Counter culture: Causes, extent and solutions of systematic bias in the analysis of behavioural counts

Supplementary Material

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Contents

S1   Refractory Period and Stochastic Error

A Poisson process assumes an exponential distribution of inter-visit intervals (IVIs), which is a specific formulation of the gamma distribution. The gamma distribution can be described by two parameters α and β; in an exponential distribution the α parameter is fixed to 1 (Figure S1A). This results in a modal IVI of 0. When observing such a process for a certain observation period (t), the mean number of observations ($\bar{y}$) is calculated as

$$\bar{y} = \frac{t}{\mu} \tag{S1}$$

, where μ is the mean IVI. The stochastic error (σ_y) is

$$\sigma_y = \frac{t}{\alpha\mu} \tag{S2}$$

. Thus when $\alpha = 1$, as under a Poisson process, then the stochastic error is equal to the mean. This corresponds to a Poisson distribution of observations (Figure S1B).

In many scenarios it seems likely that the probability of very short IVIs would be low (i.e. modal IVI > 0), for example if there is a minimum realistic time in which a bird could find food. This can be described as there being a refractory period. Such distribution of IVIs would be described by a gamma distribution where $\alpha > 1$. Therefore, for the same μ (and $\bar{y}$), as α increases, the stochastic error decreases (Figure S1A). α describes the refractory period in terms of the expected interval length. When $\alpha = 2$ the refractory period is an average IVI long, and when $\alpha = 3$ the refractory period is 2 IVIs long, etc. The refractory period itself can be more intuitively thought of as the mode of the gamma distribution, $((\alpha - 1)/\beta)$, as this given a quantification in terms of a time period.

Using simulated data, we can demonstrate how stochastic error decreases with the presence of a refractory period, when the mean, and so observed number of visits, remains constant. We simulated visit data from a gamma distribution, with a mean IVI (μ) of

5 minutes, varying α. Assuming a total observation time (t) of 90 minutes, we counted all visits from intervals whose cumulative sum was less than or equal to 90, and repeated this 100 times to create 100 observations. Figure S1 shows the gamma distribution from which the intervals were simulated (Figure S1A) and the resulting the number of observations (Figure S1B). The mean number of observations is constant (here 18), regardless of the changing α, whilst the stochastic error decreases as a function of α (Figure S1D).

This process can be easily described with the Tweedie distribution, the variance of which is defined as

$$\sigma_y = \phi \bar{y}^\xi \tag{S3}$$

Therefore when $\xi = 1$ and $\phi = 1/\alpha$, the Tweedie distribution can be used to estimate the stochastic error. This is shown in Figure S1C.

For this to be used a population level α would have to be estimated and specified in the model. If the model was allowed to estimate ϕ, then it would include any residual or over-dispersion variance, and so would not be able to be used to estimate α.

In the main text, we mention that if the refractory period, and so α, is small then assuming Poisson distributed error results in less bias in effect size estimation than assuming no stochastic error. As the stochastic error is scaled by $1/\alpha$, we can see that when $1 \leq \alpha < 2$, the stochastic error will be closer to Poisson distributed error than zero, whilst if $\alpha > 2$ assuming no Poisson-distributed stochastic error would induce less bias than assuming Poisson-distributed stochastic error (although would still result in the underestimation of effect sizes). As can be seen from Figure S1A, when $\alpha > 2$ the refractory period is quite pronounced; this is not the case in distributions of inter-visit intervals from published studies (see text for references).
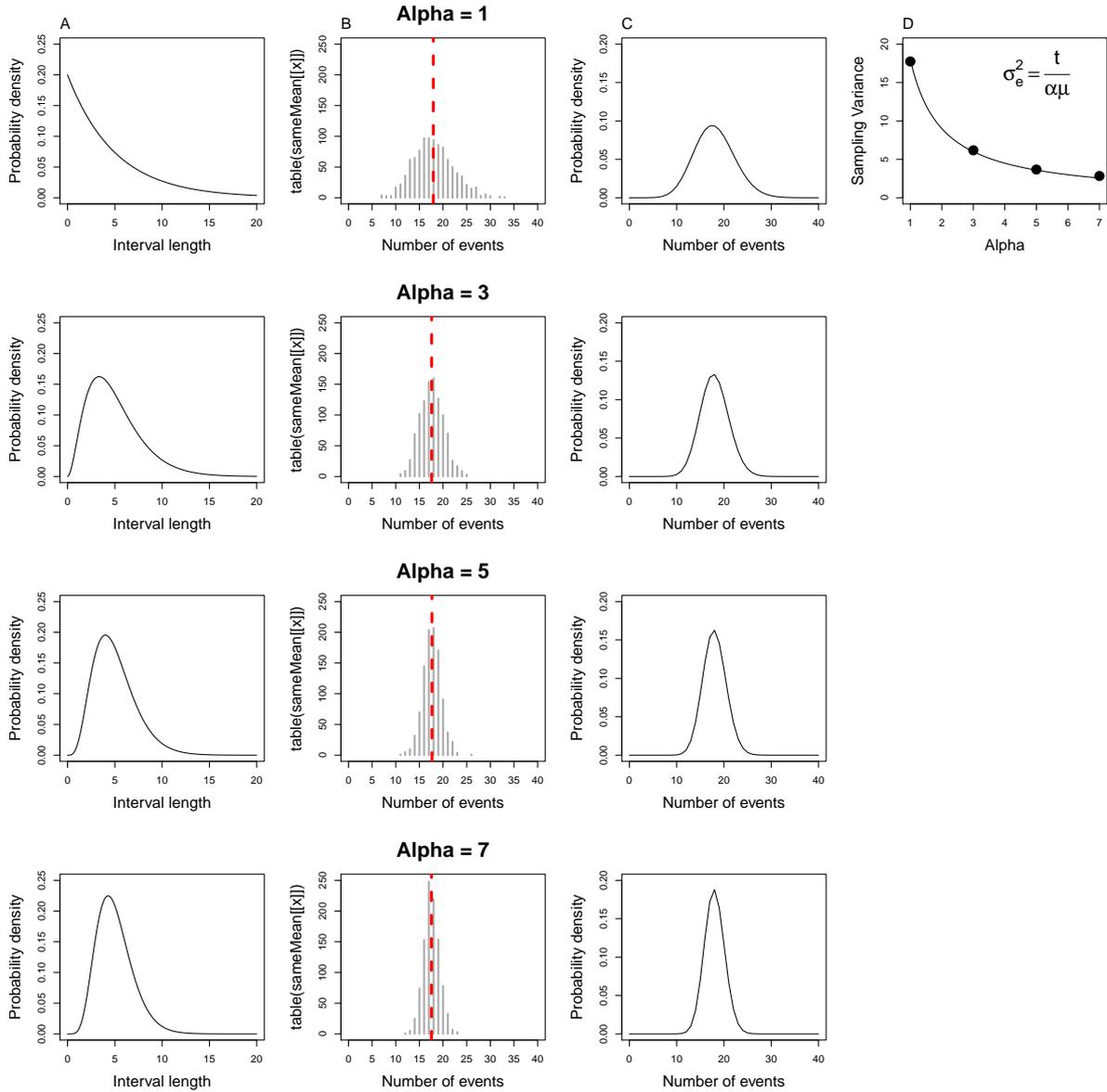
Figure S1: Effect of a refractory period on Poisson-distributed stochastic error. A) shows the gamma distributions from which inter-visit intervals were simulated, with varying values of alpha. B) shows the corresponding distributions of observation numbers from sampling these distributions over a 90 minute period. C) shows the probability density function from a Tweedie distribution that would best describe the distribution of counts arising from these gamma distributions of IVIs. D) shows the relationship between alpha and the resulting stochastic error; the points are from the simulated datasets, line represent theoretical expectations.

