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METHODOLOGICAL INSIGHTS

Clarifying the effect of toe clipping on frogs with Bayesian statistics

MICHAEL A. MCCARTHY*† and KIRSTEN M. PARRIS†
**Australian Research Centre for Urban Ecology, Royal Botanic Gardens Melbourne, South Yarra VIC 3141, Australia; and* †*School of Botany, University of Melbourne, Parkville VIC 3010, Australia*

Summary

1. Toe clipping is commonly used in population ecology to identify individual amphibians, particularly frogs and toads. Toe clipping may influence the return rate of the marked animals, although results of previous studies have appeared to be contradictory.
2. We re-analysed available data using Bayesian statistics to examine how the return rate of frogs may change with the number of toes removed.
3. Our re-analysis indicated that toe clipping reduces the return rate by 4–11% for each toe removed after the first, assuming the effect is the same for all toes.
4. A second analysis allowed the effect of removing each toe to change linearly with the number removed. This indicated that when one toe had already been removed, the return rate was reduced by 3·5% (95% credibility interval of 0–7%) upon removal of a second. The reduction in return rate on removal of an additional toe was 30% (95% credibility interval of 20–39%) when seven toes had already been removed.
5. When considering the cumulative effect of toe clipping, the return rate of frogs with two toes removed was estimated to be 96% of those with one toe removed. This ratio decreased to 28% for frogs with eight toes removed.
6. *Synthesis and applications.* We found that the effect of toe clipping on the return rate of amphibians increases with the number of toes removed. Because this effect is reasonably consistent among studies, the estimated impact should be recognized in future work that uses toe clipping to estimate population sizes and survival rates. In addition, our study has important implications for the ethical treatment of animals, the continued use of toe clipping to mark species of conservation concern, and the removal of multiple toes from an individual frog or toad.

Key-words: Bayesian statistics, estimation, mark–recapture, Markov chain Monte Carlo, null hypothesis testing, power

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Introduction

Many types of ecological studies require the unique identification of individuals, which is usually achieved by marking. Methods such as tattooing and banding are difficult to use on amphibians because of their particular anatomy and the nature of their skin (Halliday 1996). Perhaps the most common method of marking amphibians is toe clipping, in which a unique combination of digits (or part thereof) is removed from each individual (Hero 1989; Waichman 1992; Halliday 1996). For subsequent analysis, it is usual to assume that the method of marking does not influence the animal's survival or behaviour. A marking method that has adverse effects on the marked animals will violate this assumption and compromise the quality of the data, unless it is possible to account for these effects. In addition, there are ethical and conservation implications if animals are harmed.

The adverse impacts of toe clipping on amphibians, such as inflammation and infection of feet and limbs, and a reduction in the return rate of marked animals, have been reported in some cases (Clarke 1972; Humphries 1979; Golay & Durrer 1994; Lemckert 1996; Reaser & Dexter 1996; Williamson & Bull 1996) but not in others (Lemckert 1996; Williamson & Bull 1996). Parris &

Correspondence: Michael McCarthy, School of Botany, University of Melbourne, Parkville VIC 3010, Australia (fax + 61 39347 5460; e-mail mamcca@unimelb.edu.au).

McCarthy (2001) helped to resolve this apparent inconsistency by demonstrating that absences of statistically significant effects in some previously published studies could be attributed to a lack of statistical power rather than absences of actual effects. Based on fitted regression lines, we estimated that return rates declined by 6–18% for each toe removed after the first (Parris & McCarthy 2001). However, this analysis did not provide meaningful confidence intervals for the estimate, or analysis of how the impact of toe clipping might change with the number of toes removed.

