

## A power–efficiency trade-off in resource use alters epidemiological relationships

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**Abstract.** Trade-offs play pivotal roles in the ecology and evolution of natural populations. However, trade-offs are probably not static, invariant relationships. Instead, ecological factors can shift, alter, or reverse the relationships underlying trade-offs and create critical genotype  $\times$  environment ( $G \times E$ ) interactions. But which ecological factors alter trade-offs or create  $G \times E$  interactions, and why (mechanistically) do they do this? We tackle these questions using resource quality as the central ecological factor and a case study of disease in the plankton. We show that clonal genotypes of a zooplankton host (*Daphnia dentifera*) exhibit a “power–efficiency” trade-off in resource use, where powerful (fast-feeding) host clones perform well on richer algal resources, but more efficient (slow-feeding) clones perform relatively well on poorer resources. This resource-based trade-off then influences epidemiological relationships due to fundamental connections between resources and fecundity, transmission rate (an index of resistance), and replication of a virulent fungal parasite (*Metschnikowia bicuspidata*) within hosts. For instance, using experiments and dynamic energy budget models, we show that the power–efficiency trade-off overturned a previously detected trade-off between fecundity and transmission risk of hosts to this parasite. When poorer resources were eaten, transmission risk and fecundity were negatively, not positively, correlated. Additionally, poor resource quality changed positive relationships between yield of infectious stages (spores) and host fecundity: those fecundity–spore relationships with poor food became negative or nonsignificant. Finally, the power–efficiency trade-off set up an interaction between host clone and resource quality for yield of fungal spores: powerful clones yielded relatively more spores on the better resource, while efficient clones yielded relatively more on the poorer resource. Thus, the physiological ecology of resource use can offer potent, mechanistic insight linking environmental factors to epidemiological relationships.

**Key words:** *Daphnia dentifera*; dynamic energy budget; fecundity; fungal parasite; host–parasite relationship; *Metschnikowia bicuspidata*; power–efficiency relationship; trade-offs; transmission rate; virulence; zooplankton.

### INTRODUCTION

Organisms frequently must trade off one aspect of fitness with another. These trade-offs can stem from constraints imposed by allocation of limited energy reserves among competing components of fitness. Energy invested in one function, such as reproduction, is no longer available for another function, such as immune response to infection. Such trade-offs play an important role in maintaining genetic variation in natural populations and can profoundly affect their ecology and evolution (Roff 1992, Stearns 1992, Grover 1997, Tilman 2000). Not surprisingly, then, trade-offs have received prominent focus in ecological and evolutionary research (Reznick et al. 2000, Tilman

2000, Angilletta et al. 2003, Roff and Fairbairn 2007). An explicit or implicit assumption is usually made about the invariance of trade-offs: for a given organism, relationships between two traits are presumed fixed. However, environmental factors might strongly influence trade-offs (Reznick et al. 2000, Sgrò and Hoffmann 2004). In fact, ecological context can influence their strength (Coley 1986, Bohannan et al. 2002, Lopez-Pascua and Buckling 2008) and shape (Jessup and Bohannan 2008).

Environmentally driven variation in trade-offs matters because their sign, strength, and shape influence both ecological interactions and evolutionary dynamics. For example, trade-offs between resistance to parasitism and fecundity can alter the evolution of resistance in host populations (Boots and Begon 1993, Luong and Polak 2007, Boots et al. 2009, Duffy and Forde 2009, Hall et al. 2010). However, the shape of fecundity–resistance trade-offs plays a pivotal role in determining whether a host population experiences selection for increased resistance, disruptive selection, or selection for

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decreased resistance (Hoyle et al. 2008, Boots et al. 2009). But if environmental factors disrupted this trade-off altogether, evolution of increased resistance of host populations would probably ensue. These various outcomes have implications for maintenance of diversity and population dynamics (Boots et al. 2009, Duffy and Forde 2009, Penczykowski et al. 2011). Perhaps even more generally, environmentally driven changes in trade-offs are likely to involve genotype  $\times$  environment interactions, a factor that can also maintain genetic diversity (Gillespie and Turelli 1989, de Jong 1990, Gomulkiewicz and Kirkpatrick 1992). In disease systems, host genotype  $\times$  environment interactions arise commonly (Thomas and Blanford 2003, Bedhomme et al. 2004, Mitchell et al. 2005, Lazzaro et al. 2008, Vale et al. 2008). Thus, it seems critical to mechanistically explain why environment could create  $G \times E$  interactions and alter trade-offs.

Why do environmental factors influence trade-offs? Can we predict when we should expect strong context dependency of trade-offs? Could these same environmental factors create genotype  $\times$  environment interactions? To address these questions, we focus on the resources of hosts. The focus on this environmental factor makes sense when trade-offs arise due to energetic constraints (van Noordwijk and de Jong 1986, Reznick et al. 2000). We also use a case study of disease that exhibits strongly resource-dependent epidemiology. A zooplankton host (*Daphnia dentifera*) becomes infected by a virulent fungus (*Metschnikowia bicuspidata*) while consuming its algal food resource, phytoplankton (Hall et al. 2007b). As a result, feeding rate and infection risk are closely linked (Hall et al. 2007b, 2009a). Once hosts become infected, the fungus grows and produces infective stages (spores) within the blood (hemolymph), all the while consuming internal energy reserves of the host (Hall et al. 2007a, 2009a, b, 2010). Consequently, infection depresses growth and fecundity of the host before host death releases spores (Ebert 2005, Hall et al. 2007b, 2009b). However, resource quantity and quality govern the availability of energy within hosts for parasites to exploit. Thus, resources shape fecundity, depression of fecundity due to infection, spore yield, and survival of hosts (Hall et al. 2007a, 2009a, b, Frost et al. 2008).

Resources then provide an especially relevant environmental factor for epidemiological trade-offs and  $G \times E$  interactions in this system for three reasons. First, algal resource quality varies among lakes and through time (Tessier and Woodruff 2002b, Hall et al. 2009a). In fact, resource quality can shift from low (digestion resistant) to better (more digestible) during epidemics. Second, host genotypes probably trade-off use of these resources of varying quality. In particular, in the power–efficiency trade-off, some genotypes powerfully exploit richer resources while others efficiently exploit poorer-quality ones (Smith 1976, Turpin 1988, Brown 1989, Grover 1997, Tessier et al. 2000, Tessier and Woodruff

2002a). Third, variation among clonal genotypes in feeding and growth rate (i.e., acquisition and use of resources, respectively) creates key epidemiological trade-offs. For instance, when they consume rich resources, fast feeding clones have a higher risk of fungal infection, but produce more offspring when uninfected, thus generating a resistance–fecundity trade-off (Hall et al. 2010). Similarly, variation in feeding and growth rate among clones correlates with spore yield. Thus, resource traits can create relationships between fecundity, transmission rate, and spore yield (Hall et al. 2010).

