Comparing methods for estimating parasite-induced host mortality from distributional data: implementation and limitations

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Abstract

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Introduction

Infectious agents can have major impacts on animal populations through changing population dynamics and stability (Dobson & Hudson 1992), altering predator-prey interactions (Joly & Messier 2004), and even causing species decline and extinction (De Castro & Bolker 2005; McCallum 2012). Accurate estimates of parasite-induced host mortality (PIHM) in wild animals are important for understanding what regulates both host and parasite populations and to make predictions about disease transmission in natural systems. Although a negative impact on host fitness is a fundamental component of parasitism (Lafferty & Kuris 2002) [more], it is notoriously difficult to quantify PIHM in wild animal populations (Lester 1984; McCallum 2000).

To conclusively identify PIHM in wild animal populations, it is necessary to experimentally infect and track host populations; a method that is rarely possible in most wild animal systems (McCallum 2000). Instead, parasitologists are

often only able to determine the parasite intensity on some number of sampled hosts. This snapshot, distributional data is far from the ideal type of data for addressing questions regarding PIHM, but this is the type of data on which most questions regarding PIHM are asked (Ferguson *et al.* 2011; Royce & Rossignol 1990; Lanciani & Boyett 1989; Lester 1984, 1977). In particular, parasitologists are often interested in asking two questions from this data: 1) Is PIHM occurring in a host-parasite system? and if PIHM is occurring 2) Can the effect of parasite intensity on host survival be quantified? While both macro and microparasites have detrimental and possibly fatal effects on hosts, for the remainder of this paper we limit our discussion to macroparasites that can be discretely counted within a host.

The first of these PIHM questions was addressed by Crofton (1971) who developed a method to test for the presence of PIHM using the truncation of the negative binomial distribution. In short, the Crofton Method assumes that the distribution of parasites across hosts before mortality occurs follows a negative binomial distribution (Anderson & May 1978; Shaw *et al.* 1998). As heavily infected hosts begin to die, the negative binomial distribution is truncated and these hosts are no longer observed in a sample. In other words, the observed host-parasite distribution and the pre-mortality host-parasite distribution will predict substantially different numbers of hosts with high infect intensity (because those have died due to infection), but a similar number of hosts with low infection intensity (because those have survived). Crofton (1971) noted that by starting with all observed hosts and iteratively fitting a negative binomial distribution to hosts with lower and lower parasite loads, one could determine whether or not PIHM was occurring and estimate the parameters of the host distribution before parasite-induced mortality. This was done graphically by determining whether the parameters of the negative binomial distributions fit to different truncations of the data showed a substantial change as the truncation point moved from

heavily infected hosts to lightly infected hosts. The Crofton Method and this graphical technique are both still currently used to assess whether PIHM is a occurring in a system (Ferguson *et al.* 2011). We give a thorough description and implementation of the Crofton Method in *Supplementary Information* (SI) 1 and discuss the validity of its assumptions in the *Discussion*.

The second question regarding PIHM moves beyond a simple yes or no answer and attempts to quantify how parasite intensity affects host survival. Adjei *et al.* (1986) proposed a method to answer this question by first using the Crofton Method to estimate the pre-mortality parameters for a host-parasite distribution and then, given these parameters, estimating a host survival function that described how the probability of host-survival changed with increasing parasite load (see *Methods*). With this host survival function, one can estimate important host-parasite quantities such as the parasite intensity at which 50% of hosts succumb to PIHM (LD_{50}), as well as the percent of hosts in a population succumbing to PIHM (Adjei *et al.* 1986).

Despite these methods both being over three decades old, they are still the primary means of answering questions about PIHM given distributional data (but see Ferguson *et al.* 2011, for an alternative to the Crofton Method). However, both methods have a few important limitations. The Crofton Method, and more recent methods (Ferguson *et al.* 2011), rely on a visual test to determine whether or not PIHM is occurring in a system. With no clear decision rule, it can be difficult to consistently determine the significance of PIHM across different host-parasite systems. In theory, the Adjei Method can ameliorate this problem. In addition to providing information on the host-survival function, this method can also be used to assess the significance of PIHM in a system. In practice, however, the Adjei Method has never been thoroughly tested and relies on a number of questionable data manipulations.

In this study, we have three primary goals. First we wish to test reliability

of the Adjei Method for answering the aforementioned questions regarding PIHM. Second, we propose a novel method for answering these questions, compare its efficacy against the Adjei Method, and test both methods ability to detect PIHM on empirical data. Third, we discuss the limitations of inferring PIHM from distributional data alone and whether any method for inferring PIHM has a place in the future of parasitology.

Methods

The Adjei Method for estimating PIHM

The Adjei Method for estimating PIHM has two steps. The first step is to estimate the parameters of the pre-mortality host-parasite distribution using the Crofton Method. The three parameters estimated are the total number of hosts before mortality N_p, the mean number of parasites per host before mortality μ_p, and the aggregation of parasites before mortality given by the parameter k_p from a negative binomial distribution. When k_p is small, parasites are highly aggregated among hosts and when k_p is large parasites are more evenly spread out (Wilson *et al.* 2002). The implementation of the Crofton Method has been discussed at length elsewhere (e.g. Royce & Rossignol 1990; Lester 1984) and we provide a tested implementation of the method in SI 3.