Here, we present a Bayesian reanalysis of the data used by Parris & McCarthy (2001). A Bayesian analysis uses a model to combine prior information with new data to produce updated estimates of the parameters (Hilborn & Mangel 1997; Wade 2000; Link *et al*. 2002). The model defines how the parameter of interest (in this case the effect of toe clipping) is related to the data. In the present study, we developed statistical models that define the relationship between the number of frogs that are recaptured and the effect of toe clipping as a function of the number of toes removed. We demonstrated the relatively simple implementation of our analysis using WinBUGS, a freely available program developed by researchers at the MRC Biostatistics Unit and Imperial College, London, UK (Spiegelhalter *et al*. 2003). We also extended the analysis by permitting the influence of toe clipping to increase or decrease with the number of toes removed. The results presented here illustrate one way that biologically reasonable models with a focus on parameter estimation can help to clarify the results obtained in ecological studies.

Methods

DATA

The data were obtained from four previously published studies of the influence of toe clipping on the return rate of frogs (Parris & McCarthy 2001). Williamson & Bull (1996) studied 1333 individuals of *Crinia signifera*, with up to seven toes removed from each individual. *Crinia signifera* is a small ground-dwelling frog from eastern Australia that grows up to 30 mm snout–vent length (SVL). Lemckert (1996) also studied *C. signifera*, with 306 individuals and between two and four toes removed from each individual. Clarke (1972) reported the effect of removing up to eight toes from 733 individuals of *Bufo fowleri*, and Lüddecke & Amézquita (1999) reported effects of toe-disk clipping on the return rate of 1307 individuals of *Hyla labialis*, with up to seven toe-disks removed from each individual. *Bufo fowleri* is a relatively large ground-dwelling frog from the eastern USA (up to 80 mm SVL), while *H. labialis* is a medium-sized tree frog from the Colombian Andes (up to 55 mm SVL). Extra information was available in some of the studies, such as the return rate for different sexes and years, and different size and age classes. This extra information was used in the statistical analysis to account for some of the variation in the data (see Statistical models below for details of each study).

STATISTICAL MODELS

Logistic regression

The original statistical model used by Parris & McCarthy (2001) was based on logistic regression. This had the advantage over previous analyses (such as correlation analysis and linear regression) of accounting for the binomial nature of the data; each individual either returned or it did not, and the differences in sample sizes for different numbers of toes clipped could be accommodated. Logistic regression relates the return rate of frogs to the number of toes clipped using the formula:

$$\ln(R(n)/[1 - R(n)]) = A + Bn \qquad \text{eqn 1}$$

where $R(n)$ is the expected return rate of frogs that have had n toes removed, B is the regression coefficient for the effect of toe clipping and A is a value that may include terms for other covariates (such as yearly differences in return rate). When $B < 0$, the return rate decreases with the number of toes removed.

Equation 1 illustrates one of the disadvantages of using logistic regression, because the variable of most interest (the change in the return rate for each toe removed) is not included explicitly in the equation. The change in return rate can be estimated by examining how the predicted return rate changes with each additional toe that is removed beyond the first. However, in the analysis of Parris & McCarthy (2001) this procedure would lead to 87 different estimates of the effect of toe clipping, which would be difficult to interpret. Parris & McCarthy (2001) determined the change in return rate with each toe removed by inspecting the fitted regression lines. This provided useful information on the effect of toe clipping, but there was some subjectivity in estimating the magnitude of the effect, making it impossible to place meaningful confidence intervals on the estimate.

Model A

An alternative model can be developed by assuming that the return rate changes by a constant proportion for each toe removed. If the removal of a toe causes a constant change in the return rate (m), then the return rate will equal $R(0) \times (1 + m)$ following the removal of one toe. If a second toe is removed, this return rate ($R(0) \times (1 + m)$) will be further changed and the return rate will equal $R(0) \times (1 + m)^2$. It follows that the return rate following the removal of some number of toes (n) will equal $R(0) \times (1 + m)^n$. If there is a reduction in return rate due to mortality, m will be negative, $-m$ will equal the proportion of frogs that die following the removal of each toe, and $1 + m$ will be the chance of surviving the removal of a toe. If toe clipping causes a behavioural response such as aversion to recapture, or migration away from the site of initial capture, then m would be interpreted as the change in the probability of recapture (for each toe) given that the frog is alive. Positive values of m would indicate that removing toes increases the return rate, perhaps by making the individuals less mobile and more likely to remain in the study area. A value of zero for m represents no effect of toe clipping. Thus, the first model used in our reanalysis (model A) was:

