

Fitness, parasitoids, and biological control: an opinion¹

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Abstract—Fitness, defined as the *per capita* rate of increase of a genotype with reference to the population carrying the associated genes, is a concept used by biologists to describe how well an individual performs in a population. Fitness is rarely measured directly and biologists resort to proxies more easily measured but with varying connection to fitness. Size, progeny survival, and developmental rate are the most common proxies used in the literature to describe parasitoid fitness. The importance of the proxies varies between papers looking at evolutionary theories and those assessing ecological applications. The most direct measures of fitness for parasitoids are realised fecundity for females and mating ability for males, although these proxies are more difficult to measure under natural conditions. For practical purposes, measure of size, through body size or mass, is the proxy easiest to use while providing good comparative values; however, care must be taken when using a single proxy, as proxies can be affected differently by rearing conditions of the parasitoid.

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Résumé—La valeur adaptative, définie comme le taux d'accroissement *per capita* d'un génotype en référence à une population possédant les gènes associés, est un concept utilisé par les biologistes pour décrire la performance d'un individu dans une population. Cependant la valeur adaptative est rarement mesurée directement et les biologistes utilisent plutôt des indices, plus faciles à mesurer mais qui sont de valeur inégale. La taille, la survie de la progéniture et le taux de développement sont les indices les plus souvent utilisés dans la littérature scientifique pour décrire la valeur adaptative des parasitoïdes. Toutefois, l'importance des indices varie selon que les articles traitent d'écologie évolutive ou d'écologie appliquée. Les indices les plus directement reliés à la valeur adaptative des parasitoïdes sont la fécondité réalisée pour les femelles et la capacité d'accouplement pour les mâles. Cependant, ces indices sont difficiles à mesurer dans des conditions réalistes. D'un point de vue pratique la taille, mesurée par le biais des dimensions ou de la masse du corps, est l'indice donnant une bonne valeur comparative le plus facile à utiliser. Toutefois, la prudence s'impose lorsqu'un seul indice est utilisé. En effet, les indices peuvent être influencés différemment par les conditions d'élevage d'un parasitoïde.

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Introduction

Fitness is a concept that most biologists employ on a daily basis; however, why and how we do so seems to vary dramatically among scientists. The purpose of this article is to clarify this exceedingly important concept by discussing its definition and the ways fitness can be measured.

Here, we follow the lead of Sibly and Smith (1985) and define fitness as: *per capita* rate of increase of a genotype with reference to the population carrying the associated genes. Fitness is a relative measure because the spread of a gene in the population depends on the performance of other individuals. This is a Darwinian definition that clearly refers to an evolutionary process. Thus, fitness should not be confused with vigour or quality, although these may be indirect measures (proxies) of fitness (see below). This definition includes both the narrow and broad categories of individual and inclusive fitness, respectively. Individual fitness of a genotype derives from the direct descendants of an individual. Inclusive fitness of a genotype is the sum of both the fitness of the individual genotype and the effect of its action on the fitness of related genotypes (kin) (Hamilton 1964). The second term of this equation is effectively zero for the many organisms in which the action of the individual has no effect on kin fitness. In these cases, individual measures of fitness will suffice. Inclusive fitness is the appropriate measure of fitness whenever a structured population is considered. Examples include gregarious species, where several individuals, often closely related, share a habitat and resources, and quasi-gregarious species, where individuals are not gregarious but rather exploit, as solitary individuals, resources that are gregarious. Gregarious insect larvae, by definition, will almost always reside in a highly structured population, whereas adults may or may not, depending upon resource structure and differential vagility.

Few biologists ever measure fitness directly [*i.e.*, measure the relative performance of genotypes (Hoffman 1994)]. Instead, most researchers resort to proxies such as body size, fecundity, or longevity that give absolute values. One must be cautious when applying such proxies, especially when there is only a distant connection between the proxy and fitness. We thus need to consider the contribution of the proxy to somatic *versus* gametic function in relation to fitness. For example, genes associated with self-feeding decisions may contribute to growth and, ultimately, to reproduction but the connection may be weak. Conversely, decisions concerning the feeding of offspring may contribute directly to fitness. It is interesting that, originally, optimal foraging theory employed the fitness-maximising criterion for deriving the optimal self-feeding decisions (Krebs and Davies 1978), despite the sometimes tenuous connection with fitness. Still, optimal foraging theory provided a powerful new way to think about feeding despite its inadequacies (Pierce and Ollason 1987; Stearns and Schmid-Hempel 1987). Recent efforts have considered more appropriate decisions, such as the feeding of young (Krebs and Davies 1987).