Because resources modulate epidemiological traits and trade-offs, the power–efficiency trade-off could alter these trade-offs and/or create host genotype  $\times$  resource interactions. We examined these predictions using a combination of lab-based experiments and an energy-based model of parasitism. We first revealed a power–efficiency trade-off in resource use among host clones. This trade-off was produced from a link between feeding rate and the ability of hosts to assimilate poor-quality resources. Then, we showed how power–efficiency trade-off shaped epidemiological relationships. Specifically, it reversed the fecundity–resistance trade-off (i.e., more resistant clones became more fecund) and similar relationships involving spore yield. This power–efficiency trade-off also created a host genotype  $\times$  environment interaction in spore yield.

#### METHODS: EXPERIMENTS

This study combines new experiments with insights and data from a previous one (Hall et al. 2010) aimed at estimating pertinent epidemiological and life history parameters. Unlike the previous experiments that used the relatively nutritious alga *Scenedesmus* (Hall et al. 2010), here we used a field-isolated strain of *Oocystis* sp. This green alga produces a gelatinous, digestion-resistant sheath; this sheath, in turn, reduces the nutritive value of this alga for *Daphnia* grazer-hosts (DeMott et al. 2010). In both previous and current studies, juvenile growth rate assays provided an indicator of efficiency of use of resources. Additionally, transmission rate of hosts, an inverse indicator of resistance to infection, was estimated from infection assays. Finally, life tables provided information on fecundity of infected and uninfected hosts, time of and size at death of infected hosts, and spore yield from dead hosts. Experiments presented here were performed under similar conditions as in the previous study (20°C, 16:8 day:night cycle, ample levels of algal food [2.0 mg dry mass/L of algae] suspended in filtered lake water). *Daphnia* genotypes ( $N = 11$ , fewer in some experiments) came from several lakes in southwestern Michigan (Kalamazoo and Barry Counties), USA. These clones have been reared under standard laboratory conditions since 2004, minimizing environmental and maternal effects. The parasite was collected from Baker Lake in 2003 and has been farmed in vivo in a

single host clone since. Thus, we focus on genetic variation of hosts, not parasites. We have found no evidence of host genotype–parasite genotype specificity in this system (Duffy and Sivars-Becker 2007).

*Feeding rate, juvenile growth rate,  
and the power–efficiency trade-off*

We started forging links between resource-based trade-offs and their epidemiological consequences by revealing the power–efficiency relationship. We used existing feeding rate measurements (Hall et al. 2010), but here also estimated juvenile growth rate (JGR). Juvenile growth rate synthesizes variation in feeding rate with other physiological factors (e.g., conversion efficiency, maintenance costs) that jointly determine growth of hosts consuming the less digestible alga *Oocystis*. JGR was measured for all genotypes as mass accrual by neonates during a four-day assay (Lampert and Trubetskova 1996). To provide initial, mean day 0 measurements ( $\bar{m}_0$ ), 15 neonates per genotype (<24 h old) were dried at 55°C and weighed with a Mettler UMX2 microbalance (Mettler-Toledo, Columbus, Ohio, USA). Simultaneously, we placed 10–15 neonates per clone in separate 150-mL beakers of filtered lake water containing 100 mL of 2.0 mg dry mass/L of lab-grown *Oocystis*. For four days ( $d = 4$ ), we transferred these animals into fresh water with replenished *Oocystis* food; then, we similarly dried and weighed each individual animal. This procedure yielded day-four mass estimates ( $m_4$ ). Our JGR measure was then:  $\gamma = [\ln(m_4) - \ln(\bar{m}_0)]/d$  (where  $d = 4$  days).

By redrawing these growth rate data, we could show the power–efficiency trade-off in a manner analogous to Tessier et al. (2000) and Tessier and Woodruff (2002a). First, we plotted growth of each genotype of *Daphnia dentifera* vs. that of a standard grazer (a *D. pulicaria–pulex* hybrid, the “Geedey clone”; Tessier and Woodruff 2002a); see Fig. 1B. The lines connected growth on *Oocystis* (left, lower values, “O” label) and *Scenedesmus* (right, higher values, “S” label). Then, slope and  $x$ -axis intercepts were calculated from these lines for each *D. dentifera* genotype. The slope parameter indexes “power”; that is, it determines how effectively a genotype can increase growth from poorer to richer food resource (i.e., its “sensitivity” to algal resources). The  $x$ -axis intercept describes the “efficiency” of a genotype, since it denotes an index of resource threshold for growth. A positive relationship between  $x$ -intercept and slope characterizes a power–efficiency trade-off (Tessier et al. 2000, Tessier and Woodruff 2002a).

*Estimation of transmission rate of hosts  
(infection assays)*

Next, we estimated the pertinent epidemiological parameters. We used an infection assay to estimate transmission rate of the different genotypes of hosts. We placed five 6-day-old *Daphnia* raised on 2.0 mg/L of high-quality *Scenedesmus* into 100 mL of filtered lake

water containing 2.0 mg dry mass/L low-quality *Oocystis* and one of two spore levels (25 or 100 spores/mL). Each spore–clone treatment was replicated eight times and incubated for ~24 hours. Additionally, we saved 10 animals for length measurements (eye-to-base-of-tail measurements, with a micrometer at 50 $\times$ ; clonal mean sizes ranged from 1.48 to 1.68 mm). After the exposure time elapsed, we transferred animals from each beaker into fresh, spore-free, filtered lake water. Animals were fed *Scenedesmus* daily for 10 days until we could visually diagnose infection to then calculate prevalence of infection (see the Appendix for prevalence data).

Prevalence information, coupled with the size data, was used to calculate the size-specific transmission rate ( $\beta$ ), our index of host resistance. To estimate this parameter, we simplified a previously used model (Hall et al. 2007b); specifically, we assumed that host infectivity rate depended on body length ( $L$ ) raised to the 4th power ( $L^4$ ). We thus wrote equations to represent change in susceptible ( $H_S$ ) and infected ( $H_I$ ) host classes, given the spore densities ( $Z$ ) used in the experiment ( $dH_S/dt = -\beta L^4 H_S Z$ ;  $dH_I/dt = -dH_S/dt$ ). Then, we estimated  $\beta$  using a maximum-likelihood-based approach with the binomial distribution serving as the likelihood function (for more details, see Hall et al. 2010). We bootstrapped nonparametric 95% confidence intervals using 1000 random draws of data from each treatment.