$$R(n) = R(0) \times (1 + m)^n \quad \text{eqn 2}$$

To account for different return rates for different types of frogs, we estimated different values of $R(0)$ for frogs of different sizes, sexes and ages where such data were provided by the original authors. We also distinguished between individuals caught in different years to account for annual variation in return rates. For the data of Williamson & Bull (1996), we accounted for differences between juveniles, adult males and adult females in each of 3 years. For the data of Clarke (1972), we distinguished between large and small individuals. Lüddecke & Amézquita (1999; H. Lüddecke & A. Amézquita personal communication) provided us with their original data separated into each of 5 years, allowing us to account for differences among years and sex. Lemckert (1996) did not distinguish among different classes of *C. signifera*.

In addition to defining the return rate, we assumed that the fate of each individual in the same class (i.e. individuals with the same number of toes clipped, of the same age, etc.) was determined independently of the other individuals. As a result, the number of frogs recaptured was drawn from a binomial distribution, with variance equal to $NR(1 - R)$, where N is the number of frogs in the class that were marked and released, and R is their return rate.

Models B and C

In the above analysis we assumed that the influence of toe clipping was the same for each toe removed. However, the effect of removing a toe may be greatest for the first toe removed (diminishing impact) or the effect per toe may increase with each toe removed (increasing impact). It is possible to incorporate such a modification to equation 2. In this case, the effect of toe clipping may be expressed as:

$$R(n) = R(0) \times (1 + m_1) \times (1 + m_2) \times \ldots \times (1 + m_n) \quad \text{eqn 3}$$

where m_n is the change in return rate when removing the nth toe. We used a linear function to model the change in m, so $m_n = a + bn$. More complex functions could be used, but our choice has the advantages of simplicity and ease of interpretation. The estimated parameters for the chosen function were used to determine if there was an increasing or diminishing impact. In addition to analysing the data sets separately (model B), we also pooled the data from the four studies and estimated the values of m_n under the assumption that the parameters a and b were the same for all studies (model C).

BAYESIAN ANALYSIS

We used Bayesian methods in WinBUGS version 1.4 to analyse the data (Spiegelhalter *et al*. 2003). The WinBUGS code for the analyses is available at: http://www.nceas.ucsb.edu/~mccarthy/research.html, with one example provided in Appendix 1 (see Supplementary material).

Prior information in Bayesian analyses is represented by probability distributions for the parameters. We used uniform prior distributions to reflect a lack of previous data on the impacts of toe clipping. We chose not to incorporate reports of infection, anecdotal accounts and intuition that suggest that toe clipping does not increase return rates. In most cases, the results were not sensitive to this choice because the data did not indicate a possible positive effect of toe clipping on return rates. The upper bound on the change in return rate (m) was set to ensure that the return rate for the maximum number of toes clipped was not greater than 1; the lower bound on m was −1. The prior distribution was uniform between −1 and 1 for a, and between −0·2 and 0·2 for b. These limits for the prior distributions did not constrain the posterior distributions.

In addition to the models described above, we also analysed the logistic regression models used by Parris & McCarthy (2001), using uninformative normal priors (mean of 0 and SD of 1000) for the regression coefficients. The fit of the various models was compared using the deviance information criterion (DIC) as calculated in WinBUGS (Spiegelhalter *et al*. 2002). The lower the DIC value, the better the model fits the data.