Parasitic insects provide an excellent opportunity to exploit the direct connection between proxies and fitness. Several textbooks have pointed out the direct connection between parasitism and fitness and used this argument to propose that parasite species are well suited for testing theories in evolutionary ecology (Godfray 1994; Ives and Hochberg 2000). The parasite category is not limited to parasitoids; in fact, it applies to the many insects that express a parasitic life style (Price 1975; Eggleton and Gaston 1990).

Caution must be exercised when assuming that all parasite behaviours directly contribute to gametic function. For example, feeding decisions of mosquitoes on blood and nectar have direct and indirect contributions to fitness, respectively. Similar logic can be applied to host feeding and nectar in parasitoids.

Usefulness of proxies

To evaluate how fitness is measured and which proxies are applied to parasitoids, we surveyed the literature from 1990 to 1998 (Biological Abstracts, Philadelphia, Pennsylvania), using the keywords (“fitness” or “qualit*” or “vigo*”) and “parasitoid*.” This search yielded 297 papers, 87 of which used a variety of fitness proxies (Table 1); on average about three proxies per study were measured. Some proxies are favoured: size, progeny survival, development rate, longevity, and fecundity.

Parasitoid fitness may be measured for different reasons (*i.e.*, for testing evolutionary theory or for assessing ecological applications such as biological control). Evolutionary ecologists may be more interested in evolutionary and applied scientists in numerical processes because the latter are concerned with insect-pest regulation. Moreover, evolutionary ecologists employ fitness as a means of assessing within-population evolutionary trajectories, whereas applied ecologists frequently employ it to compare candidate genotypes, populations, or even species. Thus, the level of analysis may differ.

Our first survey did not differentiate measurements of fitness on the basis of evolutionary *versus* applied ecology. Therefore, to gain some insight into how evolutionary and applied ecologists employ fitness proxies, we initiated an additional literature search in which we separated the papers into two categories: those with and those without the keyword “biological control” (Table 2).

Globally, the results have similar trends in the two categories. The six proxies used in more than 20% of the papers in evolutionary studies were also used in more than 20% of the papers in applied ecology (Table 2); however, differences appear, mostly in the relative importance of the proxies. For example, size, which was used in two-thirds of the evolutionary studies, is employed in only 35% of the studies in biological control. Among the proxies that are used more in the context of biological control, progeny survival, host acquisition, and sex ratio are emphasised. The first two factors characterise natural-enemy efficacy and recruitment rather than fitness *per se*, and the greater interest in these proxies is due to their perceived importance for killing pest insects and for securing sufficient enemies for future control, respectively. Sex ratio, on the other hand, is emphasised when parasitoids are mass-reared and female-biased sex ratios facilitate high colony productivity.

In our search, we did not differentiate on the basis of classical and inoculative biological control *versus* inundative biological control. In the former categories, researchers may be as interested in population establishment and stabilisation as they are in killing power, whereas in the latter, short-term efficacy is the key criterion for evaluation. Hence, offspring survival is less important when parasitoids are released *via* inundation. So long as the host is accepted and killed, the ultimate fate of the developing parasitoid is irrelevant (Bigler 1994), except of course when the parasitoid immature is killed by the host immune system and therefore fails to kill the host. It is mostly with respect to mass rearing prior to inundation that gametic processes get consideration in this category.

Below, we consider each of the fitness proxies in turn in descending order of frequency (Table 1). We assigned the proxies to two categories, primary proxies and weighting proxies, to reflect the difference in the relationship between these proxies and fitness. In our opinion, primary proxies can be used as sole proxies because of their direct connection to fitness. Weighting proxies should only be used in conjunction with primary proxies because their principal effect is to modify the direct relationships. Although we treat each trait individually, we recognise that many such traits are genetically correlated with others (Lande and Arnold 1983). Thus, high performance in one measure may be linked with the performance of another. As such, a single proxy measure may not map directly onto fitness.