S2 Demonstrating provisioning as a Poisson process using the data of Lendvai et al. 2015

In a recent study, Lendvai *et al.* (2015) demonstrated that, as observation periods increase, the correlation between number of visits in the observations and in the whole day increases. We can use this data (Lendvai *et al.* 2015 Supplementary Materials) to further demonstrate how provisioning data matches the assumptions a Poisson process. Lendvai *et al.* (2015) measured provisioning over the course of a whole day, broken up into the number of visits per 15 minute period. We subset their data to include records from 10:30 to 20:45; we discarded data before this time period, as there was a high proportion of individuals with missing data, and after this time as most individuals had stopped provisioning (Fig S2A and B). This left us with 41, 15 minute observation periods, of 128 individuals.

With this data set we combined adjacent 15 minute time blocks to create new, longer, observation periods, i.e. to make 30 minute observations, we combined pairs of adjacent time blocks to make 20 new 30 minute time blocks. We did this to create observation periods increasing in length by 15 minutes, up to 615 minutes (i.e. 41 *15 minutes). Depending on the length of the observation period, we could not use all the time blocks (i.e. if the length of the new observation period did not divide exactly into 615 minutes). We therefore preferentially took observation from the latter part the day, as there were less missing values here (see Figure S2C).

To calculate the observed coefficient of variation ($CV = \sigma_y/\bar{y}$), for each observation period we pooled the new data and calculated CV across this data. Using the observed CV (CV_{obs}) and mean ($\bar{y}$) across different observation periods, we estimated the expected CV

(CV_{exp}) using a nonlinear model with the `nls` function in R with the form

$$CV_{obs} = \frac{\sqrt{\bar{y} + (\bar{y}CV_{exp})^2}}{\bar{y}} \tag{S4}$$

The predictions from this model are plotted in Figure 2B.

To calculate repeatability, we use these new observation periods as repeated measures, and calculated repeatability across the new data, in a linear mixed model, with individual ID as a random effect, using the *lme4* package in R (Bates *et al.*, 2015). Repeatability was then calculated as individual variance / (individual variance + residual variance). This was only possible for observation periods up to 300 mins, as at least two time blocks were needed to estimate repeatability. Using the observed repeatability (ICC_{obs}), mean $(\bar{y})$ across different observation periods and the expected CV (CV_{exp}) as calculated above, we estimated the true repeatability (ICC) using a nonlinear model with the form