*Estimation of virulent effects on survival and fecundity,  
and spore production (life table)*

We conducted a life table experiment to estimate virulent effects of the parasite on host survival and fecundity, size at death, and spores produced. Using four-day-old juveniles of each clone (mean size ranged from 1.10 to 1.29 mm), we exposed “infection” treatment animals (10 per clone) to a high spore dose (1000 spores/mL incubated for 24 hours at room temperature; this yielded 4–8 infected animals per clone). Uninfected animals ( $N = 8$ ) from each genotype received similar treatment, except that they did not receive spores. Then, when starting the experiment, we placed individual unexposed and exposed *Daphnia* in fresh water (150-mL beakers filled with 100 mL of filtered lake water with 2.0 mg dry/L *Oocystis*). During daily changes, we noted the number of offspring produced, date of death, and size reached on death. Size at death matters because larger hosts yield more spores (Hall et al. 2009a, b, 2010, Duffy et al. 2011). To estimate spore yield, we placed infected animals into 0.25 mL of lake water in plastic centrifuge tubes. Then, we gently smashed corpses using tweezers and counted spores in the slurry with a hemocytometer (200 $\times$ ). Using these data, we estimated several parameters: size (length) at death, time until death, spores contained in infected hosts, and fecundity, i.e., total offspring released divided by time until death or end of the experiment (at day 16).

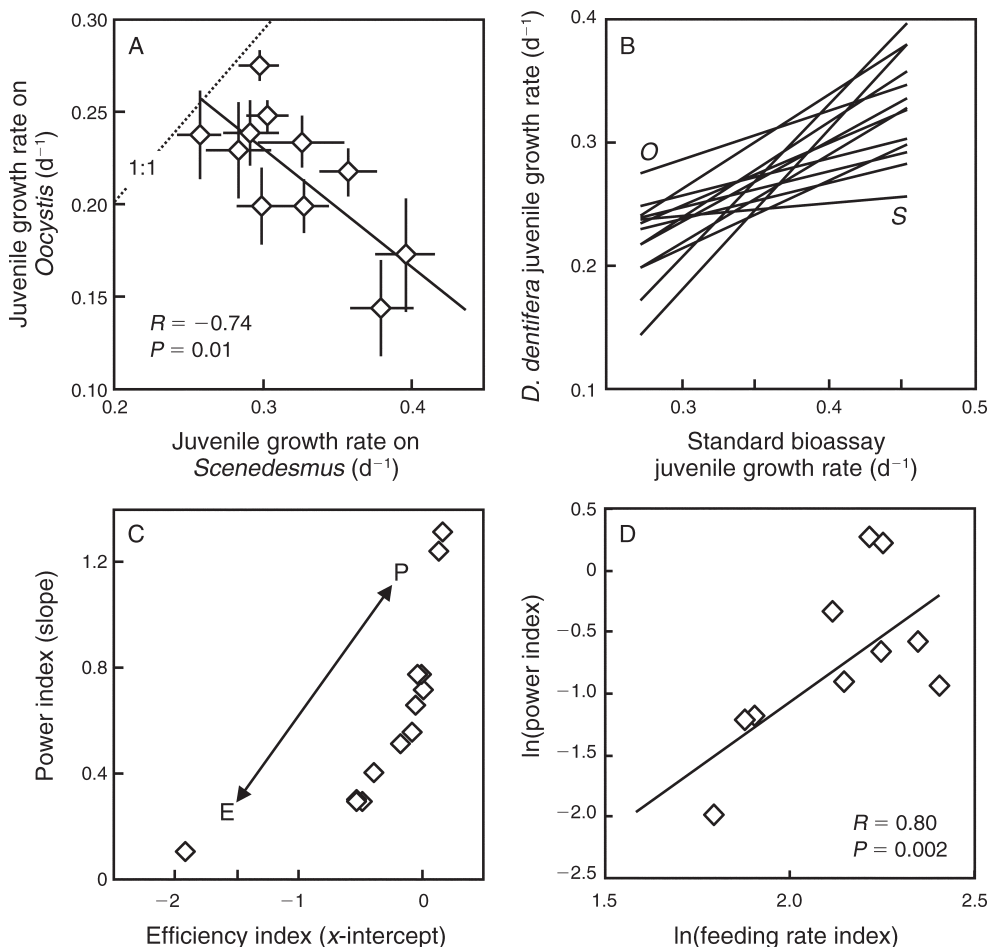


FIG. 1. The power–efficiency trade-off and its relationship to feeding rate. (A) Growth rate of juvenile *Daphnia dentifera* on two algal species, *Oocystis* and *Scenedesmus*, were negatively correlated (note the dotted 1:1 line). Error bars show  $\pm$ SE. (B) Growth rate of juvenile *D. dentifera* genotypes on *Oocystis* (“O,” smaller values) or *Scenedesmus* (“S,” larger values) vs. growth rate of a standard grazer, a *Daphnia pulex-pulcarica* hybrid used in previous studies (Tessier and Woodruff 2002a, b). Lines show reaction norms for each clonal genotype. Growth is expressed as a per-day rate, based on the equation  $\gamma = [\ln(m_4) - \ln(\bar{m}_0)]/d$  (where  $d = 4$  days). (C) A positive relationship between two indices for powerful genotypes (P, slope) and efficient genotypes (E, x-intercept) calculated from those lines (see *Methods*). (D) The log-transformed power index was positively correlated with log-transformed feeding rate (originally measured as mL/d) for the 1.25-mm size class of *Daphnia*: the fast-feeding *Daphnia* clones were the powerful clonal genotypes. Each point is a clonal mean.

#### RESULTS: EXPERIMENTS

The host clones exhibited a power–efficiency trade-off. Host clones that grew relatively rapidly on *Oocystis* grew relatively slowly on higher-quality *Scenedesmus* (Fig. 1A). More specifically, clones that grew fastest on *Scenedesmus* responded most sensitively to resource quality (i.e., fell well below the 1:1 line in Fig. 1A); meanwhile, the slower growing genotypes experienced much less growth reduction when feeding on *Oocystis* (i.e., were closer to the 1:1 line; Fig. 1A). When we redrew the growth rate data relative to growth rate of the reference clone (Fig. 1B) and estimated  $y$ - and  $x$ -axis intercepts from those resulting regression relationships, the power–efficiency trade-off could be visualized even more clearly (Fig. 1C). Efficient genotypes (low values of  $x$ -axis, denoted as “E” in Fig. 1C) were not powerful

(i.e., had low values of the  $y$ -axis), but powerful genotypes (denoted as “P” in Fig. 1C) were not efficient. Powerful clones were the fast-feeding clones (Fig. 1D). Thus, a deep connection arises between feeding rate and relative performance on good- vs. poor-quality food resources.