The second step of the Adjei Method is to estimate the shape of the host survival function. Adjei *et al.* (1986) assume that the host survival function follows the logistic form

$$h(x|a,b) = h_x = \frac{e^{a-b\log(x)}}{1+e^{a-b\log(x)}} \tag{1}$$

where x is the parasite intensity in a given host and a and b are the two parameters of the logistic function. Generally, a larger a allows for hosts to tolerate larger

parasite intensities before experiencing parasite-induced mortality and a larger b leads to a more rapid decline in the probability of host survival as parasite intensity increases. The value $\exp(a/b)$ is referred to as the LD_{50}, which gives the parasite intensity at which 50% of hosts experience mortality.

To estimate this function the Adjei Method proceeds as follows. First, it calculates the expected number of hosts with a given parasite load x by using the equation $g(x; \mu_p, k_p) * N_p$ where $g(x; \cdot)$ is the negative binomial pre-mortality distribution. Second, the observed and predicted number of hosts with x parasites are paired as a single data point and the method then assumes that this data point follows a binomial distribution with the total number of "trials" equal to the predicted number of hosts and the total number of "successes" equal to the observed number of hosts. In some cases, the observed number of hosts is greater than the expected number of hosts and the Adjei Method alters the data so that the observed is equal to the predicted (Adjei *et al.* 1986). After this questionable manipulation, the (observed, predicted) pairs are fit to a standard Generalized Linear Model (McCullagh & Nelder 1989) with a binomial response variable and a logistic link function given by equation 1. This model provides estimates for parameters a, b and LD_{50}.

While not included in the original implementation of the Adjei Method, a χ^2 test with a degrees of freedom of 1 can be used to assess whether a GLM model that includes parasite intensity as a predictor of host survival probability is a "better" model than a GLM without this predictor. This allows the Adjei Method to determine whether PIHM is a significant factor in a host-parasite system.

The Adjei Method's most glaring deficiency is the need to alter the observed data in order to fit the model into the binomial GLM framework. A second more subtle problem with the Adjei Method is the potential need to bin data in order to predict greater than one host in a given parasite intensity class. For example, if the total number of hosts pre-mortality was 50, the mean number of parasites

per host pre-mortality was 100 and the aggregation parameter was 1, applying the equation $g(x; \mu_p = 100, k_p = 1) * 50$ would result in less than 1 individual in all parasite intensities x. In other words, the Adjei Method cannot be applied to samples with either very high mean parasite loads, small sample sizes, or both without some sort of binning of the data. While this is not a flaw *per se*, it does add a certain level of subjectivity (i.e. which bins should you use?) to a method that already has serious potential issues. In this analysis, we always assume the Adjei Method is not binning the data, though we provide code for applying the binning method in SI 3.

The Likelihood Method for estimating PIHM

Given the potential deficiencies of the Adjei Method, we provide an alternative approach for estimating parasite-induced host mortality (PIHM) that makes less assumptions and provides more reliable answers to the PIHM questions outlined above. The Likelihood Method we propose does not require any binning or alteration of the data, potentially reduces the number of parameters that need to be estimated, and allows for standard statistical techniques to be used to assess the significance of PIHM in a system.

As with all previously proposed methods for estimating PIHM, the Likelihood Method first assumes that the pre-mortality distribution follows a negative binomial distribution $g(x; \mu_p, k_p)$. The second assumption is that the host survival function takes the form of a logistic curve given by equation 1. With these two explicit assumptions, the Likelihood Method estimates the 4 parameters μ_p, k_p, a, and b.

To estimate these parameters, we need to define a probability distribution that gives the probability of having a parasite load of x parasites conditional on host survival. Using standard rules of conditional probability this distribution can

be written as

$$P(x|\text{survival}) = \frac{P(\text{survival}|x) * P(x)}{P(\text{survival})} \tag{2}$$

One can see that $P(\text{survival}|x)$ is the survival function $h(x; a, b)$, $P(x)$ is the pre-mortality parasite distribution $g(x; \mu_p, k_p)$ and $P(\text{survival}) = \sum_0^\infty P(\text{survival}|x) * P(x) = \sum_{x=0}^\infty h(x; a, b) * g(x; \mu_p, k_p)$. Therefore equation 2 can be written as

$$P(x|\text{survival}) = \frac{h(x; a, b) * g(x; \mu_p, k_p)}{\sum_{x=0}^\infty h(x; a, b) * g(x; \mu_p, k_p)} \tag{3}$$

Using this probability distribution, one can then find the parameters μ_p, k_p, a, and b that maximize the likelihood of an observed host-parasite dataset. Alternatively, one could apply the Crofton Method to estimate μ_p and k_p and then find the maximum likelihood estimates of a and b and the corresponding LD_{50}.

To estimate that significance of PIHM in a host-parasite system, a likelihood ratio test can be used in which the full model is given by equation 3 and the reduced model is given by a negative binomial distribution. If PIHM is not significant in the system, the resulting likelihood ratio statistic should approximately follow a χ^2 distribution with degrees of freedom equal to 2. We provide the code for implementing this Likelihood Method in SI 3.

