSELL, J. BALBONTIN, S. BENSCH, C. RELINQUE, L. RODRIGUEZ, L. GARCIA-LONGORIA, AND F. DE LOPE. 2013. Malaria infection and feather growth rate predict reproductive success in house martins. *Oecologia* **171**: 853–861.
- MCLACHLAN, A. J., T. W. PIKE, AND J. C. THOMASON. 2008. Another kind of symmetry: Are there adaptive benefits to the arrangement of mites on an insect host? *Ethology, Ecology and Evolution* **20**: 257–270.
- MEDOC, V., AND J.-N. BEISEL. 2008. An acanthocephalan parasite boosts the escape performance of its intermediate host facing non-host predators. *Parasitology* **135**: 977–984.
- MOLES, A., AND J. HEIFETZ. 1998. Effects of the brain parasite *Myxobolus arcticus* on sockeye salmon. *Journal of Fish Biology* **52**: 146–151.
- MØLLER, A. P., F. DE LOPE, AND N. SAINO. 2004. Parasitism, immunity, and arrival date in a migratory bird, the barn swallow. *Ecology* **85**: 206–219.
- MOORE, J. 2002. *Parasites and the behavior of animals*. Oxford series in ecology and evolution, Oxford University Press, Oxford, U.K., 338 p.
- . 2012. A history of parasites and hosts, science and fashion. In *Host manipulation by parasites*, D. P. Hughes, J. Brodeur, and F. Thomas (eds.). Oxford University Press, Oxford, U.K., p. 1–13.
- . 2013. An overview of parasite-induced behavioral alterations and some lessons from bats. *Journal of Experimental Biology* **216**: 11–17.
- MOURITSEN, K. N. 2001. Hitch-hiking parasite: A dark horse may be the real rider. *International Journal for Parasitology* **31**: 1417–1420.
- MÜNDERLE, M., B. SURES, AND H. TARASCHEWSKI. 2004. Influence of *Anguillicola crassus* (Nematoda) and *Ichthyophthirius multifiliis* (Ciliophora) on swimming activity of European eel *Anguilla anguilla*. *Diseases of Aquatic Organisms* **60**: 133–139.
- NAGAMI, P. 2001. *The woman with a worm in her head and other true stories of infectious disease*. St. Martin's Press, New York, New York, 288 p.
- NEAR, T. J., A. DORNBERG, R. I. EYTAN, B. P. KECK, W. L. SMITH, K. L. KUHN, J. A. MOORE, S. A. PRICE, F. T. BURBRINK, M. FRIEDMAN ET AL. 2013. Phylogeny and tempo of diversification in the super-radiation of spiny-rayed fishes. *Proceedings of National Academy of Sciences USA* **110**: 12738–12743.
- , R. I. EYTAN, A. DORNBERG, K. L. KUHN, J. A. MOORE, M. P. DAVIS, P. C. WAINWRIGHT, M. FRIEDMAN, AND W. L. SMITH. 2013. Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of National Academy of Sciences* **109**: 13698–13703.
- NENDICK, L., M. SACKVILLE, S. TANG, C. J. BRAUNER, AND A. P. FARRELL. 2011. Sea lice infection of juvenile pink salmon (*Oncorhynchus gorbuscha*): Effects on swimming performance and postexercise ion balance. *Canadian Journal of Fisheries and Aquatic Sciences* **68**: 241–249.
- OPPLIGER, A., M. L. CÉLÉRIER, AND J. CLOBERT. 1996. Physiological and behavior changes in common lizards parasitized by haemogregarines. *Parasitology* **113**: 433–438.
- ÖSTLUND-NILSSON, S., L. CURTIS, G. E. NILSSON, AND A. S. GRUTTER. 2005. Parasitic isopod *Anilocra apogonae*, a drag for the cardinal fish *Cheilodipterus quinquelineatus*. *Marine Ecology Progress Series* **287**: 209–216.
- PALSTRA, A. P., D. F. M. HEPPENER, V. J. T. VAN GINNEKEN, C. SZÉKELY, AND G. E. E. J. M. VAN DEN THILLART. 2007. Swimming performance of silver eels is severely impaired by the swim-bladder parasite *Anguillicola crassus*. *Journal of Experimental Marine Biology and Ecology* **352**: 244–256.
- PAP, P. L., C. I. VAGASI, L. BARBOS, AND A. MARTON. 2013. Chronic coccidian infestation compromises flight feather quality in house sparrows *Passer domesticus*. *Biological Journal of the Linnean Society* **108**: 414–428.