Transmission rate of hosts consuming digestion-resistant *Oocystis* increased with an index of feeding rate of hosts (Fig. 2A; feeding rate data from Hall et al. [2010]). Transmission rate of these host genotypes eating *Scenedesmus* also increased with this same index of feeding rate (Hall et al. 2010). Not surprisingly then, infectivity rates on both food resources were correlated positively (Fig. 2B). In other words, clones that had a higher transmission rate when consuming *Scenedesmus* retained a higher transmission rate when consuming the

poorer-quality *Oocystis* (probably because fast-feeding clones remain fast feeders on various algal food resources). However, the slope of this relationship was less than 1 (i.e., compare to the 1:1 dashed line in Fig. 2B). Clones with higher transmission rate became infected at a higher rate when feeding on higher-quality *Scenedesmus* than on lower-quality *Oocystis* (i.e., deviated farther from the 1:1 line in Fig. 2B). Meanwhile, transmission rate of the more resistant clones varied little with resource quality (i.e., fell close to the 1:1 line). Clones with faster feeding rate showed the largest deviation in transmission rate from the 1:1 line (marginally significant; Fig. 2C). This positive trend suggests that the transmission rate of fast-feeding clones to infection is more sensitive to algal nutrition than that of slower feeding clones.

Several sets of key relationships reversed or disappeared when hosts consumed poorer-quality algal resources. A major driver of these reversals is fecundity. When host clones ate the low-quality *Oocystis*, feeding rate became decoupled from fecundity, i.e., fast-feeding genotypes (powerful genotypes) did not produce more offspring than did slower feeding ones (Fig. 3A, B; a similar lack of relationships arose for fecundity of infected clones, not shown). Once feeding and fecundity became decoupled, trade-offs involving fecundity and transmission rate disappeared. In fact, whether uninfected or infected, clones that were more vulnerable to infection produced fewer offspring when consuming poorer-quality *Oocystis* (Fig. 3C, D, respectively). These results destroyed the resistance–fecundity trade-offs previously seen when hosts consumed the higher-quality resource (inset of Fig. 3C, D; see Hall et al. 2010). Now, hosts with lower transmission rate were also more fecund. Second, when eating the poorer-quality resource, clones that yielded more spores produced fewer offspring when uninfected (Fig. 3E). This result again reversed a trend seen using higher-quality *Scenedesmus* (inset of Fig. 3E). (That trade-off was expected, at least when food quality was good, because clones that grow fast tend to produce more spores when infected, but also more offspring, regardless of infection status.) Furthermore, no relationship arose between spore yield and fecundity of infected hosts (Fig. 3F). As a consequence, the relationship between spore yield and fecundity of infected hosts (inset of Fig. 3F), which was detected when food quality was good, disappeared.

The power–efficiency trade-off and variation in resource quality produced a host genotype × resource quality (environment) interaction for spore yield. Spore yield when hosts ate *Oocystis* was negatively correlated with spore yield when they ate *Scenedesmus* (Fig. 4A). This negative inter-environment clonal correlation, an indicator of a  $G_H \times E$  interaction (Pigliucci 2001), reflects the similar, negative relationship in juvenile growth rate (Fig. 1A). These mirrored, negative relationships stem from links between spore yield and juvenile growth rate. Spore yield of host clones

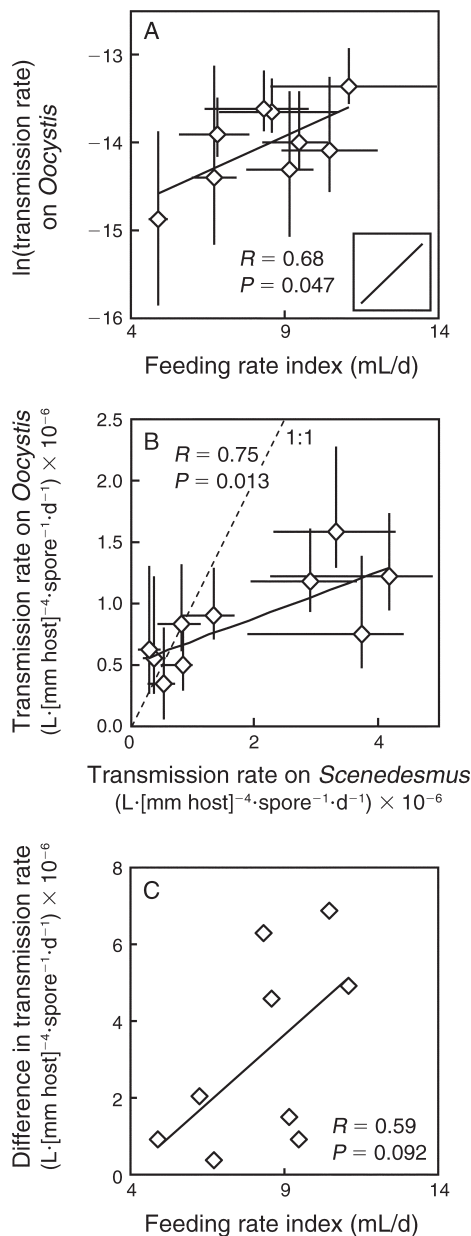


FIG. 2. Transmission rate of *Daphnia* hosts and quality of algal resources. Each point is a clonal mean; error bars are bootstrapped 95% confidence intervals. (A) Log-transformed transmission rate of *Daphnia* hosts eating poorer-quality algae (*Oocystis*) correlated positively with an index of feeding rate (from Hall et al. 2010). The inset box qualitatively denotes the trend seen in a companion study using higher-quality alga (*Scenedesmus*; Hall et al. 2010). (B) Transmission rate of clones feeding on the poorer resource correlated positively with that estimated from clones feeding on the higher-quality resource. However, the slope of this relationship is less than 1 (note the dashed 1:1 line). (C) Host clones with faster feeding rate showed the strongest change (difference) in transmission rate on the two algal resource types. Note that transmission rate scales with *Daphnia* (length)<sup>4</sup> (gut surface area × body surface area).