WinBUGS was used to generate 100 000 samples from the posterior distributions for each of the analyses after discarding the initial 10 000 samples as a 'burn in'. The mean of each of the parameters was calculated, as was the 2·5th and 97·5th percentiles of the distribution. This interval was used to represent a 95% Bayesian confidence interval (95% credibility interval).

Results

For the analysis assuming a constant effect of toe clipping for each toe removed (model A), the results were broadly consistent with those of Parris & McCarthy (2001), with return rates reduced by approximately 4–11% for each toe removed (Fig. 1). There was strong evidence for a negative effect of toe clipping in the studies of Williamson & Bull (1996), Lüddecke & Amézquita (1999) and Clarke (1972), because the 95% credibility intervals were less than zero. This was equivalent to the conclusion of Parris & McCarthy (2001), who determined that the observed decline (or a larger decline) was

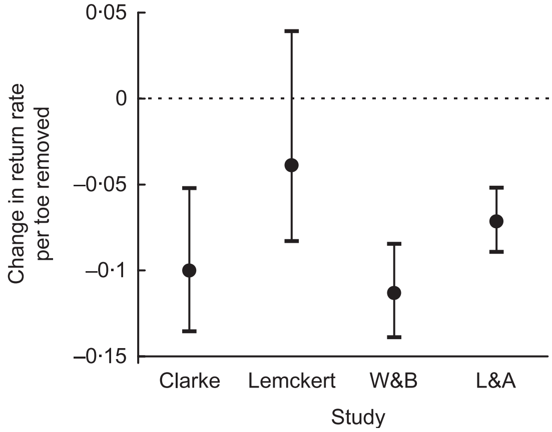

Fig. 1. Predicted change in return rate for each toe removed, with the four studies analysed separately [model A; Clarke 1972; Lemckert 1996; Williamson & Bull 1996 (W & B); Lüddecke & Amézquita 1999 (L & A)]. The circle is the mean of the posterior distribution and the bars represent 95% credibility intervals. Negative values represent an adverse effect of toe clipping.

unlikely to have occurred if the number of toes removed did not affect the return rate. For the study of Lemckert (1996), the negative mean provided some evidence that toe clipping reduces return rates (Fig. 1), although it is possible that there is no effect or that toe clipping increases return rates (the credibility interval encompassed zero). The wide credibility interval for this study was consistent with its low statistical power (Parris & McCarthy 2001).

By using credibility intervals to present the results, the predicted impacts of toe clipping can be compared with values that might be considered biologically important, not just statistically significant (Fig. 1). For example, we can be confident that the reduction in return rate was greater than 0·02 (equivalent to one frog not returning due to toe clipping for every 50 toes removed) for three of the four studies. In the case of Lemckert (1996), the results were also consistent with an impact of at least 1 in 50.

The analysis in which the effects of toe clipping were permitted to change with each toe removed (model B) provided evidence for increasingly negative effects with each toe removed in the studies of Williamson & Bull (1996) and Lüddecke & Amézquita (1999) (Fig. 2). The study of Clarke (1972) suggested an increasing impact, although the possibilities of no impact or a declining impact could not be eliminated given the width of the credibility intervals. The data from Lemckert (1996) provided little insight into this particular question, with few data to indicate a trend and relatively wide credibility intervals.

The influence of toe clipping on return rates appeared to be relatively consistent across the different studies, because the credibility intervals for the different studies largely overlapped (Fig. 2). Thus, model C seemed to be appropriate for the data. Removing the second toe was estimated to reduce recapture rates by approximately