Question 1: Is PIHM occurring?

To test the ability of the Adjei Method and the Likelihood Method to identify whether or not PIHM was occurring in a system, we randomly generated data using the following procedure. First, we drew N_p randomly infected hosts from a negative binomial distribution with parameters μ_p and k_p. This represented the dataset observed before mortality. Second, we chose values of a and b and

calculated the probability of survival for all N_p hosts using equation 1. Third, we drew N_p random numbers from a uniform distribution between 0 and 1 and if host survival probability was less than this random number, the host experienced parasite-induced mortality. The surviving hosts comprised the dataset that would be obtained in the field, after PIHM.

Using both the pre-mortality and post-mortality simulated datasets, we assumed that the values of N_p, μ_p, and k_p were known and tested the ability of both methods to correctly determine whether or not PIHM was occurring. While this scenario is unrealistic because the parameters N_p, μ_p, and k_p are always unknown, we implemented this scenario as a baseline to establish the efficacy of the methods independent of the estimates of N_p, μ_p and k_p. For the Adjei Method, N_p, μ_p, and k_p are estimated using the Crofton Method, while μ_p and k_p in the Likelihood Method can be estimated jointly with a and b or via the Crofton Method. If a method could not correctly predict whether or not PIHM was occurring under these idealistic conditions, we considered this strong evidence of the unreliability of this method.

We used three different values of μ_p (10, 50, 100) and for each μ_p we examined three different survival functions that had graduate, moderate, and steep decreases in host survival with increasing parasite intensity (Figure 1). For a given μ_p, each survival function had the same LD_{50} ($[\mu_p = 10,\ LD_{50} = 7.39]$, $[\mu_p = 50,\ LD_{50} = 35.57]$, $[\mu_p = 100,\ LD_{50} = 77.3]$), but different values of a and b. We examined each μ_p-survival function pair at three levels of parasite aggregation, $k_p = 0.1$, 0.5, and 1 — realistic values of parasite aggregation in natural populations (Shaw *et al.* 1998). For each of these parameter combinations we simulated 150 datasets and tested the probability of each method incorrectly identifying PIHM in the pre-mortality dataset (Type I error) and correctly identifying PIHM in the post-mortality dataset (power). For each method, we used a likelihood ratio test to determine whether the full model with PIHM provided a

significantly better fit than the reduced model without PIHM at significance level $\alpha = 0.05$. We tested each parameter combinations for pre-mortality population sizes of N_p = [50, 100, 200, 300, 400, 500]. N_p is not technically the sample size on which the methods are being tested on the post-mortality data because PIHM reduces N_p for each simulated dataset. We therefore used the average number of surviving hosts over all 150 simulations for a given parameter combination as our measure of sample size in the power simulations.

Question 2: Can the effect of parasite intensity on host survival be quantified?

To compare the ability of the Adjei Method and the Likelihood Method to recover LD_{50} and the parameters a and b of the survival function, we used the same simulation procedure and parameter combinations described above.For each parameter combination we simulated 150 datasets, estimated a, b, and LD_{50} and calculated the standardized bias and precision (Walther & Moore 2005) for these estimates over varying pre-mortality host population sizes N_p = [300, 500, 1000, 2000, 5000, 7500, 10000]. We used the average number of surviving hosts over all 150 simulations for a given parameter combination as our measure of sample size.

Application to data

We tested the ability of the Adjei Method and the Likelihood Method to identify PIHM in 6 host-parasite datasets given in Crofton (1971) and 4 datasets given in Adjei *et al.* (1986) (Table 1). In the Crofton (1971) datasets, the host was the snail *Gammarus pulex* which acts as the intermediate host for the acanthocephalan *Polmorphus minutus*. In the Adjei *et al.* (1986) datasets, the hosts were two species of lizard fish *Saurida tumbil* and *Saurida undosquamis* that were infected by the cestode parasite *Callitetrarhynchus gracilis*. Males and females of both fish species

were considered separately.

In both these studies, the authors reported PIHM in some of the datasets and we test whether the Adjei Method and/or the Likelihood Method also predicted PIHM. For the 6 datasets from Crofton (1971), we truncated the data at 4 parasites, applied the Crofton Method to estimate the pre-mortality distribution, and then ran the Likelihood Method and Adjei Method using these pre-mortality parameters. For the Adjei *et al.* (1986) datasets, we followed the same procedure as the authors and first truncated the data at 2 parasites and then fit the Crofton Method for the female fish of both species. We then parameterized the male pre-mortality distributions for each species with the results from the females. Finally, we applied the Adjei Method and the Likelihood Method to determine whether or not PIHM was significant for these species and compared our results to those given by the authors. All fitting to data was done with the Python code provided in SI 3.

Results

Question 1: Is PIHM occurring?

The Adjei Method showed highly inflated Type I error rates (i.e. falsely detected PIHM) for all parameter combinations that we considered (Figure 2; SI2 Figs 1, 2). This method also showed the unintuitive pattern of Type I error rate decreasing as sample size decreased. This pattern is due to the issue of binning discussed in the *Methods*. For small samples sizes, the applicability of the Adjei Method is compromised without binning the observed data in some way. In contrast, the Likelihood Method showed a Type I error rate at or near the pre-set level of 0.05 for all parameter combinations and sample sizes considered.