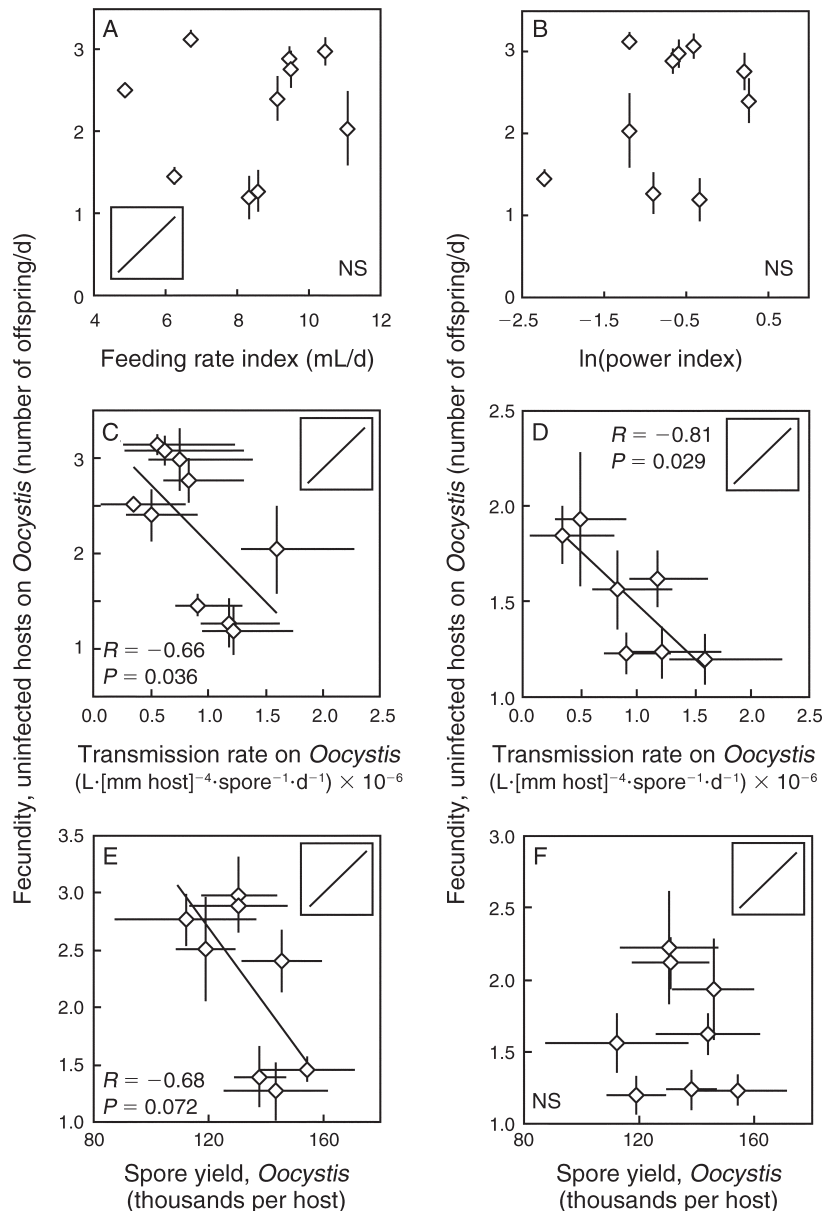


FIG. 3. Two sets of relationships that arose when hosts consumed higher-quality resources (*Scenedesmus*) were overturned when hosts consumed a poorer-quality alga (*Oocystis*). Neither (A) feeding rate nor (B) the power index correlated with fecundity of uninfected hosts feeding on *Oocystis*. The transmission–fecundity rate relationship was reversed on a diet of the lower-quality alga: hosts with lower transmission rate produced more offspring when (C) uninfected and (D) infected. Relationships involving spore yield and fecundity either (E) become reversed, in the case of uninfected hosts, or (F) blurred for infected hosts. Each point is a clonal mean  $\pm$  SE except for the transmission rate estimates (where error bars are 95% bootstrapped CIs). The inset boxes qualitatively denote trends from a companion study, when hosts consumed *Scenedesmus*, the higher-quality alga (Hall et al. 2010).

correlated positively with juvenile growth rate, whether clones fed on higher-quality *Scenedesmus* (Hall et al. 2010) or on lower-quality *Oocystis* (Fig. 4B; see the Appendix for other factors correlating with spore yield). As a result, we found that powerful clones produced fewer spores than efficient clones when consuming *Oocystis* (using the ln-transformed power axis,  $R = -0.76$ ,  $P = 0.018$ ; not shown). Additionally, powerful clones produced relatively more spores when growing on

the more nutritious *Scenedesmus* than on the poorer-quality *Oocystis* (indexed by the ratio of spore yields on the two food types; Fig. 4C).

#### THEORETICAL EXPLANATION

Poor quality of algal resources dramatically changed several key relationships seen in a previous study (Hall et al. 2010). It also created a host genotype  $\times$  resource quality interaction in spore yield. We looked for an

explanation for these changes based on variation in feeding rate among clones and the related power–efficiency trade-off in a dynamic energy budget model. The model cannot explain all results, but it does provide key insight into several of them.

*Model: implementation of the power–efficiency trade-off into a DEB–parasite model*

We built the power–efficiency trade-off into a dynamic energy budget (DEB) model to help explain why changing resource quality influences epidemiological relationships among host clones that vary in feeding rate (Fig. 5A). This model (see Appendix for details) shows how resource use among clones produces variation in fecundity, growth, survivorship, and spore yield (Hall et al. 2007a, 2009b, 2010). It tracks the flow of energy from ingestion and assimilation to storage in a reserve pool (Kooijman 1993). That reserve energy is then used for growth, reproduction in adults and development in juveniles, and metabolic costs associated with maintenance of body structure, reproduction, and growth. Parasites consume energy from the reserve, before it can be used by the host, and replicate within the host. The parasite eventually kills its host once parasite mass reaches a certain threshold, a proportion of the structural mass of the host. Before killing it, however, the parasite inflicts energetic stress on its host by depleting its internal energy reserves. By consuming these internal resources, parasites cause virulent reductions in fecundity and growth of the host.

To implement the power–efficiency trade-off in the energy model, we focused on conversion efficiency and feeding rate (based on insights gleaned from DeMott et al. 2010). Conversion efficiency ( $\epsilon$ ) governs how much ingested food (at ingestion rate  $I$ ) is assimilated (at assimilation rate  $A$ ;  $\epsilon \equiv A/I$ ). Conversion efficiency of high-quality resources typically remains constant and high, regardless of feeding rate, body size, and so forth (DeMott et al. 2010). However, when *Daphnia* eat less digestible algae like *Oocystis*, conversion efficiency increases with body length ( $L$ ) and gut passage time ( $T_G$ ); gut passage time, in turn, increases linearly with body length (DeMott et al. 2010). Kooijman (1993) formulated an empirically justified model for gut passage time as a function of body size (gut volume,  $V_G$ ) and feeding rate,  $I(R)$ , on resource  $R$ :

$$T_G = \frac{\phi V_G}{I(R)} = \frac{k_V \phi L^3}{c L^2 R / (h + R)} = \frac{k_V \phi L}{c} \left( \frac{h + R}{R} \right). \quad (1)$$

According to this variation on Kooijman’s model, gut volume ( $V_G$ ) is proportional to  $L^3$  (governed by a proportion constant  $k_V$ , where parameter  $\phi$  converts volume [ $\text{mm}^3$ ] into mass [ $\text{mg C}$ ]; Hall et al. 2009b), and feeding rate ( $I$ ) is a type II-based function of maximal, surface area ( $L^2$ )-specific feeding rate ( $c$ ), algal food density ( $R$ ), and a half-saturation constant ( $h$ ). Thus, gut passage time should increase linearly with body length ( $L$ ) and decrease with maximal feeding rate,  $c$  (Fig. 5B).