TABLE 1. Fitness proxies used, number of papers in which they were used, and proportion of papers that used them (total number of papers = 87).

Proxy	No. of papers using proxy	Proportion (%) of papers using proxy
Size	42	48.3
Progeny survival	38	43.7
Developmental rate	37	42.5
Longevity	31	35.6
Realised fecundity—lifetime	26	29.9
Sex ratio	26	29.9
Host acquisition	17	19.5
Vagility	13	14.9
Potential fecundity	10	11.5
Mating ability	9	10.3
Oviposition propensity	4	4.6
Realised fecundity—daily	3	3.5

TABLE 2. Fitness proxies used, number of papers in which they were used, and proportion of papers that used them (number of papers used: without biological control, 41; with biological control, 46).

Proxy	Without biological control		With biological control	
	No. of papers using proxy	Proportion (%) of papers using proxy	No. of papers using proxy	Proportion (%) of papers using proxy
Size	26	63.4	16	34.8
Developmental rate	18	43.9	19	41.3
Progeny survival	15	36.6	23	50.0
Longevity	13	31.7	18	39.1
Realised fecundity—lifetime	10	24.4	16	34.8
Sex ratio	9	22.0	17	37.0
Potential fecundity	7	17.1	3	6.5
Mating ability	5	12.2	4	8.7
Vagility	5	12.2	8	17.4
Host acquisition	4	9.8	13	28.3
Oviposition propensity	2	4.9	2	4.4
Realised fecundity—daily	1	2.4	2	4.4

Finally, explicit calculation of fitness depends upon life history and ecological circumstances. When generations are discrete and (or) the focal population is stable, R_0 , the net reproductive rate or the number of offspring produced by an individual during her lifetime, suffices. Otherwise, the intrinsic rate of increase, r , is the appropriate measure of fitness (Stearns 1992). In the latter case, a proxy such as fecundity may be a weak surrogate for fitness because age-specific rates of mortality and rates of offspring production need to be considered as well. In the Discussion, we make note of this distinction.

Proxies

Size (primary proxy – weighting proxy)

Body size or mass was the most commonly used metric in our survey, although it has no direct relation to fitness. This proxy, however, may be used as a primary proxy, when we know its relationship with another primary, such as fecundity, mating ability,

longevity, *etc.* This relationship is generally positive (Vet *et al.* 1994). Nicol and Mackauer (1999) discuss the allometry of body size and body mass. Relative to biological control, body size has also been positively correlated with field performance of parasitoids (Kazmer and Luck 1995; Bennett and Hoffmann 1998).

Progeny survival (weighting proxy)

The metric employed is survival probability on a *per capita* basis (Sequeira and Mackauer 1994). This proxy includes the ability to overcome host defences, larval competitors (Ueno 1997), and hyperparasitism (van Baaren *et al.* 1995). Progeny survival is not suitable as a sole proxy because its effect on fitness acts through fecundity. To serve as a primary proxy the assumption that fecundity's are randomly distributed among genotypes must hold; this is not realistic (Cronin and Strong 1996). When super- and multi-parasitism are common, progeny survival may be an important weighting parameter (Visser 1996). In biological control programmes using either classic introduction or inoculative releases, progeny survival, or host suitability as it is often termed, is an essential element for programme success.

Developmental rate (primary proxy)

The value of this proxy is highly conditional on population dynamics and temporal structure. For example, in populations with overlapping generations, generation time links directly to fitness (Roff 1992). In a discrete generation, population development rate can still map directly onto fitness, when there is some temporal dependence of performance; for example, when there is a limited time window for parasitism or time-dependent competition for mate acquisition (Roitberg *et al.* 1992).

From a biological-control perspective, development rate is important in two ways. First, this rate can determine the population growth rate of the natural enemy. Second, it can determine the degree of synchronisation with the pest insect and, thus, its importance as a proxy varies according to the type of programme used. It is highly important in classical biological control programmes where the parasitoid must develop in synchrony with its host, less important in inoculative release programmes, and almost non-existent in inundative programmes where the parasitoid is released at the right developmental stage of the host (Bigler 1994).