The ability of the Adjei Method to detect PIHM given that it was occurring

in a system (i.e. the power) was close to 1 for larger sample sizes and tended to decrease as sample size decreased (Figure 2; SI2 Figs 1, 2). The Likelihood Method had a power close to one for all parameter combinations and sample sizes considered. With gradual survival functions (solid black lines; Figure 2, SI2 Figs 1, 2), the Likelihood Method showed a decreased power to detect PIHM for small sample sizes.

Question 2: Can the effect of parasite intensity on host survival be quantified?

The Likelihood Method gave asymptotically unbiased estimates of the LD_{50} for all combinations of parameters examined in this study (Figure 3, SI2 Fig 3, 4). Even for small sample sizes (< 500 hosts), the Likelihood Method's estimate of LD_{50} was largely unbiased, with small biases occurring for host survival functions that were gradual. On the other hand, the Adjei Method always produced more biased estimates of the LD_{50} than the Likelihood Method across all parameter combinations (Figure 3, SI2 Fig 3, 4). For $\mu_p = 10$, the LD_{50} estimates from the Adjei Method were largely unbiased for large samples sizes, but showed increasing bias as sample size decreased, particularly for steep survival functions. As μ_p increased, the Adjei method produced biased estimates of LD_{50} across all sample sizes, with bias increasing as sample size decreased (SI2 Fig 3, 4).

The precision of the LD_{50} estimates for the Likelihood Method decreased (increasing coefficient of variation) as sample size decreased for all parameter combinations we examined (Figure 3, SI2 Fig 3, 4). The LD_{50} estimates from the Adjei Method showed a similar pattern, with large decreases in precision occurring for the steepest survival function across all values of μ_p (Figure 3, SI2 Fig 3, 4).

In terms of the host survival function, the Likelihood Method gave asymptotically unbiased estimates of a and b as sample size increased for all

parameter combinations considered (Figure 4, SI2 Fig 5, 6). However, as sample size decreased, the Likelihood Method tended to produce severely biased estimates of a and b. This was generally more pronounced for steeper survival functions and more aggregated pre-mortality distributions (e.g. Figure 4). The Adjei Method produced biased estimates of a and b across all sample sizes, with the bias consistently being larger when the survival function was steeper. The bias of the Adjei Method's estimate of a also increased as μ_p increased (Figure 4, SI2 Fig 5, 6).

Application to data

Of the 10 datasets we considered, the previous authors visually detected PIHM in 7 of them (Table 1). The Likelihood Method parameterized from the pre-mortality parameters of the Crofton Method detected significant PIHM in 6 of these 7 datasets at a significance level of 0.05. The only dataset in which the the Likelihood Method did not detect a significant effect of PIHM was the Adjei dataset for female *S. tumbil*. For this dataset there was a marginally significant effect of PIHM ($\chi^2_{df=2} = 5.34; p = 0.069$).

The Adjei Method detected significant PIHM in 9 of the 10 datasets given (Table 1). This is consistent with the previous results which show that the Adjei Method has a very high Type I error rate.

Discussion

Determining whether PIHM is a significant factor for a host populations is critically important in many systems, but detecting and describing PIHM given only observational data is notoriously difficult. We show that the Adjei Method, the only currently proposed method to estimate the host survival function and

the LD_{50} from observational data, has some serious methodological problems that result in biased estimates even under the most idealistic conditions. Moreover, we show that the Adjei Method has a seriously inflated Type I error rate, meaning it will often detect PIHM even when it is not present. Moreover, for small, realistic sample sizes the Adjei Method behaves erratically; a consequence of the need to subjectively bin the data in order to predict parasite intensity classes with at least one host.

To attempt to ameliorate the flaws in the Adjei Method, we proposed a more general method to determine both whether or not PIHM is occurring in a system and to quantify the survival function. We show that this method is asymptotically unbiased when estimating the host-survival function for all of the parameter space that we explored and we found that it produces unbiased and precise estimates of the LD_{50} for small, realistic sample sizes. Moreover, this novel method has a Type I error rate close to the pre-set level of $\alpha = 0.05$ and high power for detecting PIHM for realistic samples sizes. However, we note that the Likelihood Method produces seriously biased estimates of the host survival function (a and b) for sample sizes typically observed in many host- parasite studies. The bias was most severe for steep host survival functions, due to large changes in the values of a and b only slightly changing an already steep survival function. Given these results, neither the Likelihood Method or the Adjei Method could confidently recover the exact shape of the host survival function for small, realistic sample sizes.

We also fit both the Likelihood Method and the Adjei Method to empirical data to determine whether they could detect PIHM that had been previously reported based on visual assessments. Consistent with our simulation results, we found that the Adjei Method tended to detect PIHM where it had not been previously reported, while the Likelihood Method's detection of PIHM was consistent with previously reported PIHM in a given dataset. Taken together, these

results suggest that the Adjei Method is fundamentally flawed. We recommend using the Likelihood Method for detecting PIHM and describing attributes of the host survival function.