$$ICC_{obs} = \frac{ICC\bar{y}CV_{exp}^2}{1 + \bar{y}CV_{exp}^2} \tag{S5}$$

The predictions from this model are plotted in Figure 2D.
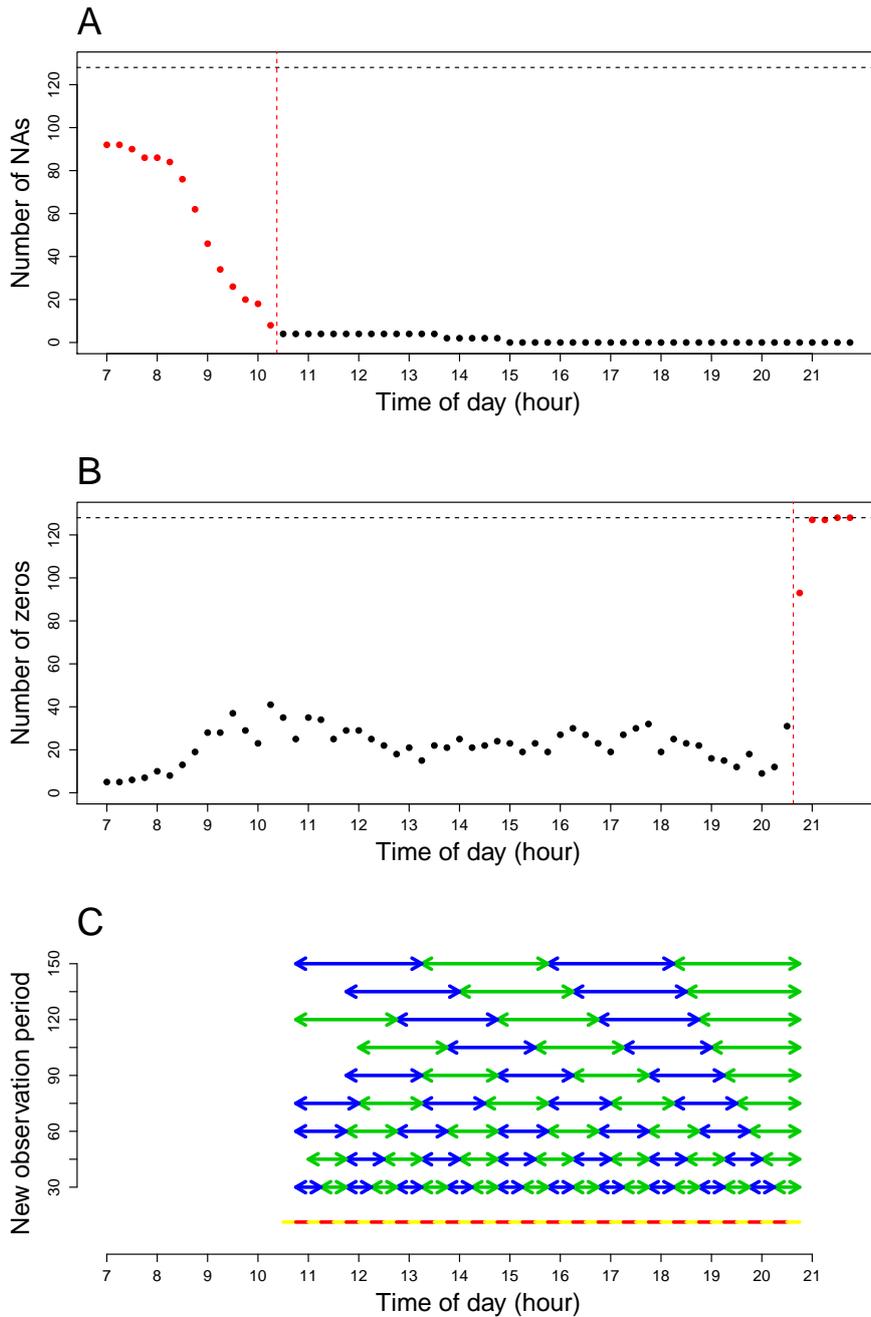
Figure S2: Selection and manipulation of data from Lendvai et al. 2015. A) and B) show time periods that were excluded because of A) high level of missing data and B) high level of individuals that had stopped provisioning. Red points are those that were excluded. Black dotted line shows total number of individuals. C) shows how new observation periods were made; the red and yellow line shows that 15 minute observation periods, and the blue and green line show how there were combined to make longer observation periods.

S3 Studies Included in Literature Survey

The reference numbers refer to the study reference in table S1.

5. Blas, J., Abaurrea, T., D'Amico, M., Barcellona, F., Revilla, E., Roman, J. & Carrete, M. (2016) Management-related traffic as a stressor eliciting parental care in a roadside-nesting bird: the european bee-eater *Merops apiaster*. *Plos One*, **11**, e0164371.

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11. Barger, C.P., Young, R.C., Will, A., Ito, M. & Kitaysky, A.S. (2016) Resource partitioning between sympatric seabird species increases during chick-rearing. *Ecosphere*, **7**, e01447.

19. Auer, S.A., Islam, K., Wagner, J.R., Summerville, K.S. & Barnes, K.W. (2016) The diet of cerulean warbler (*Setophaga cerulea*) nestlings and adult nest provisioning behaviors in southern indiana. *Wilson Journal Of Ornithology*, **128**, 573-583.

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38. Liebl, A.L., Browning, L.E. & Russell, A.F. (2016) Manipulating carer number versus brood size: complementary but not equivalent ways of quantifying carer effects on offspring. *Behavioral Ecology*, **27**, 1247-1254.

40. Endo, S. & Ueda, K. (2016) Factors affecting female incubation behavior in the bullheaded shrike. *Ornithological Science*, **15**, 151-161.

42. Dzielski, S.A., Van Doren, B.M., Hruska, J.P. & Hite, J.M. (2016) Reproductive

biology of the Sapayoa (*Sapayoa aenigma*), the "old world suboscine" of the new world. *Auk*, **133**, 347-363.

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S4   Simulations

We ran simulations to demonstrate the difference between analysing provisioning rate when correcting and not correcting for Poisson-distributed stochastic error, with provisioning rate as both response and predictor variables, across different mean number of observed visits. For each mean, we simulated a dataset of 100 observations of provisioning rate with an expected CV of 0.3. For provisioning as a response variable, we simulated provisioning rate being affected by a single variable, which accounted to 50% of variation in provisioning rate on the expected scale ($R^2 = 0.5$). We ran two models; a linear model and a GLMM with Poisson error distribution and observation level random effect, the latter using the *lme4* package in *R* (Bates *et al.*, 2015). Both models included the observed number of visits as a response variable. For provisioning as a predictor variable, we simulated provisioning rate explaining 50% of variation in a another variable, on the expected scale ($R^2 = 0.5$). Again we ran two models; a linear model and a measurement error model, the latter using *Stan* (Carpenter *et al.*, 2017). Both models had number of visits as a predictor variable, but the measurement error model accounted for the uncertainty in observed number of visits. In both cases R^2 was calculated as

$$\frac{\sigma_f^2}{\sigma_f^2 + \sigma_r^2} \tag{S6}$$

where σ_f^2 is the variance due to the fixed effects calculated following Nakagawa & Schielzeth (2013) and σ_r^2 is the residual variance, which in the GLMM was the variance associated with the observation level random effect. All code for these simulations can be found at https://doi.org/10.5281/zenodo.7439115.