- PARADIS, E., J. CLAUDE, AND K. STRIMMER. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**: 289–290.
- PARKER, G. A., M. A. BALL, J. C. CHUBB, K. HAMMERSCHMIDT, AND M. MILINSKI. 2008. When should a trophically transmitted parasite manipulate its host? *Evolution* **63**: 448–458.
- PENNISI, E. 2014. Parasitic puppeteers begin to yield their secrets. *Science* **343**: 239.
- PERROT-MINNOT, M.-J., AND F. CÉZILLY. 2009. Parasites and behaviour. In *Ecology and evolution of parasitism*, F. Thomas, J.-F. Guégan, and F. Renaud (eds.). Oxford University Press, Oxford, U.K., p. 49–67.
- , AND ———. 2013. Investigating candidate neuromodulatory systems underlying parasitic manipulation: Concepts, limitations and prospects. *Journal of Experimental Biology* **216**: 27–35.
- , M. MADDALENO, A. BALOURDET, AND F. CÉZILLY. 2012. Host manipulation revisited: No evidence for a causal link between altered photophobia and increased trophic transmission of amphipods infected with acanthocephalans. *Functional Ecology* **26**: 1007–1014.
- PFENNIG, K. S., AND R. C. TINSLEY. 2002. Different mate preferences by parasitized and unparasitized females potentially reduces sexual selection. *Journal of Evolutionary Biology* **15**: 399–406.
- PIZZATTO, L., AND R. SHINE. 2011a. Ecological impacts of invading species: Do parasites of the cane toad imperil Australian frogs? *Austral Ecology* **36**: 954–963.
- , AND ———. 2011b. You are what you eat: Parasite transfer in cannibalistic cane toads. *Herpetologica* **67**: 118–123.
- , AND ———. 2012. Typhoid Mary in the frogpond: Can we use native frogs to disseminate a lungworm biocontrol for invasive cane toads? *Animal Conservation* **15**: 545–552.
- PONTON, F., F. OTALORA-LUNA, T. LEFÈVRE, P. M. GUÉRIN, C. LEBARBENCHON, D. DUNEAU, D. G. BIRON, AND F. THOMAS. 2011. Water-seeking behavior in worm infected crickets and reversibility of parasitic manipulation. *Behavioral Ecology* **22**: 392–400.
- POULIN, R. 1994. Meta-analysis of parasite-induced behavioural changes. *Animal Behaviour* **48**: 137–146.
- . 1995. “Adaptive” change in the behaviour of parasitized animals, a critical review. *International Journal for Parasitology* **25**: 1371–1383.
- . 2000. Manipulation of host behaviour by parasites: A weakening paradigm? *Proceedings of the Royal Society B: Biological Sciences* **267**: 787–792.
- . 2010. Parasite manipulation of host behavior: An update and frequently asked questions. *Advances in the Study of Behavior* **1**: 151–186.
- . 2013. Parasite manipulation of host personality and behavioural syndromes. *Journal of Experimental Biology* **216**: 18–26.
- , AND E. P. LEVRI. 2012. Applied aspects of host manipulation by parasites. In *Host manipulation by parasites*, D. P. Hughes, J. Brodeur, and F. Thomas (eds.). Oxford University Press, Oxford, U.K., p. 172–194.
- , AND S. MORAND. 2000. The diversity of parasites. *The Quarterly Review of Biology* **75**: 277–293.
- , AND F. THOMAS. 1999. Phenotypic variation induced by parasites: Extent and evolutionary implications. *Parasitology Today* **15**: 28–32.
- POWELL, M. D., M. J. LEEF, S. D. ROBERTS, AND M. A. JONES. 2008. Neoparamoebic gill infections: Host response and physiology in salmonids. *Journal of Fish Biology* **73**: 2161–2183.
- PRANDOVSKY, E., E. GASKELL, H. MARTIN, J. P. DUBEY, J. P. WEBSTER, AND G. A. MCCONKEY. 2011. The neurotropic parasite *Toxoplasma gondii* increases dopamine metabolism. *PLoS ONE* **6**: e23866.
- PYRON, R. A., F. T. BURBINK AND J. J. WIENS. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* **13**: 93. Available at: <http://www.biomedcentral.com/1471-2148/13/93>. Accessed 6 March 2014.
- R CORE DEVELOPMENT TEAM. 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Version 3.0.1. Available at: <http://www.R-project.org/>. Accessed 6 March 2014.
- REILLY, S. M., AND P. C. WAINWRIGHT. 1994. Conclusion: Ecological morphology and the power of integration. In *Ecological morphology*:

- Integrative organismal biology, P. C. Wainwright and S. M. Reilly (eds.). University of Chicago Press, Chicago, Illinois, p. 339–354.