While we have improved upon the previously existing methods for answering questions about PIHM, we cannot belie the fact that estimating PIHM from observational data alone is ladened with assumptions and difficulties (McCallum 2000). The most fundamental assumption of all methods for estimating PIHM is that the shape of the pre-mortality host-parasite distribution is known and follows a negative binomial distribution. While there is substantial empirical and theoretical evidence to justify the use of the negative binomial distribution as the pre-mortality distribution for macroparasites across hosts (Calabrese *et al.* 2011; Anderson & Gordon 1982; Shaw *et al.* 1998), it is widely recognized that different processes can lead to a variety of distributions of parasites across hosts (Isham 1995; Grenfell *et al.* 1995; Wilson *et al.* 2002; Duerr *et al.* 2003). However, the critical assumption of the pre-mortality distribution is not that the processes leading to the pre-mortality distribution generate a negative binomial distribution, but rather that the pre-mortality distribution is well-fit by a negative binomial. The extreme flexibility of the negative binomial distribution makes it a reasonable candidate distribution for the pre-mortality distributions. Therefore, we do not see this assumption as central problem in any of the proposed methods.

However, to use the pre-mortality distribution to infer whether or not the PIHM is occurring in a system requires an explicit assumption about the host survival function and the shape of the post-mortality distribution. Regarding the host-survival function, all currently proposed methods of PIHM assume that the host-survival function is such that uninfected individuals and individuals with low parasite intensity experience essentially no PIHM. Lanciani & Boyett (1989) illustrated the importance of this assumption by showing that when hosts experienced a linear decrease in survival probability the Crofton Method could not

detect PIHM. As the most fundamental models of host- parasite dynamics assume a linear decrease in host survival probability with increasing parasite intensity (Anderson & May 1978), the failure of these methods to detect this relationship is a significant disconnect between empirical and theoretical disease ecology [though I haven't explicitly tested this with the likelihood method]. However, empirical work has shown that non-linear functions of host survival are not uncommon in host-parasite systems (Benesh 2011), so this assumption alone does not preclude the use of PIHM methods on empirical data.

Regarding the shape of the post-mortality distribution, all of these methods require that the post-mortality distribution be significantly different from a negative binomial distribution. This is necessary because none of the above methods will be able to detect PIHM if a negative binomial distribution is an adequate fit to the post-mortality distribution. This is simply because there will be no need for a more complex model (either truncation of the negative binomial or the model given in equation 3) if a negative binomial distribution already fits the data. As many observed host-parasite distributions are not significantly different from a negative binomial distribution, there may be limited cases where these PIHM methods can even be considered.

Finally, all of these methods assume that the truncation of a negative binomial distribution is due to PIHM, but previous studies have shown that a variety of other processes can lead to the truncation of a negative binomial distribution such as within host parasite density-dependence, age- dependent variation in host resistance and heterogeneous rate of infection (McCallum 2000; Anderson & Gordon 1982; Rousset *et al.* 1996). Therefore, even detecting "significant" PIHM in a dataset does not mean that PIHM is cause of the truncation.

Given these numerous caveats, is there a place in parasitology for methods that estimate PIHM from distributional data? We are in agreement with Lester (1984) that, at the very least, methods for estimating PIHM can provide prelim-

inary insight into whether or not PIHM is worth further exploration. However, we stress that these methods should only be used as an exploratory tool when assessing the role of PIHM in a system and potential users should critically evaluate whether they think they have a large enough sample sizes and an appropriate host survival function/post-mortality distribution for the methods developed in this paper to be applicable. Even if they are applicable, inferring PIHM from distributional data is no substitute for field or laboratory experiments and/or in depth understanding of the natural history of the host-parasite system under consideration.

Acknowledgments

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Table 1: Comparison of the PIHM predictions of previously used host-parasite datasets to those given by the Adjei Method and the Likelihood Method. The first column specifies the identity of the dataset, the second column specifies whether or not the author indicated that PIHM was occurring in the system, the third column indicates whether or not the Likelihood Method with parameters from the Crofton Method detects significant PIHM, and the final column indicates whether the Adjei Method with pre-mortality parameters estimated from the Crofton Method detects PIHM. If a method detected significant PIHM the predicted LD_{50} is given in parentheses

Data Set (sample size)	Author detected PIHM?	Likelihood Method?	Adjei Method?
Crofton, Station 1 ($n = 538$)	Yes	Yes (7.27)	Yes (9.33)
Crofton, Station 2 ($n = 507$)	Yes	Yes (6.92)	Yes (14.95)
Crofton, Station 3 ($n = 633$)	Yes	Yes (5.93)	Yes (5.98)
Crofton, Station 4 ($n = 486$)	No	No	Yes (7.99)
Crofton, Station 5 ($n = 276$)	No	No	Yes (10.58)
Crofton, Station 6 ($n = 191$)	No	No	No
Adjei, *S. tumbil* female ($n = 446$)	Yes (5.7)	No	Yes (6.37)
Adjei, *S. tumbil* male ($n = 452$)	Yes (3.4)	Yes (3.42)	Yes (3.66)
Adjei, *S. undosquamis* female ($n = 2573$)	Yes (3.2)	Yes (3.04)	Yes (3.11)
Adjei, *S. undosquamis* male ($n = 2440$)	Yes (1.8)	Yes (1.83)	Yes (1.78)