In order to explore the conditions under which we might see increased bias and lower precision, we again simulated provisioning rate as a response variable, being affected by a single variable, with an R^2 of 0.5 (θ). In these simulations we also varied the expected CV. For each expected CV and mean combination we simulated 1000 datasets, of 100
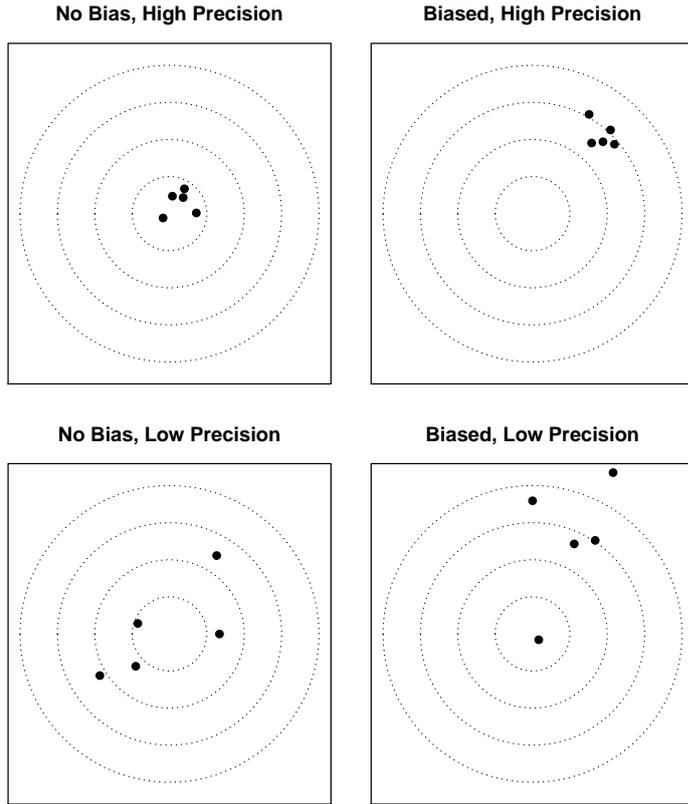
Figure S3: Bias and Precision

observations. For each dataset, we ran a GLMM with Poisson error distribution and observation level random effect, and estimated R2 $(\hat{\theta})$. Bias was calculated as $\theta - E(\hat{\theta})$, precision as $1/\sigma_{\hat{\theta}}$. Bias is measure of whether, and how much, estimates differ from the true value, whilst precision is a measure of variability in the estimates. This is shown graphically in Figure S3

For these latter simulations, we also calculated expected CV from the simulated datasets, following the equations in Box 2 to explore the conditions under which expected CV cannot be calculated, shown in Figure II.

S5 Calculating CV of expected rates

To calculate the expected CV, we can use the mean ($\bar{y}$) and variance of the observed number of arrivals (σ_y^2) in a population:

$$CV_{exp} = \frac{\sqrt{\sigma_y^2 - \bar{y}}}{\bar{y}} \tag{S7}$$

This formula works specifically for observations of the same length. When observation periods differ this can be accounted for by removing the variation due to observation period (t)

$$\hat{y} = y\bar{t}/t \tag{S8}$$

where $\hat{y}$ is the adjusted arrival rate. Here we have derived a rate, but importantly we have kept the mean number of visits the same. $\hat{y}$ can then be substituted into equation 3, in place of y.

Once the number of observed arrivals are transformed to a different scale (e.g. the number of arrivals is standardised to arrivals/hour) equation S7 is no longer valid, as Poisson distributed stochastic error does not scale in the same way as the expected variance in arrival rates. Therefore, the mean no longer represents the stochastic variance. Imagine a 120 min observation period with a mean of 20 ± 8 arrivals; the expected CV would be calculated as 0.332. However, when transformed to arrivals/hour, the mean±SD becomes 10±4 arrivals/hour, and expected CV is calculated as 0.245, as we are overestimating the amount of Poisson sampling error. In order to estimate the true expected CV, the mean and SD of number of observed arrivals should therefore be back transformed to the scale on which the data was collected (i.e. by multiplying by the mean observation period; $\bar{t}$). This allows us to see why using rates instead of observed counts in a Poisson models results in an under- or overestimation of effect size. The model estimates the stochastic error based on the counts it is presented with. When the scale is changed, the model does

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this incorrectly - if the counts are smaller than those observed, as in the example above, the stochastic error is overestimated, and so are effect sizes (Supplementary Material S6).