Longevity (primary proxy)

Assuming that all else is equal (*i.e.*, reproductive opportunities per unit time are equally distributed over genotypes), longevity can be a good estimate of lifetime reproductive success. Generally, it is measured in the laboratory (Fernandez and Netwig 1997; Ueno 1998); however, physiological longevity is quite different from ecological longevity (Heimpel *et al.* 1998). Furthermore, longevity is a weak proxy under conditions of egg limitation.

In males, longevity can be almost completely irrelevant for within-patch mating, as in the case of gregarious or quasi-gregarious parasitoids, but is important for extra-patch mating. Here, both longevity and vagility (see below) become important.

Fecundity (primary proxy)

As discussed for longevity, there can be significant differences between physiological (Ellers *et al.* 1998) and ecological fecundity (Bourchier and Smith 1996), more commonly called potential and realised fecundity, respectively (Ito 1980). Fecundity is important in egg-limited situations, both for pro- and syn-ovigenic species. In the latter

species, we must consider the temporal dynamics of egg limitation, whereas in the former, we measure the egg load at eclosion.

As a proxy, there is a great difference in the value of potential and realised fecundity because of the unlikely assumption that mortality is equally distributed over the population. Realised fecundity includes age-specific fecundity and mortality schedules, vagility, host acquisition, and propensity to oviposit. Hence, the best way to measure realised fecundity is under realistic field conditions. In conjunction with progeny survival, realised fecundity is an excellent proxy, especially when the aforementioned net reproductive rate is the appropriate measure of fitness.

Fecundity is important in all forms of biological-control programmes because it directly influences the number of hosts parasitised. Realised fecundity can impact both field efficacy and mass rearing.

Sex ratio (weighting proxy)

More than any other proxy, sex ratio has no value as an absolute measure [*i.e.*, it must be evaluated against the population sex ratio and mating structure (Charnov 1976)]. Like offspring survival, sex ratio can be an important weighting term in conjunction with realised fecundity as a determinant of fitness (Baker *et al.* 1998).

Host acquisition (weighting proxy)

This proxy measures the ability to get to the host, respond to infochemicals, and accept hosts, and the capacity to oviposit in the host. It is a weighting proxy that can serve as an important bridge between potential and realised fecundity (Bouchier and Smith 1996). In parasitoid species in which the larva rather than the ovipositing female must locate and parasitise the host (*e.g.*, most species of Coleoptera, Diptera, Neuroptera, Lepidoptera, and Trichoptera parasitoids), host acquisition becomes a primary proxy. In Hymenoptera, only species of Perilampidae, Eucharitidae, and Eucerotinae exhibit this behavior (Godfray 1994). Fecundity, either potential or realised, is less important in these species, where most of the mortality occurs during the first instar. This proxy is of similar importance in classic introduction, inoculative, and inundative biological control programmes (Bigler 1994).

Vagility (weighting proxy)

Vagility can be thought of as the ability to move through the environment to access opportunities (King and Lee 1994; Visser 1994). There is an assumed positive correlation between vagility and host or mate encounter rate. This correlation greatly depends on the structure of the resources sought. For example, when species are highly clumped, there may be extremely high variance in host encounter rates between individuals who are and those who are not successful in locating host clusters (Janssen 1989).

Mating ability (primary proxy – weighting proxy)

The categorisation of this proxy is conditional on gender. For males, it is the ability to transfer genome *via* sperm. Hence, for males it is a primary proxy and is comparable with realised fecundity for females (Sorati *et al.* 1996). For females, this proxy is a weighting factor when they are sperm-limited and (or) males vary in quality. For parasitoids, the importance of this weighting factor may differ between species that are haplodiploid and those that are diploid.

Oviposition propensity (weighting proxy)

This proxy is measured as a tendency to accept hosts (van Bergeijk *et al.* 1989; Bouchier and Smith 1996). The value of this proxy depends on the assumption that fecundity is randomly distributed across the population, which is unlikely. Like host acquisition, it is a weighting proxy that can serve as an important bridge between potential and realised fecundity. Host acceptance is a major component of a successful biological-control agent, whatever type of programme is used (Bigler 1994).

Other proxies

A few papers considered other proxies, such as deformation (Romeis *et al.* 1998) and fluctuating asymmetries (Bennett and Hoffmann 1998), which we classify as measures of vigour or quality. These measures can correlate with fitness proxies, such as size or longevity, but they are not directly linked to fitness as defined here.