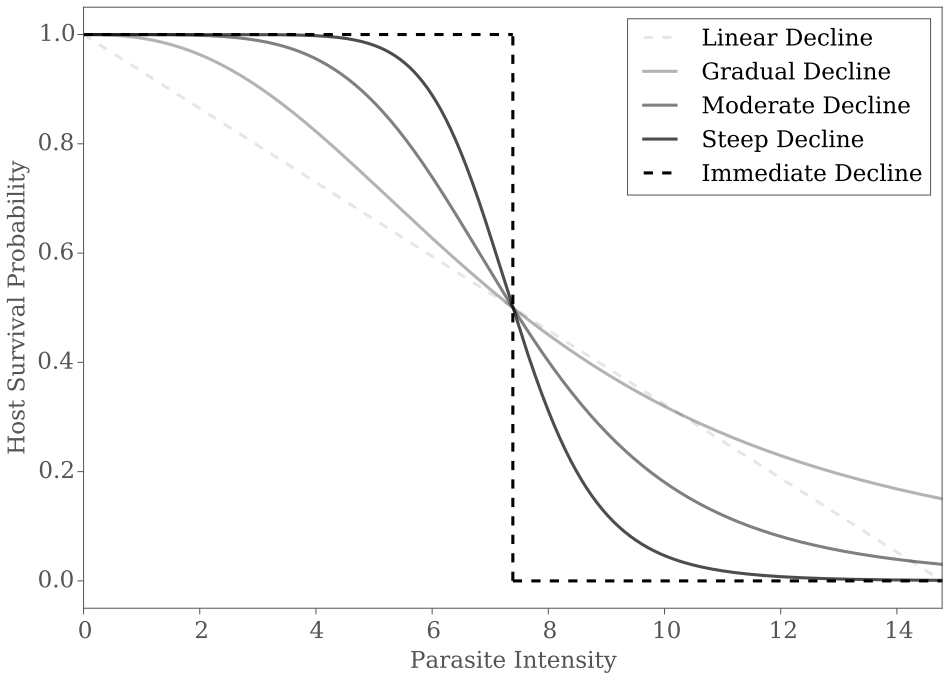

Figure 1: Five potential shapes for a host-survival functions. PIHM should be easier to detect for steeper host survival functions (Lanciani & Boyett 1989), but we may expect the bias in the parameter estimates to increase as it becomes increasingly difficult to distinguish between steep survival functions.