It is also important to note that when the mean number of observed visits is low, the estimation of expected CV may not be possible. As the variance is so dominated by stochastic error, random fluctuations in this error (induced by sampling error) can lead to the mean being larger than the variance meaning that $\sigma_y^2 - \bar{y}$ is negative. We can see this pattern in both simulated data, and in data from the literature review (Figure S4). Moreover, this is likely why we see an upward bias in effect size occur in the Poisson models, as the residual (i.e. expected) variance is underestimated.
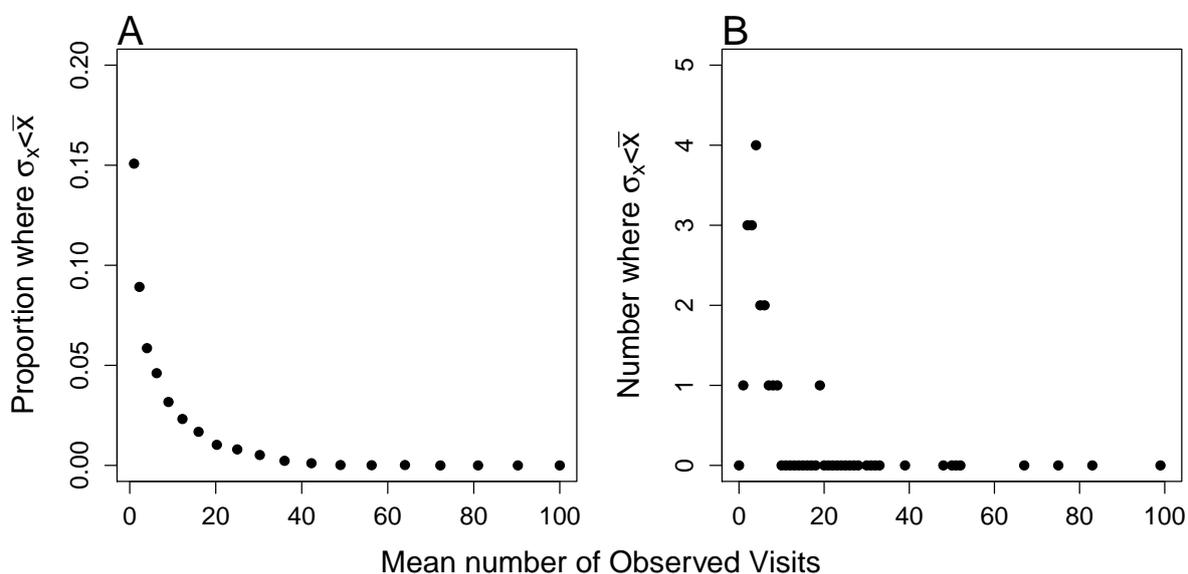

Figure S4: The proportion of samples in which the mean is greater than the variance declines with increasing mean number of observed arrivals, in both A) simulated and B) observed data (from literature review). In B) the mean number of observed arrivals is rounded to the nearest integer. See Supplementary Material S5 for further details of simulations.

S6 Tutorial - Analysing Provisioning Data

Data for this tutorial is included in supplementary files S7, S8 and S9.

S6.1 Exploring Provisioning Rate

Imagine we have collected some provisioning data; we observed 100 nests, each 3 times for 2 hours. Using R, lets find out some properties of this provisioning data (`id` is the nest ID, `visits` is the number of visits observed and `time` is the observation time)

```r
data_ICC <- read.csv("S7_data_ICC.csv")
head(data_ICC)
```

```
##   id visits time
## 1  1     24    2
## 2  1     13    2
## 3  1     24    2
## 4  2     23    2
## 5  2     13    2
## 6  2     27    2
```

```r
plot(table(data_ICC$visits), xlab="Number of visits", ylab="Frequency", xaxt="n")
axis(1,seq(5,60,5))
```
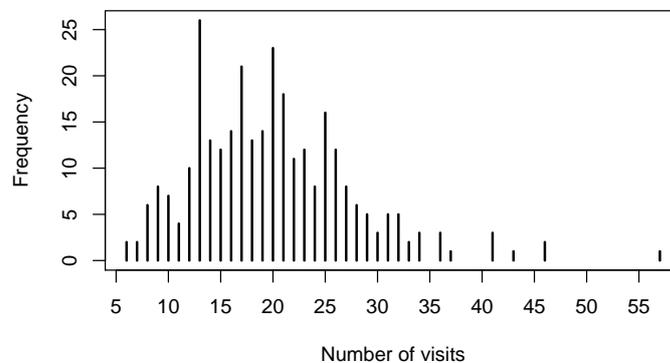
```
c(mean = mean(data_ICC$visits), variance = var(data_ICC$visits))
```

```
##     mean variance
## 19.94333 57.65230
```

We know that the stochastic error is equal to the mean, so we can calculate the variance in expected provisioning rates

```
var(data_ICC$visits) - mean(data_ICC$visits)
```

```
## [1] 37.70896
```

From this we can then calculate the CV of expected provisioning rate

```
sqrt(var(data_ICC$visits) - mean(data_ICC$visits)) / mean(data_ICC$visits)
```

```
## [1] 0.3079105
```

As discussed in Box 2, we may want to present our results as visits/hour; however if we do this, we cannot calculate any of the descriptive statistics mentioned above on this new measure, as we would miscalculate the amount of Poisson-distributed stochastic error. For example if we calculate the expected CV, in this case it is underestimated (and Poisson-distributed stochastic error overestimated).

```
visits_per_hour <- data_ICC$visits / data_ICC$time
sqrt(var(visits_per_hour) - mean(visits_per_hour)) / mean(visits_per_hour)
```

```
## [1] 0.2113453
```

S6.2   Analysing Provisioning Rate as a Response Variable

S6.2.1   Estimating repeatability with and without Poisson-distributed stochastic error

We want to know if the provisioning rate observed at a nest is repeatable. We can run a linear mixed model, as is commonly done in the literature. This assumes no Poisson-distributed stochastic error.

```
## run LMM using lme4 package

library(lme4)

mod_LMM <- lmer(visits ~ 1 + (1|id), data=data_ICC)


## extract ID variance

V_id_LMM <- as.numeric(summary(mod_LMM)$var$id)


## extract residual variance

V_e_LMM <- summary(mod_LMM)$sigma^2


## calculate ICC

ICC_LMM <- V_id_LMM / (V_id_LMM + V_e_LMM)
```