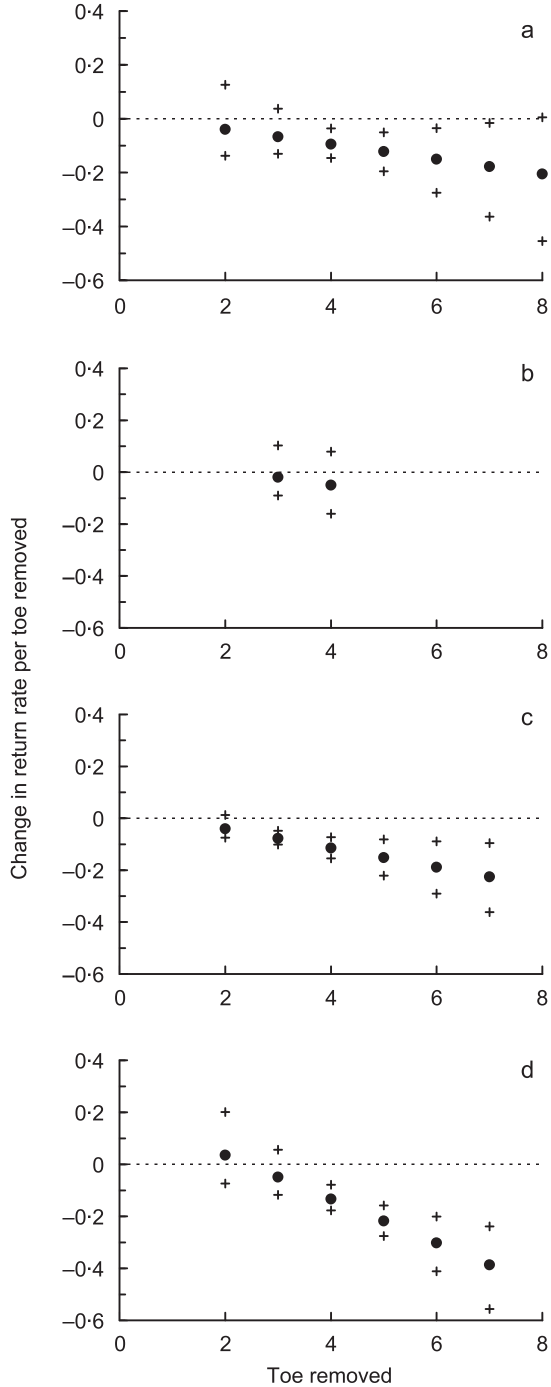

Fig. 2. Predicted change in return rate for each toe removed, allowing for linear changes in the effect of toe clipping with each toe removed (equation 3, model B): (a) Clarke (1972); (b) Lemckert (1996); (c) Williamson & Bull (1996); (d) Lüddecke & Amézquita (1999). Circles are the means of the posterior distribution and the crosses represent the limits of the 95% credibility intervals. Negative values represent an adverse effect of toe clipping.

3·5% ($m_2 = -0{\cdot}035$), with the impact increasing to approximately 30% for the eighth toe ($m_8 = -0{\cdot}3$) (model C). These impacts were in addition to the effect of removing previous toes. Because the 95% credibility interval for toe number two had an upper bound of approximately zero, it is possible that removing a second toe could

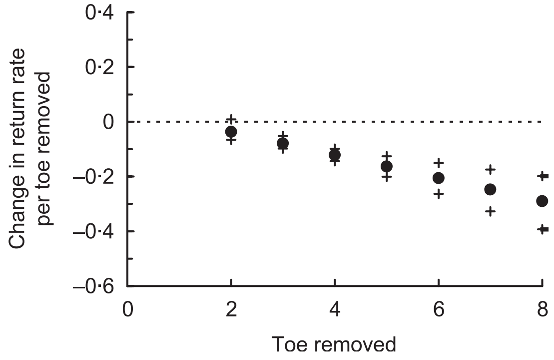

Fig. 3. Predicted change in return rate for each toe removed, allowing for linear changes in the effect of toe clipping with each toe removed (equation 3, model C). Data were pooled from the four studies in Fig. 2. Circles are the means of the posterior distribution and the crosses represent the limits of the 95% credibility intervals. Negative values represent an adverse effect of toe clipping.