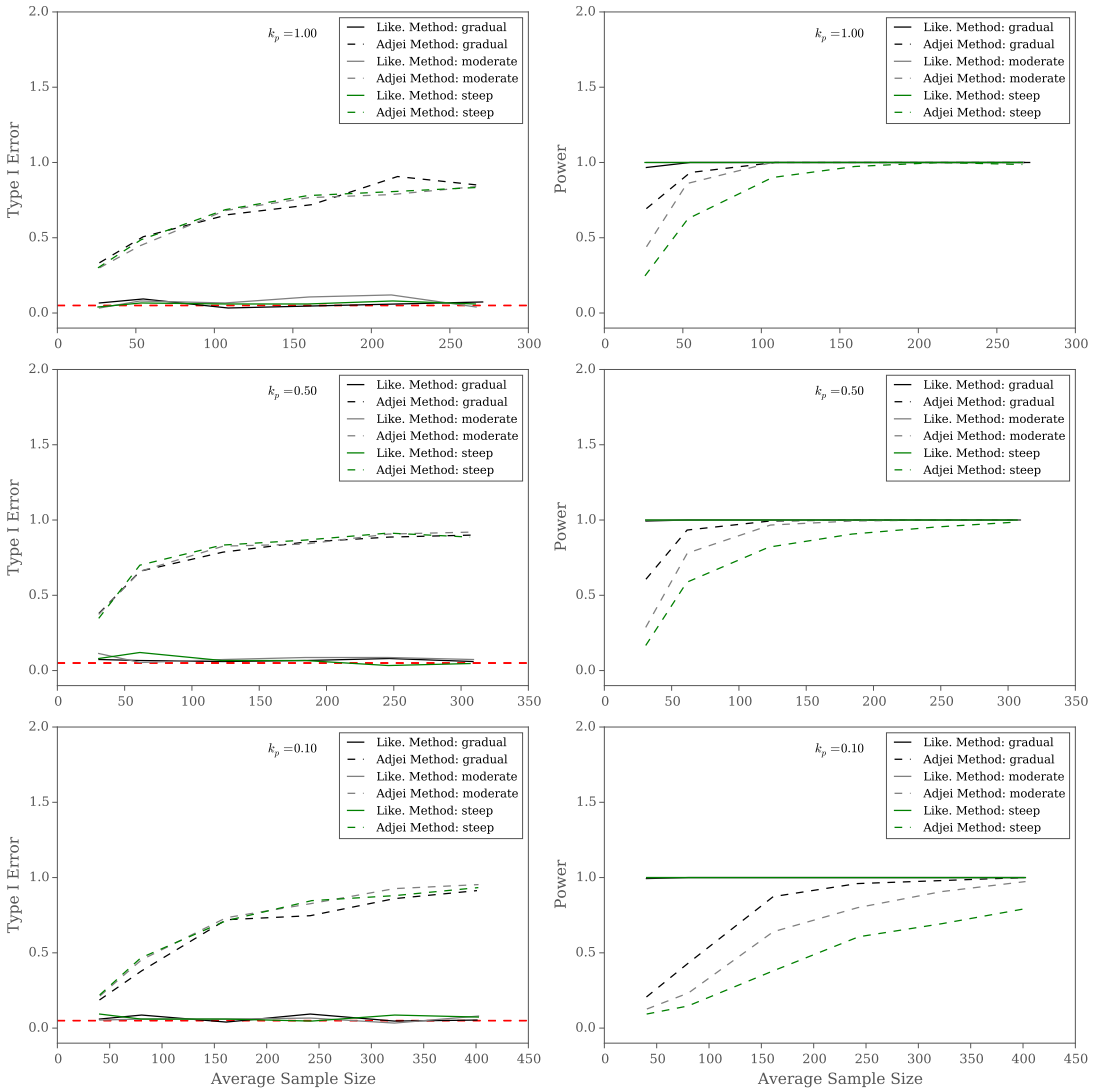

Figure 2: The Type I error rate and the power of the Likelihood Method (solid line) and the Adjei Method (dashed lines) when $\mu_p = 10$ for various shapes of the host survival function and levels of aggregation k_p. The first column gives the Type I error rate of each method for falsely detecting PIHM when none is present. The red line gives the the pre-set Type I error rate of $\alpha = 0.05$. The second column gives the power of a given method to detect PIHM when it is actually occurring.