For comparison, we can also run a GLMM, with Poisson error distribution, in order to calculate ICC, which accounts for Poisson-distributed stochastic error. We add in an observation level random effect to calculate over-dispersion variance (Harrison, 2014).

```
## create observation level random effect, i.e a different level for each data point

data_ICC$obs <- 1:nrow(data_ICC)


## run GLMM using lme4 package

mod_GLMM <- glmer(visits ~ 1 + (1|id) + (1|obs), data=data_ICC, family="poisson")

V_id_GLMM <- as.numeric(summary(mod_GLMM)$var$id)

V_e_GLMM <- as.numeric(summary(mod_GLMM)$var$obs)

ICC_GLMM <- V_id_GLMM / (V_id_GLMM + V_e_GLMM)
```

This model can also be run in *MCMCglmm* (Hadfield, 2010), but here we do not have to specify a observation level random effect, as this is done by default. As we get a posterior distribution from *MCMCglmm*, we can calculate the error associated with our ICC estimate.

```
library(MCMCglmm)

mod_MCMCglmm <- MCMCglmm(visits ~ 1, random = ~id, data = data_ICC,
    family = "poisson", verbose = FALSE)
## posterior distribution of individual variance
```

```
V_id_MCMCglmm <- mod_MCMCglmm$VCV[, "id"]
## posterior distribution of residual variance
V_e_MCMCglmm <- mod_MCMCglmm$VCV[, "units"]
## posterior distribution of ICC
ICC_MCMCglmm <- V_id_MCMCglmm/(V_id_MCMCglmm + V_e_MCMCglmm)
```

Comparing the three, we see that the estimate from the LMM is much lower than when we account for the Poisson-distributed stochastic error in the GLMMs.

```
cat("LMM =", round(ICC_LMM, 3), "\nGLMM =", round(ICC_GLMM, 3), "\nMCMCglmm =",
    paste0(round(mean(ICC_MCMCglmm), 3), " +/- ", round(sd(ICC_MCMCglmm),
        3)))

## LMM = 0.39
## GLMM = 0.604
## MCMCglmm = 0.607 +/- 0.088
```

Previous work has suggested estimating ICC on the observed rather than expected scale (Nakagawa & Schielzeth, 2010, 2013). This can be done by adding the Poisson-distributed stochastic error back on to the total variance , using the trigamma function (Nakagawa *et al.*, 2017)

```
## from Nakagawa & Schielzeth 2017
P_error <- trigamma(mean(data_ICC$visits))
V_id_GLMM / (V_id_GLMM + V_e_GLMM + P_error)

## [1] 0.3793103
```

which you can see is similar to what we would predict when not accounting for this stochastic error (i.e. in the LMM). Note this is not what we recommend in this particular case. Conversely, we could 'correct' the ICC estimate from the linear model for the presence of Poisson-distributed stochastic error, by directly removing it

```
V_id_LMM / (V_id_LMM + V_e_LMM - mean(data_ICC$visits))

## [1] 0.5957898
```

which gives a result similar to that from the Poisson model.

It is common for researchers to log transform this kind of data when analysing it using a LMM, as count data is highly skewed at low means. Repeatability is unaffected by this transformation (here we use log(y+0.5) following Yamamura 1999),

```
mod_LMM_log <- lmer(log(visits + 0.5)~ 1 + (1|id), data_ICC)

V_id_LMM_log <- as.numeric(summary(mod_LMM_log)$var$id)

V_e_LMM_log <- summary(mod_LMM_log)$sigma^2

V_id_LMM_log / (V_id_LMM_log + V_e_LMM_log)


## [1] 0.3736332
```

and Poisson-distributed stochastic error can similarly be corrected for post-hoc using the trigamma function (as it on the log scale).

```
P_error <- trigamma(mean(data_ICC$visits))

V_id_LMM_log / (V_id_LMM_log + V_e_LMM_log - P_error)


## [1] 0.5916202
```

S6.2.2   Estimating CV_B

In a linear mixed model context, CV_B is intuitively calculated as

$$CV_B = \frac{\sqrt{V_B}}{\bar{x}} \tag{S9}$$

, where V_B if the between individual variation (i.e. the individual variance component) (?).

```
CV_B_LMM <- sqrt(V_id_LMM) /  mean(data_ICC$visits)
```

This is less simple for non-Gaussian traits. From de Villemereuil *et al.* (2016), we can derive CV_B from a Poisson GLMM as

$$CV_B = \sqrt{V_{B_l}} \tag{S10}$$

, where V_{B_l} is the between individual variance estimated on the link scale (i.e. the individual variance component from the Poisson GLMM). We can compare these values from different models

```
CV_B_GLMM <- sqrt(V_id_GLMM)

CV_B_MCMCglmm <- sqrt(V_id_MCMCglmm)

cat("LMM =", round(CV_B_LMM, 3), "\nGLMM =", round(CV_B_GLMM, 3),

    "\nMCMCglmm =", paste0(round(mean(CV_B_MCMCglmm), 3), " +/- ",

        round(sd(CV_B_MCMCglmm), 3)))


## LMM = 0.238

## GLMM = 0.229

## MCMCglmm = 0.23 +/- 0.026
```

As you can see, CV_B is not affected by the scale (observed or expected) on which it is calculated, as it does not depend on the calculation of total variance.