- ROBAR, N., G. BURNES, AND D. L. MURRAY. 2010. Tropics, trophics and taxonomy: The determinants of parasite-associated host mortality. *Oikos* **119**: 1273–1280.
- , D. L. MURRAY, AND G. BURNES. 2011. Effects of parasites on host energy expenditure: The resting metabolic rate stalemate. *Canadian Journal of Zoology* **89**: 1146–1155.
- ROBERTS, L. W. 1981. Probing by *Glossina morsitans morsitans* and transmission of *Trypanosoma (nannomonas) congolense*. *American Journal of Tropical Medicine and Hygiene* **30**: 948–951.
- ROCHE, D. G., S. A. BINNING, L. E. STRONG, J. N. DAVIES, AND M. D. JENNIONS. 2013. Increased behavioural lateralization in parasitized coral reef fish. *Behavioural Ecology and Sociobiology* **67**: 1339–1344.
- RYCE, K. N., A. V. ZALE, AND R. B. NEHRING. 2001. Lack of selection for resistance to whirling disease among progeny of Colorado River rainbow trout. *Journal of Aquatic Animal Health* **13**: 63–68.
- SANTOS, E. G. N., R. A. CUNHA, AND C. PORTES SANTOS. 2011. Behavioral responses of *Poecilia vivipara* (Osteichthyes: Cyprinodontiformes) to experimental infections of *Acantho collaritremia umbilicatum* (Digenea: Cryptogonimidae). *Experimental Parasitology* **127**: 522–526.
- SCHALL, J. J. 1990. Virulence of lizard malaria: The evolutionary ecology of an ancient parasite–host association. *Parasitology* **100**: S35–S52.
- , A. F. BENNETT, AND R. W. PUTNAM. 1982. Lizards infected with malaria: Physiological and behavioral consequences. *Science* **217**: 1057–1059.
- SCHIEFER, B. A., R. A. WARD, AND B. F. ELDRIDGE. 1977. *Plasmodium cynomolgi*: Effects of malaria infection on laboratory flight performance of *Anopheles stephensi* mosquitoes. *Experimental Parasitology* **41**: 397–404.
- SCHWANZ, L. E. 2006. Schistosome infection in deer mice (*Peromyscus maniculatus*): Impacts on host physiology, behavior and energetics. *Journal of Experimental Biology* **209**: 5029–5030.
- SHIRAKASHI, S., K. TERUYA, AND K. OGAWA. 2008. Altered behaviour and reduced survival of juvenile olive flounder, *Paralichthys olivaceus*, infected by an invasive monogenean, *Neoheterobothrium hirame*. *International Journal for Parasitology* **38**: 1513–1522.
- SJÖBERG, N. B., E. PETERSSON, H. WICKSTRÖM, AND S. HANSSON. 2009. Effects of the swimbladder parasite *Anguillicola crassus* on the migration of European silver eels *Anguilla anguilla* in the Baltic Sea. *Journal of Fish Biology* **74**: 2158–2170.
- STEPHAN, S. J., R. M. ADKINS, AND J. ANDERSON. 2004. Phylogeny and divergence-based estimates of rapid radiations in murid rodents based on multiple nuclear genes. *Systematic Biology* **53**: 533–553.
- SUKHDEO, M. V. K., AND A. D. HERNANDEZ. 2005. Food web patterns and the parasite's perspective. In *Parasitism and ecosystems*, F. Thomas, F. Renaud, and J.-F. Guegan (eds.). Oxford University Press, Oxford, U.K., p. 54–67.
- TAEUBERT, J.-E., AND J. GEIST. 2013. Critical swimming speed of brown trout (*Salmo trutta*) infested with freshwater pearl mussel (*Margaritifera margaritifera*) glochidia and implications for artificial breeding of an endangered mussel species. *Parasitology Research* **112**: 1607–1613.
- THOMAS, F., S. ADAMO, AND J. MOORE. 2005. Parasitic manipulation: Where are we and where should we go? *Behavioral Processes* **68**: 185–199.
- , R. POULIN, AND J. BRODEUR. 2010. Host manipulation by parasites: A multidimensional phenomenon. *Oikos* **119**: 1217–1223.
- , F. RENAUD, AND R. POULIN. 1998. Exploitation of manipulators: 'Hitch-hiking' as a parasitic transmission strategy. *Animal Behaviour* **56**: 199–206.