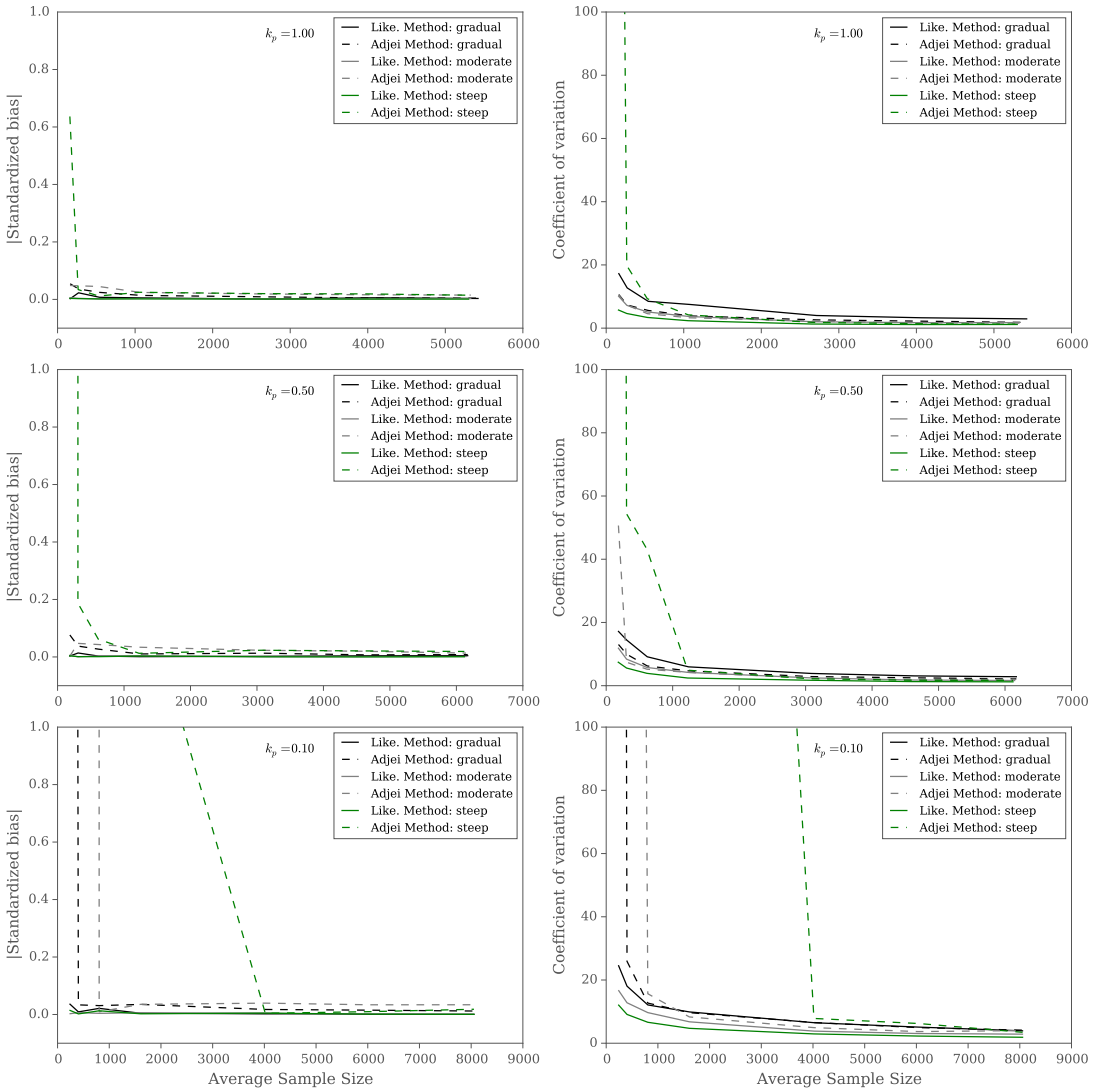

Figure 3: The bias and the precision of the Likelihood Method (solid line) and the Adjei Method (dashed lines) when $\mu_p = 10$ for various shapes of the host survival function and levels of aggregation k_p when estimating LD_{50}. The first column gives the bias of each methods LD_{50} estimate over 150 simulations. The second column gives the precision of each methods LD_{50} estimate over 150 simulations.

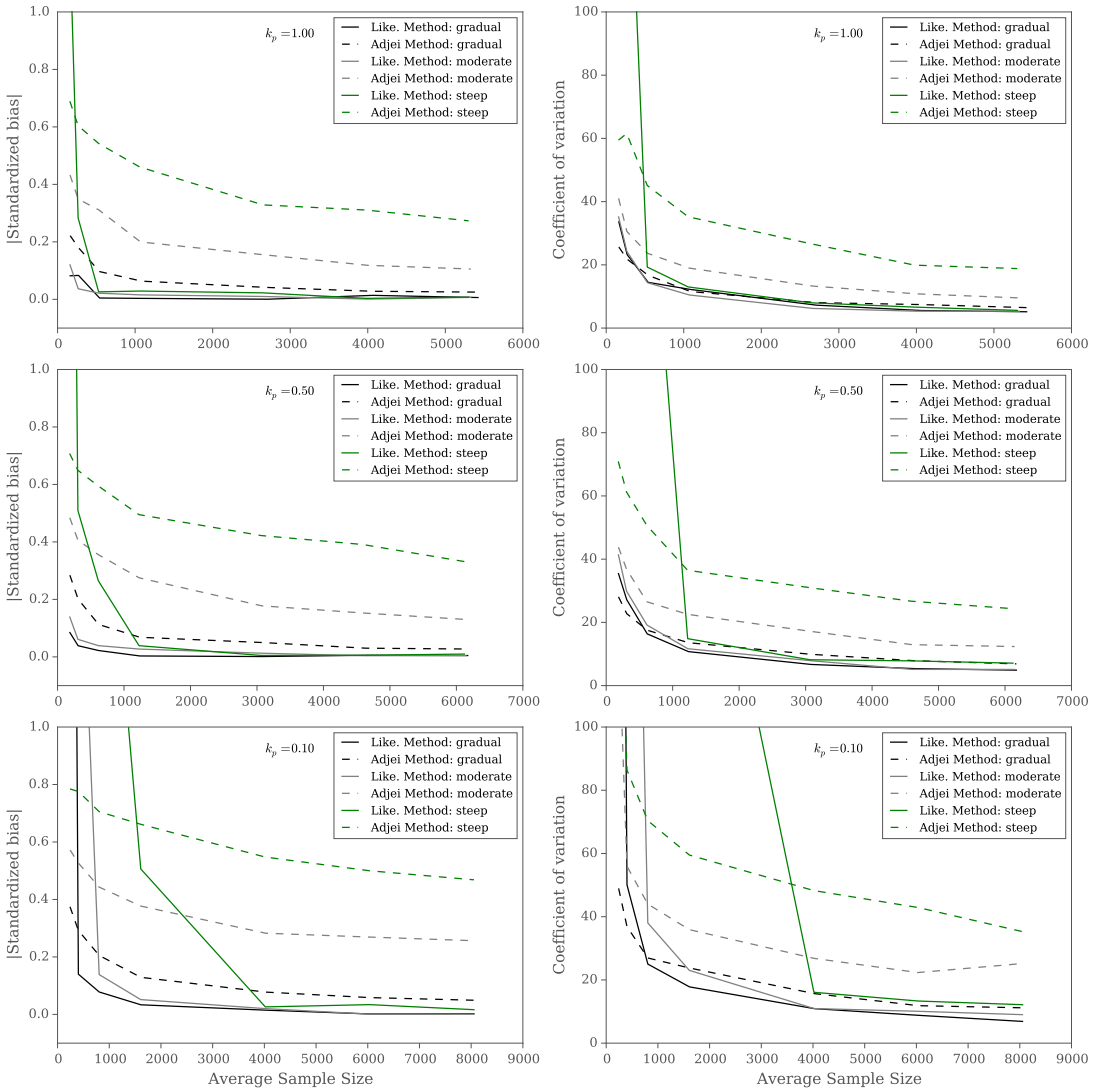

Figure 4: The bias and the precision of the Likelihood Method (solid line) and the Adjei Method (dashed lines) when $\mu_p = 10$ for various shapes of the host survival function and levels of aggregation k_p when estimating the a parameter of the host survival function. The first column gives the bias of each methods a estimate over 150 simulations. The second column gives the precision of each methods a estimate over 150 simulations.