It is worth noting that if CV_B is estimated using a LMM with log transformed provisioning rate, then CV_B should be calculated as $\sqrt{V_B}$ (again because it is on the log scale).

```
sqrt(V_id_LMM_log)


## [1] 0.2283472
```

S6.2.3 Problems associated with analysing rate

As mentioned in Box 2, some authors have analysed transformed provisioning rate in Poisson model. We presume that authors do this by rounding to the nearest whole number, as most GLMM softwares to not take non-integers as input when a Poisson error distribution is specified.

```
mod_GLMM_rate <- glmer(round(visits_per_hour) ~ 1 + (1 | id) + (1 |

    obs), data = data_ICC, family = "poisson")

V_id_GLMM_rate <- as.numeric(summary(mod_GLMM_rate)$var$id)

V_e_GLMM_rate <- as.numeric(summary(mod_GLMM_rate)$var$obs)

V_id_GLMM_rate/(V_id_GLMM_rate + V_e_GLMM_rate)
```

```
## [1] 1
```

```
sqrt(V_id_GLMM_rate)/mean(round(visits_per_hour))
```

```
## [1] 0.02269032
```

In this extreme case, the ICC has been estimated as 1 which is clearly a large overestimation, as the model has estimated there being no residual (over-dispersion) variance, whilst CV_B has been hugely underestimated.

S6.2.4   Accounting for observation period

Imagine we observed the same population, but this time we had a large amount of variation in our observation periods.

```
data_ICC_time <- read.csv("S8_data_ICC_time.csv")
head(data_ICC_time)
```

```
##   id visits     time
## 1  1     38 4.860166
## 2  1     32 3.847738
## 3  1     39 4.913166
## 4  2     25 2.397478
## 5  2     41 4.788769
## 6  2     32 3.220871
```

Firstly, we can calculate expected CV

```
adj_visits <- (data_ICC_time$visits * mean(data_ICC_time$time))/data_ICC_time$time
sqrt(var(adj_visits) - mean(adj_visits))/mean(adj_visits)
```

```
## [1] 0.3218552
```

When estimating ICC, we can correct for this variation in observation period by adding an offset of log observation period. An offset is a covariate where the slope is fixed to 1.

Mathematically, this is equivalent to dividing by the observation period (t), but allows the model to remove the Poisson error before this occurs.

$$log(y) = \beta x + log(t) + \epsilon \tag{S11}$$

$$log(y/t) = \beta x + \epsilon \tag{S12}$$

We can do this with the *lme4* package by using the offset function

```
## create observation level random effect, i.e a different level
## for each data point
data_ICC_time$obs <- 1:nrow(data_ICC_time)
## run GLMM using lme4 package
mod_GLMM_time <- glmer(visits ~ 1 + offset(log(time)) + (1 | id) +
    (1 | obs), data = data_ICC_time, family = "poisson")
V_id_GLMM_time <- as.numeric(summary(mod_GLMM_time)$var$id)
V_e_GLMM_time <- as.numeric(summary(mod_GLMM_time)$var$obs)
ICC_GLMM_time <- V_id_GLMM_time/(V_id_GLMM_time + V_e_GLMM_time)
```

We can also run this in the *MCMCglmm* package, but here the offset function does not work. instead we have to fix the prior of the slope to 1 (or at least make a very informative prior with mean 1 and extremely low variance)

```
## create priors for fixed effects - intercept and obs. time, with
## large variance
prior <- list(B = list(V = diag(2) * 1e+07, mu = c(0, 1)), G = list(G1 = list(V = 1,
    nu = 0.002)))
## make obs. time variance very small
prior$B$V[2, 2] <- 1e-07
mod_MCMCglmm_time <- MCMCglmm(visits ~ log(time), random = ~id, data = data_ICC_time,
    family = "poisson", prior = prior, verbose = FALSE)
V_id_MCMCglmm_time <- mod_MCMCglmm_time$VCV[, "id"]
V_e_MCMCglmm_time <- mod_MCMCglmm_time$VCV[, "units"]
```

```
ICC_MCMCglmm_time <- V_id_MCMCglmm_time/(V_id_MCMCglmm_time + V_e_MCMCglmm_time)
## compare results
c(GLMM = round(ICC_GLMM_time, 3), MCMCglmm = paste0(round(mean(ICC_MCMCglmm_time),
    3), "+/-", round(sd(ICC_MCMCglmm_time), 3)))
```

```
##           GLMM        MCMCglmm

##         "0.483" "0.485+/-0.074"
```

S6.3 Analysing Provisioning Rate as a Predictor Variable

Imagine we have collected some provisioning data of 100 nests in 2 hour observations.
We also collected data on chick mass at the end of the provisioning period.

```
data_pred <- read.csv("S9_data_pred.csv")
head(data_pred)
```

```
##   visits time      mass
## 1     18    2 196.7587
## 2     26    2 181.4664
## 3     17    2 196.4869
## 4     40    2 228.1916
## 5     30    2 222.9193
## 6     25    2 212.5197
```

```
par(mfrow=c(1,2))
plot(table(data_pred$visits), xlab="Provisioning Rate", ylab="Frequency", xaxt="n")
axis(1,seq(5,60,5))
hist(data_pred$mass, col="grey", main="", xlab="Chick Mass")
```
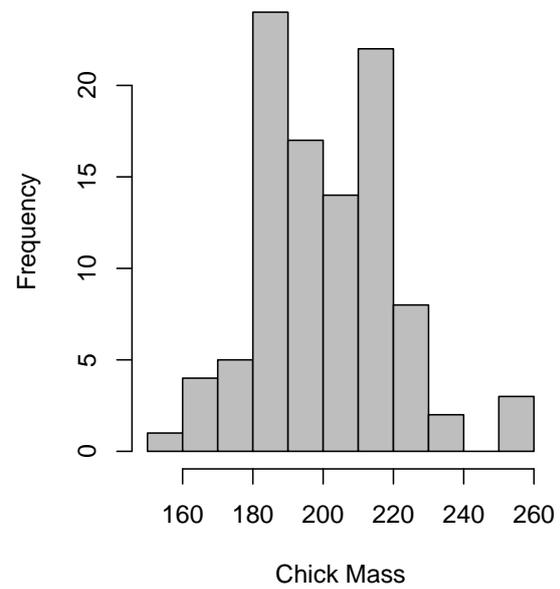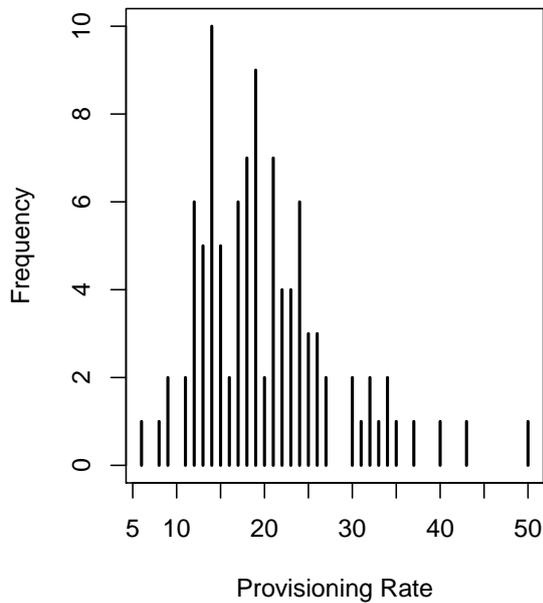
We want to estimate the effect of provisioning rate on chick mass. Traditionally this is done in a linear model

```
mod_LM <- lm(mass~visits, data_pred)

V_f_LM <- var(model.matrix(mod_LM) %*% coef(mod_LM))

V_e_LM <- summary(mod_LM)$sigma^2

R2_LM <- V_f_LM / (V_f_LM + V_e_LM)

R2_LM


##             [,1]
## [1,] 0.4270903
```