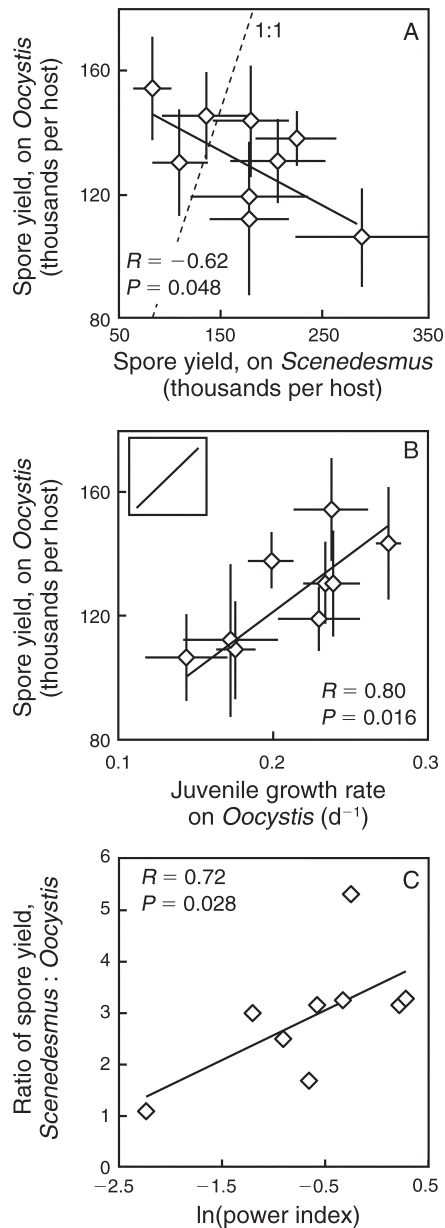


FIG. 4. A host genotype  $\times$  resource quality (environment) interaction in spore yield. (A) A negative relationship between spore yield on higher-quality (*Scenedesmus*) vs. lower-quality (*Oocystis*) algal resources arose, indicating a  $G_H \times E$  interaction. (B) Spore yield from host genotypes consuming the poorer-quality alga *Oocystis* correlated positively with juvenile growth rate of those genotypes (as seen for higher-quality *Scenedesmus* [inset box: a similar trend from Hall et al. (2010)]). (C) More powerful clones (i.e., higher values on the x-axis) produced relatively more spores when consuming *Scenedesmus* than when consuming *Oocystis* (shown by their ratio).

As shown in the Appendix, however, conversion efficiency increases with length to some power (between 0.7 and 2.5 for algae of varying nutritional qualities in experiments with *Daphnia*; DeMott et al. 2010). Thus, conversion efficiency is a power function of gut passage