- , T. RIGAUD, AND J. BRODEUR. 2012. Evolutionary routes leading to host manipulation by parasites. In *Host manipulation by parasites*, D. P. Hughes, J. Brodeur, and F. Thomas (eds.). Oxford University Press, Oxford, U.K., p. 16–33.
- THOMPSON, R. M., R. POULIN, K. N. MOURITSEN, AND D. W. THIELTGES. 2013. Resource tracking in marine parasites: Going with the flow? *Oikos* **122**: 1187–1194.
- TOWNSON, H. 1970. The effect of infection with *Brugia pahangi* on the flight of *Aedes aegypti*. *Annals of Tropical Medicine and Parasitology* **64**: 411–420.
- UMBERGER, C. M., I. DE BURON, W. A. ROUMILLAT, AND E. J. MCELROY. 2013. Effects of a muscle-infecting parasitic nematode on the locomotor performance of their fish host. *Journal of Fish Biology* **82**: 1250–1258.
- VAN HOUTE, S., V. I. D. ROS, AND M. M. VAN OERS. 2013. Walking with insects: Molecular mechanisms behind parasitic manipulation of host behavior. *Molecular Ecology* **22**: 3458–3475.
- VIECHTBAUER, W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**: 1–48.
- VILLACIDE, J. M., AND J. C. CORLEY. 2008. Parasitism and dispersal potential of *Sirex noctilio*: Implications for biological control. *Agricultural and Forest Entomology* **10**: 341–345.
- VON REUMONT, B. M., R. A. JENNER, M. A. WILLS, E. DELL'AMPIO, G. PASS, I. EBERSBERGER, B. MEYER, S. KOENEMANN, T. M. ILIFFE, A. STAMATAKIS ET AL. 2012. Pancrustacean phylogeny in the light of new phylogenomic data: Support for Remipedia as the possible sister group of Hexapoda. *Molecular Biology and Evolution* **29**: 1031–1045.
- WAGNER, G. N., S. G. HINCH, L. J. KUCHEL, A. LOTTO, S. R. M. JONES, D. A. PATTERSON, J. S. MACDONALD, G. VAN DER KRAAK, M. SHRIMPTON, K. K. ENGLISH ET AL. 2005. Metabolic rates and swimming performance of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) after a controlled infection with *Parvicapsula minibicornis*. *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 2124–2133.
- WAINWRIGHT, P. C., W. L. SMITH, S. A. PRICE, K. L. TANG, J. S. SPARKS, L. A. FERRY, K. L. KUHN, R. I. EYTAN, AND T. J. NEAR. 2012. The evolution of pharyngognathy: A phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. *Systematic Biology* **61**: 1001–1027.
- WEBSTER, J. P., S. GOWTAGE-SEQUEIRA, M. BERDOY, AND H. HURD. 2000. Predation of beetles (*Tenebrio molitor*) infected with tapeworms (*Hymenolepis diminuta*): A note of caution for the manipulation hypothesis. *Parasitology* **120**: 313–318.
- WEDEKIND, C., AND M. MILINSKI. 1996. Do three-spined sticklebacks avoid consuming copepods, the first intermediate host of *Schistocephalus solidus*? An experimental analysis of behavioural resistance. *Parasitology* **112**: 371–383.
- WEINREICH, F., D. P. BENESH, AND M. MILINSKI. 2013. Suppression of predation on the intermediate host by two trophically-transmitted parasites when uninfected. *Parasitology* **140**: 129–135.
- WELSH, J. 2012. These animals are zombified by parasites. Available at: <http://www.businessinsider.com/how-insects-and-animals-are-turned-into-zombies-by-parasites-2012-12?op=1#ixzz2q6ergCrc>. Accessed 6 March 2014.
- WIEGMANN, B. M., M. D. TRAUTWEIN, I. S. WINKLER, N. B. BARR, J. KIM, C. LAMBKIN, M. A. BERTONE, B. K. CASSEL, K. M. BAYLESS, A. M. HEIMBERG ET AL. 2011. Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences USA* **108**: 5690–5695.
- YORINKS, N., AND C. T. ATKINSON. 2000. Effects of malaria on activity budgets of experimentally infected juvenile Apapane (*Himatione sanguinea*). *Auk* **117**: 731–738.
- ZIMMER, C. 2001. Parasite rex: Inside the bizarre world of nature's most dangerous creatures. First Touchstone Edition, Simon and Schuster, Inc., New York, New York, 298 p.
- ZIUGANOV, V. V. 2005. A paradox of parasite prolonging the life of its host. Pearl mussel can disable the accelerated senescence program in salmon. *Biology Bulletin* **32**: 360–365.