This model does not take into account the Poisson-distributed stochastic error in provisioning rate, which leads to an underestimation of effect size. We can account for this using a measurement error model. We can specify such a model in *Stan* (Carpenter *et al.*, 2017) using the following code

```
//modelling uncertainty in a Poisson predictor variable
data {                              // data being input:
```

```
  int <lower=0> N;                     // number of data points

  vector[N] a;                         // chick body mass

  int <lower=0> v[N] ;                 // number_of_visits

}

parameters {                           // parameters to be estimated:

  real beta_0;                         // intercept

  real beta_1;                         // slope of provisioning rate

  real <lower=0> meanPR;               // mean provisioning rate

  real <lower=0> sigmaPR;              // sd provisioning rate

  vector <lower=0> [N] PR;             // provisioning rate

  real <lower=0> sigma;                // residual sd

}

model {

  PR ~ lognormal(meanPR,sigmaPR);

  v ~ poisson(PR);

  a ~ normal(beta_0 + beta_1 * PR,sigma);

}
```

In this code we first tell *Stan* what data we are using, then we define the parameters we want the model to estimate, and then we specify the model and any priors. In essence, what we are doing with this model is creating a latent (unobserved) variable, 'PR', for provisioning rate, and we use this variable in the model for chick mass. For more details about specifying models in *Stan* see http://mc-stan.org.

We can run this model in *R* using the package *rstan*. To do this we can save the stan code in a '.stan' file, and input to *rstan* along with the data, formatted as a list

```
stan_data <- list(N = nrow(data_pred), a = data_pred$mass, v = data_pred$visits)
library(rstan)
## compile the model - this takes a bit of time
stanModel <- stan_model(file = "Poisson_measurement_error_model.stan")
## run the model
```

```
fit <- sampling(stanModel, data = stan_data, iter = 2000, chains = 1,
    open_progress = F, control = list(max_treedepth = 15, adapt_delta = 0.91))
## extract posterior distirbutions of estimated parameters
ex_fit <- extract(fit, permute = FALSE)
## posterior distributions of latent provisioning rate variable
PR_pred <- ex_fit[, , grep("PR\\[", dimnames(ex_fit)[[3]])]
## posterior distributions of predicted values
outmat <- ex_fit[, , "beta_0"] + ex_fit[, , "beta_1"] * PR_pred[,
    ]
## posterior distribution of fixed effect variance
V_f_stan <- apply(outmat, 1, var)
## posterior distribution of residual variance
V_e_stan <- ex_fit[, , "sigma"]^2
## posterior distribution of R2
R2_stan <- V_f_stan/(V_f_stan + V_e_stan)
```

Comparing the two we can see that that the R^2 from the measurement error model is substantially higher, as the covariance between provisioning rate and chick mass has been better estimated.

```
c(LM=round(R2_LM,3), stan=paste0(round(mean(R2_stan),3), "+/-", round(sd(R2_stan),3)))

##            LM            stan
##       "0.427" "0.615+/-0.093"
```

S6.3.1   Accounting for observation period

Below is some example code for accounting for observation period when including provisioning rate as a predictor variable. The highlighted code shows the difference with the last code. We have an additional data variable - time (t), and we know that the visits (v) are a function of the provisioning rate (PR) and time, observed with Poisson-distributed stochastic error.

```
//modelling uncertainty in a Poisson predictor variable
```

```
data {                                 // data being input:

  int <lower=0> N;                     // number of data points

  vector[N] a;                         // chick body mass

  int <lower=0> v[N] ;                 // number_of_visits

  vector <lower=0> [N] t;              //observation time

}

parameters {                           // parameters to be estimated:

  real beta_0;                         // intercept

  real beta_1;                         // slope of provisioning rate

  real <lower=0> meanPR;               // mean provisioning rate

  real <lower=0> sigmaPR;              // sd provisioning rate

  vector <lower=0> [N] PR;             // provisioning rate

  real <lower=0> sigma;                // residual sd

}

model {

  PR ~ lognormal(meanPR,sigmaPR);

  v ~ poisson(t .* PR);

  a ~ normal(beta_0 + beta_1 * PR,sigma);

}
```

References

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