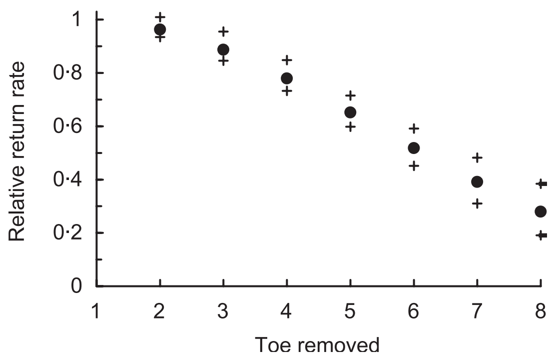

Fig. 4. Predicted return rate of frogs with more than one toe removed relative to those with one toe removed, allowing for linear changes in the impact of toe clipping with each toe removed. Data were pooled from the four studies in Fig. 2. Circles are the means of the posterior distribution and the crosses represent the limits of the 95% credibility intervals.

have a negligible effect on the return rate. There are no animals in the data sets without toes removed, so it is not possible to estimate the impact of removing the first toe. Extrapolation suggests this impact may be small (Fig. 3), although this should be regarded as speculative because we cannot be sure that the relationship is even approximately linear beyond the range of the data.

The results in Fig. 3 (which are on a per toe basis) were also expressed in terms of the cumulative effect of toe clipping by plotting $R(n)/R(1)$ vs. n using the relationship in equation 3 (Fig. 4). This demonstrated how, relative to those with one toe removed, the return rate of animals with n toes removed decreases with toe clipping. Expressing the results in this form, rather than including the effect of removing the first toe, avoided extrapolation beyond the range of the data (Fig. 4). Thus, the return rate of frogs with two toes removed was estimated to be approximately 96% of those with one toe removed. This ratio decreased to 65% for frogs with five toes removed and 28% for those with eight toes removed. The precision of these estimates decreased as the number of toes clipped increased, with the range of the 95% credibility intervals being 7% for two toes and 18% for eight toes.

Table 1. Deviance information criteria (DIC; Spiegelhalter *et al.* 2002) indicating the goodness-of-fit of the original logistic regression of Parris & McCarthy (2001) and the three new models (models A, B and C)

Model	DIC
Logistic regression	532·6
A, constant effect of toe clipping	522·9
B, changing effect varying among studies	506·2
C, changing effect consistent across studies	507·2

Models B and C, in which the effect of toe clipping increased with each toe removed, fit the data better than model A, based on the calculated DIC values (Table 1). Model A in turn provided a better fit than the original logistic regression model of Parris & McCarthy (2001).

Discussion

The return rate following marking is the product of the probability of survival and the probability of recapturing an animal that is alive. Thus, the observed changes in return rate following removal of the second and subsequent toes are due to changes in the probability of survival, changes in the probability of recapture conditional on survival, or both. Reductions in the probability of survival (Clarke 1972; Humphries 1979; Williamson & Bull 1996) may result from infection, a reduction in the mobility or dexterity of marked animals, and a consequent increased susceptibility to predation or starvation. A number of studies have observed infection of feet and limbs following toe clipping (Clarke 1972; Humphries 1979; Golay & Durrer 1994; Lemckert 1996; Reaser & Dexter 1996; Williamson & Bull 1996). Reductions in the probability of recapturing living, marked animals may result from changes in their behaviour such as reduced activity or a propensity to leave the study area following toe removal (an anti-predator response; Lemckert 1996).

A change in the return rate of marked individuals following toe clipping invalidates one of the basic assumptions of mark–recapture studies, unless this effect is known and accounted for in subsequent analyses (Donnelly & Guyer 1994). Mark–recapture analyses that estimate recapture and survival probabilities could incorporate the effects of toe clipping by including the number of clipped toes as a covariate. The results of our analyses should be included in future studies that use population data based on toe clipping of frogs and toads. For example, the predicted change in return rate with each toe removed (Fig. 3) could be used as a model against which alternative models (e.g. with no change in return rate following toe clipping) could be compared.