Discussion

In summary, of all proxies considered, realised fecundity and mating ability (weighted by progeny survival) are the most commonly used. This is likely because they appear to be the most direct measures of fitness for females and males, respectively. All other proxies require highly restrictive assumptions. Unfortunately, our best proxies may also be those to which it is most difficult to assign realistic scores because they require evaluation under realistic field conditions, a situation rarely found in studies measuring fitness proxies (but see Heimpel *et al.* 1998).

Now, are the objectives of evolutionary ecology and applied ecology, when using fitness, so different? We suggested earlier that biocontrol practitioners mostly employ proxies of fitness for ecological but not evolutionary reasons. Although this may appear pragmatic, because proxies that characterise parasitoid efficacy and recruitment are more likely to predict the control value of a natural enemy, evolutionary processes can also determine whether a biological-control programme will succeed. For example, Roitberg (2000) recently considered the potential risk associated with the release of exotic biocontrol agents. He showed that good proxies of fitness are critical for the development of risk-assessment protocols at two levels: immediate and long-term risks. These estimates refer more to proxies related to evolutionary processes. Here, "immediate" refers to the likelihood that a parasitoid possesses sufficient phenotypic plasticity to attack nontarget organisms, whereas "long-term" refers to the likelihood that a parasitoid population will evolve an expanded host range that includes nontarget organisms. Both of these risks are contentious and poorly understood (Simberloff and Stiling 1996; Roitberg 2000).

Immediate risk is difficult to assess because host fidelity can be affected by a large set of disparate factors, including egg load (Minkenberg *et al.* 1992), presence of conspecifics (Visser 1995), host availability (Speirs *et al.* 1991), adult experience (van Baaren and Boivin 1998), weather (Roitberg *et al.* 1993; Carrière and Boivin 1997), and season (Roitberg *et al.* 1992). Thus, it is difficult to design and implement elegant yet effective risk-assessment protocols. Roitberg (2000) shows that evolutionary theory and proxies of fitness can be used to identify those factors that are most likely to impact host acceptance and, thus, risk to nontarget hosts.

How and why host range evolves is determined by three factors: (i) the expression of host-range phenotype in a particular environment (note: environment is defined, in broad terms, to include endogenous state, such as egg load), (ii) the fitness of genotypes expressing a particular phenotype in its respective environment, and (iii) the frequency with which different environments are encountered (Stearns 1989; Carrière and

Roitberg 1996). Again, good fitness proxies (point *ii*) are crucial to accurate prediction. Thus, choice of appropriate fitness proxies should be carefully considered.

Conclusion

We initiated our discussion by noting the ubiquity with which biologists employ concepts and measures of fitness (de Jong 1994). How and why we measure fitness is open to debate. We contend that some surrogates are better than others, although these might not be the easiest to measure. What is certain, however, is that fitness is a key element in the successful application of ecological and evolutionary principles and choice of the appropriate fitness proxy depends upon a good working knowledge of Darwinian theory.

No single proxy emerged as the best one in all situations. Several elements influence the way a proxy relates to the true fitness of an individual, among them the biology and ecology of species. Therefore, the value of proxies will vary from species to species, as their biological and ecological characteristics change. For example, we already mentioned that the stage searching for hosts (females for most parasitoids but first-instar larvae in most Coleoptera and Diptera; see Vagility) changes the relative weight of several proxies.

For practical purposes, the measure of size, through body size or mass, is probably the easiest proxy to use; it provides good comparative values between individuals, as size has often been shown to vary in a positive way with fitness. However, variations in size relate differently to other fitness proxies. For example, in *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae), females reared on old host eggs (69 h) showed a reduction in size (head width) of 13.5%, but reductions in walking speed of 48.8% and in lifetime fecundity of 77.9% (G. Boivin, unpublished data), when compared with females reared on young host eggs (3 h). These data caution against the use of a single proxy to quantify an effect on fitness.

Ideally, we could measure several proxies and integrate them into a global measure of fitness. The contribution of each of these proxies to the production of progeny should be quantified and included in a model. However, this requires a level of knowledge of the biology and ecology of species that is available for only a few species. Without the understanding of the contribution of proxies such as vagility or longevity to the production of progeny, accurate global measures of fitness remain elusive.

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