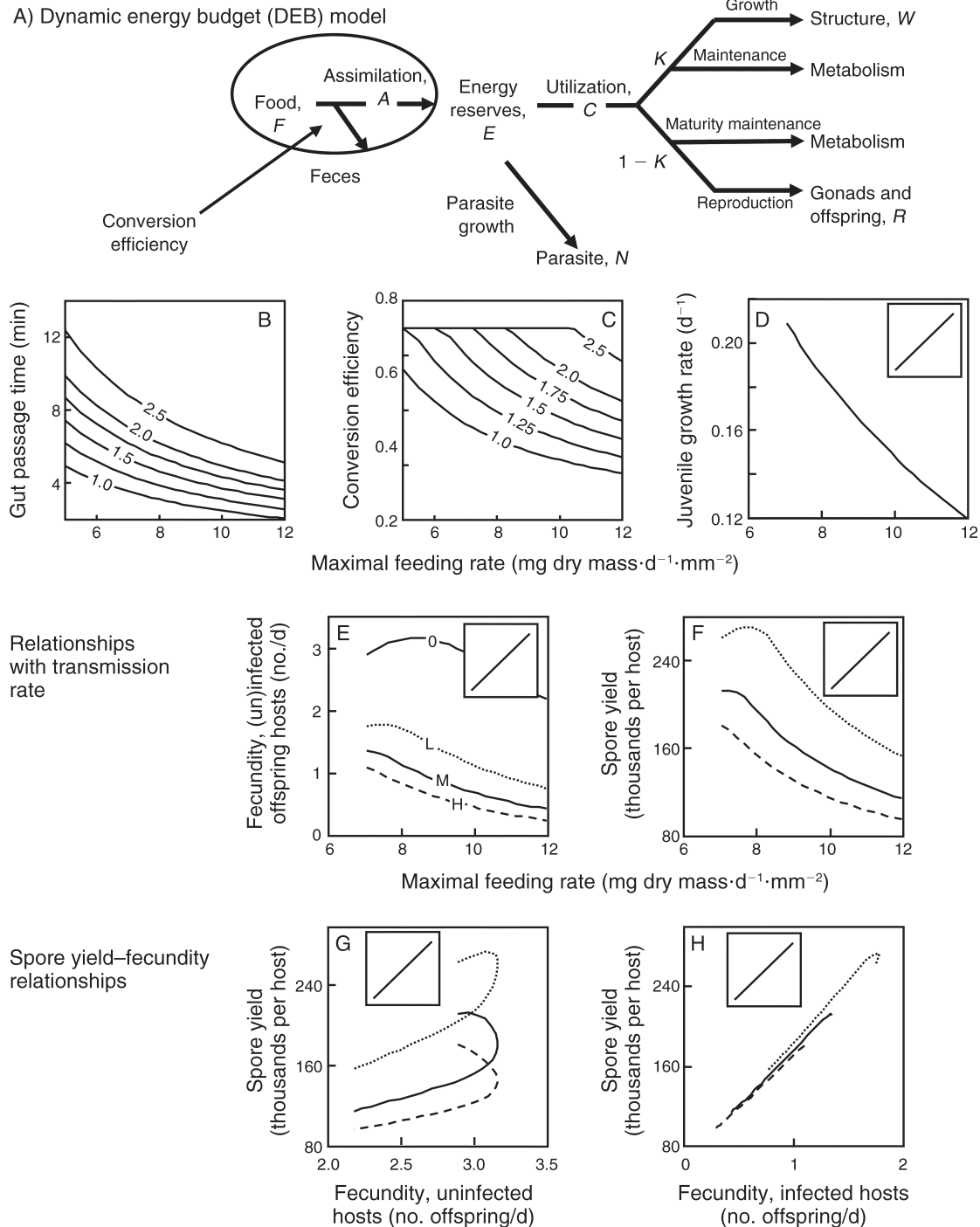


FIG. 5. Development of and predictions from a dynamic energy budget (DEB) model of parasite growth within a host. (A) The DEB model tracks energy flow through an individual host. Ingested food is first assimilated, as governed by conversion efficiency. (B) Gut passage time and (C) conversion efficiency decrease with maximal feeding rate ( $x$ -axis) but increase with body length of *Daphnia* hosts (labeled contours, in mm). (D) Through this mechanism, hosts with higher feeding rate grew more slowly on poor resources like *Oocystis*. (E) Transmission rate (which is proportionate to feeding rate, used here as a surrogate for transmission) correlates negatively with fecundity of uninfected (solid line labeled 0) and infected hosts. Contours in panels E–H correspond to lower (L; dotted, 1000 spores/mL), intermediate (M; solid, 1500 spores/mL), and higher (H; dashed, 2000 spores/mL) levels of spores to which hosts in the simulations were initially exposed. (F) Hosts with higher transmission rate should also produce fewer spores than more resistant hosts (i.e., those with lower transmission rate). (G) Spore yield has a complicated relationship with uninfected fecundity: sometimes increasing, sometimes decreasing. (H) Spore yield is positively correlated with fecundity of hosts when infected. Insets (panels D–H) indicate predictions assuming hosts consumed higher-quality *Scenedesmus* (Hall et al. 2010).



time. Furthermore, conversion efficiency can level off at some maximal level,  $\epsilon_{\max}$ , as animals become larger. To semi-mechanistically implement these results, we assume that

$$\epsilon = \min[\epsilon_{\max}, (\alpha T_G)^b]. \quad (2)$$

This model (Eq. 2) says that a minimum function,  $\min[\dots]$ , determines whether conversion efficiency is maximal (at  $\epsilon_{\max}$ ) or a power function of gut passage time ( $T_G$ ), governed by parameter  $\alpha$  and exponent  $b$ . With this model, conversion efficiency decreases nonlinearly with feeding rate, because higher feeding rates cause lower gut passage time. However, it increases nonlinearly with length, because large animals have larger gut passage times (Fig. 5C).

*Theoretical results (and more insights from and into the data)*

The modified model shows how the power–efficiency trade-off can help to explain many of the experimental results. First, the gut passage time mechanism, as implemented (Eq. 2), predicts that conversion efficiency should decline with feeding rate when resources are less digestible. Due to the drop in conversion efficiency, juvenile growth rate declines with feeding rate when hosts eat poor-quality resources like *Oocystis* (Fig. 5D). (This negative but nonsignificant relationship between juvenile growth rate and feeding rate appeared in the data:  $R = -0.34$ ,  $P = 0.30$ ; not shown). This result contrasts with predictions of this model when conversion efficiency remains constant with higher-quality resources like *Scenedesmus* (DeMott et al. 2010, Hall et al. 2010); then, growth rate increases with feeding rate (as would be anticipated even without the model, all else equal). Therefore, the model confirms the connection between feeding rate and the power–efficiency trade-off (as seen in Fig. 1D). Because growth rates produced from the two food resources diverge as feeding rate increases, a negative relationship emerges between growth rates on these resources (as in Fig. 1A). Thus, clones with a rapid feeding rate become most sensitive to the quality of their resource. These clones are “powerful” yet sensitive, whereas slower feeding, “efficient” clones respond less sensitively to resource quality.

Second, the modified DEB model provides insight into the switch in the fecundity–transmission rate relationship. We have shown, here and previously, positive correlations between feeding rate and transmission rate (Fig. 2; see Hall et al. 2007b, 2010); thus, in these simulations, we equate feeding rate with transmission rate. The model predicts that fecundity of both uninfected and infected hosts can decline with feeding rate (transmission rate), but this relationship can also become unimodal (nonlinear; Fig. 5E; see Appendix for more details). Most importantly, the model predicts that poor food quality should decouple feeding rate from fecundity. When food quality is high, strong, positive relationships between feeding rate and fecundity would

otherwise naturally arise (Hall et al. 2010). In the present experimental results, this feeding rate–fecundity relationship became uncoupled for uninfected hosts (Fig. 3A) and infected hosts (not shown). In both the data and model, then, poor food quality catalyzes a switch from positive to negative transmission rate–fecundity relationships.

Third, the model provides some insight into relationships involving spore yield. When hosts consume poor-quality resources, spore yield should decline with feeding rate and therefore with transmission rate (Fig. 5F). Thus, hosts with higher transmission rate should produce fewer spores when eating poor-quality resources (as compared to more resistant hosts). In the data, the feeding rate–spore yield relationship was negative when hosts consumed *Oocystis* ( $R = -0.76$ ,  $P = 0.029$ ; not shown); however, the transmission rate–spore yield relationship trended negatively ( $R = -0.52$ ,  $P = 0.18$ ). The model provided less insight into the fecundity–spore yield relationships. When food quality was high, clones that fed and grew faster had more energy reserve to fuel higher fecundity and higher production of fungal spores (Hall et al. 2010). Now, with poor resource quality, the model predicted a complicated relationship between uninfected fecundity and spore yield, but a positive relationship with uninfected fecundity and spore yield (Fig. 5G, H), contrary to the negative relationships in the data (Fig. 3E, F).

Finally, the model anticipated the host genotype  $\times$  resource quality interaction for spore yield. Again, when resource quality is poor, juvenile growth rate becomes a negative function of feeding rate (Fig. 5D; i.e., the growth rate of powerful clones is sensitive to poor resource quality). However, juvenile growth rate should still correlate positively with spore yield among clones when hosts consume poor-quality resources (not shown but observed in the data; see Fig. 4B). Thus, powerful clones should grow less and yield fewer spores when eating *Oocystis*. In contrast, when resource quality is higher and conversion efficiency remains constant, high feeding rates produce high growth rates and spore yields (Hall et al. 2010). In other words, when resource quality is good, powerful clones should grow quickly and yield more spores. Thus, the power–efficiency trade-off in growth rate produced by the conversion efficiency mechanism in the model predicts the negative correlation in spore yield seen in the data (Fig. 4A).