The results of our reanalysis of published data on the effects of toe clipping on the return rate of frogs are consistent with those of Parris & McCarthy (2001).

However, the present reanalysis also suggests that apparent differences among previous studies in the effect of toe clipping on return rates may be due to the different number of toes that were removed from individual animals. The model with a consistent, linear change in the effect of toe clipping with each toe removed (model C) demonstrated that the impact of clipping each toe increases as more toes are removed, corresponding to a rapidly compounding effect on the behaviour and/or survival of the marked frogs. Frogs have 18 toes in total, four on each of the fore feet and five on the hind feet. As well as assisting with balance and locomotion, the enlarged, adhesive disks on the toes of many tree frogs enable them to climb steep or vertical surfaces. It is perhaps not surprising that the fewer the toes a frog still possesses, the greater the effect of removing one more could have on its probability of return.

The observed changes in the survival and/or behaviour of frogs following toe clipping raises concerns about the ethics of using the technique for mark–recapture studies, particularly if the study species is endangered or a large number of toes is removed. These ethical concerns are magnified if possible biases in the data are ignored, thereby reducing their scientific value. The recommendations made by Parris & McCarthy (2001) for minimizing the impacts of toe clipping on individual animals remain relevant. Of particular importance will be the use of a planned marking scheme, such as those suggested by Hero (1989) and Waichman (1992), to minimize the number of toes that are removed.

In addition to providing data for estimating the survival rate and movement of individuals, toes clipped from frogs can provide material for genetic analysis and bone for skeletochronology for estimating age (Friedl & Klump 1997; Driscoll 1998; McGuigan *et al*. 1998). Usually only one toe is required for the latter two purposes, so the impact on individuals and the population is likely to be substantially less than that of studies that require the removal of multiple toes. While it is not possible to comment on specific situations, the scientific and conservation benefits of marking frogs with toe clipping need to be weighed against the likely impacts that we have identified in this study, and the possible impacts of alternative marking methods.

The statistical models we used are relatively simple representations of possible effects of toe clipping. More complex models could be developed, although we do not believe they are necessary for the purpose of exploring our particular questions. Despite their relative simplicity, most standard statistical packages cannot be used to analyse the statistical models in this study. By using the program WinBUGS, we were able to design specific models rather than relying on the statistical models that are available in standard software packages. WinBUGS is freely downloadable and relatively user-friendly. Some experience with computer programming is useful when using WinBUGS, although there is also a graphical user interface for constructing the models, reducing the need for programming skills. Further, the program includes examples for numerous different statistical models, making it relatively easy to learn the WinBUGS language.

Our results illustrate how the regression models and extensive power analyses of Parris & McCarthy (2001; which required 24 figure panels and several tables) can be represented simply within a single figure by using a relevant statistical model and focusing on parameter estimation rather than significance testing (Fig. 1). Bayesian methods are sometimes criticized because of the possibility of subjectivity in defining the prior distributions (Oakes 1986). We avoided this problem to some degree by using flat priors that did not constrain the width of the posterior distribution, making the results numerically similar to a likelihood-based analysis (Link *et al*. 2002). Likelihood-based methods could also be used to analyse the models in this study (Anderson, Burnham & Thompson 2000; Burnham & Anderson 2002). While we acknowledge there is debate about which statistical approach is the most appropriate for particular circumstances (Oakes 1986; Anderson, Burnham & Thompson 2000; Johnson 1999, 2002; Robinson & Wainer 2002), our results support calls for a greater emphasis on estimation rather than null hypothesis significance testing. As we found with our reanalysis, focusing on parameter estimation can clarify the representation and interpretation of the statistical analysis. We recommend this approach because of its relevance, robustness and relative simplicity.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE919/JPE919sm.htm

Appendix 1. An example of the WinBUGS code used to generate the results presented in Fig. 1.

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