## DISCUSSION

This study uncovered connections between epidemiological relationships and a seemingly unrelated trade-off in resource ecology. In this power–efficiency trade-off, fast-feeding host clones more powerfully exploited a richer resource (*Scenedesmus*), whereas slower feeding clones more efficiently exploited a poorer one (*Oocystis*). This trade-off also appears among *Daphnia* species (Tessier et al. 2000, Tessier and Woodruff 2002a) and other diverse taxa (Turpin 1988, Brown 1989, Sommer

1989, Winemiller and Rose 1992, Schmitt 1996). From a disease perspective, the power–efficiency trade-off matters for two reasons. First, it can promote and maintain diversity of host genotypes if resource conditions vary spatiotemporally: periods of time when resource quality is high could favor powerful clones, whereas times with poor resource quality could favor efficient clones, all else being equal (Grover 1997). Because variation in feeding rate connects to both the power–efficiency trade-off and core epidemiological traits such as transmission rate (Hall et al. 2007b, 2010), enhancement of clonal diversity by power–efficiency trade-offs could indirectly maintain genetic diversity of epidemiological traits. Second, the power–efficiency trade-off and its relationship with feeding rate can provide direct insight into why poor resource quality reverses or disrupts key trade-offs between epidemiological traits and create a  $G \times E$  interaction in spore yield.

To connect the power–efficiency trade-off with these epidemiological relationships, we first focus on transmission rate. There are two ways to view the transmission rate data. On the one hand, infection risk for clonal genotypes eating the poorer-quality resource correlated strongly and positively with infection risk for clones eating the richer resource. Thus, clones with a high transmission rate remained relatively more vulnerable to infection, most likely because fast-feeding clones remain relatively fast feeders, regardless of what they eat. Consequently, clonal variation in feeding rate seems to dominate this stage of the infection process. This result echoes findings from a plantain–mildew system in which specific infection outcomes among host and parasite genotypes remained constant along environmental gradients (Laine 2007; but see Blanford et al. 2003, Fels and Kaltz 2006). On the other hand, estimates of transmission rate did not increase in a 1:1 fashion. Instead, infection risk of the more vulnerable (faster feeding) clones responded most sensitively to resource quality. In contrast, transmission rate of the less vulnerable (slower feeding) clones responded little to resource quality. Therefore, feeding rate, a driver of the power–efficiency trade-off in resource use, influenced sensitivity of the transmission rate trait to resource quality.

The power–efficiency trade-off can provide insight into the context dependency of two sets of relationships involving fecundity and epidemiological parameters. When host clones consumed higher-quality *Scenedesmus*, a trade-off arose between resistance (transmission rate) and fecundity: clones that fed more slowly had lower transmission rate but produced fewer offspring when uninfected (Hall et al. 2010). In the other relationship, fast-growing host clones that yielded more spores upon death produced more offspring when infected and uninfected. Both of these sets of trade-offs emerged predictably from a dynamic energy budget (DEB) model of parasitism (Hall et al. 2010). However, the set of experiments reported here show that, when

hosts consumed the poor resource (*Oocystis*), these relationships changed. Instead, the more fecund hosts had a lower transmission rate and produced fewer spores. Once equipped with the feeding rate–gut passage time–conversion efficiency mechanism, our DEB model predicted that clones with a higher transmission rate (faster feeders) should produce fewer offspring than those with a lower transmission rate (slower feeders) when consuming poorer resources. Additionally, the model forecast that, when fed the fairly indigestible resource, less resistant clones should produce fewer offspring and spores when infected. Thus, the model helps us to understand the context dependency of these relationships. However, this enhanced DEB model could not quite capture the reversal or disappearance of the spore yield–fecundity relationships seen in the experiments. Some other factor beyond the power–efficiency trade-off (at least as implemented in the model) may influence these relationships.

Regardless, the dependence of these two sets of relationships on resource quality could have implications for host evolution during epidemics. Theory predicts that resistance (transmission rate)–fecundity and spore yield–fecundity relationships can both produce parasite-mediated disruptive selection (Miller et al. 2005, Boots et al. 2009, Duffy and Forde 2009). Disruptive selection, as seen in a fungal epidemic in *Daphnia* (Duffy et al. 2008), can maintain genetic variation in the transmission rate trait in host populations (Boots et al. 2009). Changes in those trade-offs might promote parasite-mediated directional selection toward increased resistance (as seen in Duffy and Sivars-Becker 2007, Duffy et al. 2009). Thus, variation in resource quality, mediated through physiological mechanisms of hosts, may influence the type of selection that operates during epidemics. This scenario could matter in nature. Digestibility of algal resources often varies considerably in space and time, particularly through the course of epidemics from summer to autumn (DeMott and Tessier 2002, Tessier and Woodruff 2002b, Hall et al. 2009a). Although other factors such as predation intensity and water temperature vary simultaneously, such changes in resource quality during epidemics (Hall et al. 2009a) might influence evolutionary trajectories of host populations. Some of our future work will explore this possibility.

The power–efficiency trade-off can also anticipate a host genotype  $\times$  resource quality interaction in spore yield. Clones of the host that produced relatively more spores when consuming higher-quality *Scenedesmus* produced relatively fewer spores when consuming poorer-quality *Oocystis*. This  $G_H \times E$  interaction can be understood through links between spore yield, growth rate of clones, and this resource-based trade-off. In the present study, clones that grew more quickly when consuming *Oocystis* produced more spores when they died from infection. A similar positive correlation between spore yield and juvenile growth rate arose

among host clones consuming *Scenedesmus* (Hall et al. 2010). However, the clones showed the trade-off in growth rate on the two resources. Thus, the power–efficiency trade-off in growth rate produced the  $G_H \times E$  interaction in spore yield. Furthermore, spore yield from more powerful clones responded most sensitively to resource quality, whereas spore yield from more efficient clones responded much less sensitively to it. These results suggest that similar relationships involving resource-related trade-offs might arise whenever resources influence parasite production (mosquitoes–parasites [Bedhomme et al. 2004]; ladybirds–mites [Ryder et al. 2007]; monarch butterflies–protozoans [de Roode et al. 2008]; snails–trematodes [Johnson et al. 2007]).

The influence of environmental factors on genotype  $\times$  environment interactions and trade-offs can have implications for host evolution, population dynamics, and maintenance of genetic diversity during epidemics. However, we need to better understand and predict how and why these environmental dependencies arise in the first place. Factors such as the energetic cost of immunity and antagonistic pleiotropy may sometimes explain these environmental effects (Lazzaro and Little 2009). Our major message here is complementary. Seemingly unrelated strategies of resource use among hosts (e.g., power–efficiency trade-offs) can provide potent insight into environment–host–parasite relationships. However, to uncover and anticipate these insights, we must develop theory that fuses the physiological roles of animals as resource consumers and hosts of parasites. That perspective proved useful here because variation in resource acquisition traits among clones ties to energy flow and allocation through hosts, and therefore to parasite production and virulence of infection. These fundamental connections between resources and infection genetics could provide predictive insight into other disease systems in which resource use and energetics influence epidemiological traits.

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#### SUPPLEMENTAL MATERIAL

##### Appendix

More data, derivation of the DEB model, and further development of the conversion efficiency mechanism (*Ecological Archives* E093-056-A1).