

## Effects of environmental variables on invasive amphibian activity: using model selection on quantiles for counts

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**Abstract.** Many different factors influence animal activity. Often, the value of an environmental variable may influence significantly the upper or lower tails of the activity distribution. For describing relationships with heterogeneous boundaries, quantile regressions predict a quantile of the conditional distribution of the dependent variable. A quantile count model extends linear quantile regression methods to discrete response variables, and is useful if activity is quantified by trapping, where there may be many tied (equal) values in the activity distribution, over a small range of discrete values. Additionally, different environmental variables in combination may have synergistic or antagonistic effects on activity, so examining their effects together, in a modeling framework, is a useful approach. Thus, model selection on quantile counts can be used to determine the relative importance of different variables in determining activity, across the entire distribution of capture results. We conducted model selection on quantile count models to describe the factors affecting activity (numbers of captures) of cane toads (*Rhinella marina*) in response to several environmental variables (humidity, temperature, rainfall, wind speed, and moon luminosity) over eleven months of trapping. Environmental effects on activity are understudied in this pest animal. In the dry season, model selection on quantile count models suggested that rainfall positively affected activity, especially near the lower tails of the activity distribution. In the wet season, wind speed limited activity near the maximum of the distribution, while minimum activity increased with minimum temperature. This statistical methodology allowed us to explore, in depth, how environmental factors influenced activity across the entire distribution, and is applicable to any survey or trapping regime, in which environmental variables affect activity.

**Key words:** animal activity; cane toad; model selection; quantile count model; quantile regression; *Rhinella marina*.

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### INTRODUCTION

Animal activity is influenced by a complex web of factors (Tester and Figala 1990), including a range of environmental variables (Chamaillé-Jammes et al. 2007, Upham and Hafner 2013). Animal activity can vary widely in response to a variety of different environmental variables, but rather than determining the mean number of active animals, such variables may impose a limit

on the maximum or minimum number of active animals. In such cases, it should be more appropriate to analyze particular portions of an activity distribution, rather than simply describing the rate of change of the mean, which may or may not change with the variable of interest. Examining the rate of change of the mean may underestimate, overestimate, or neglect changes at the minimum and maximum extents of a heterogeneous distribution (Terrell et al. 1996).

Quantile regression is especially useful for examining distributions with heterogeneous variances (Koenker and Bassett 1978), a common characteristic of distributions in ecology (Cade and Noon 2003), including animal activity in relation to environmental variables (Johnson et al. 2014). Specifically, rates of change near the maximum (i.e., 0.95 quantile) or minimum (i.e., 0.05 quantile) of the distribution are often a better representation of the influence of the measured variable than the mean (Thomson et al. 1996, Cade et al. 1999). If, for example, a particular measured variable imposes a limit on activity, the organism's response cannot increase to more than the upper limit set by that factor; however, it can be any value less than that, for example, if other, unmeasured, factors are also influencing activity (Cade and Noon 2003).

Our motivating example was estimating effects of various environmental variables on cane toad (*Rhinella marina*) activity in northern Australia. Cane toads are large, nocturnal, terrestrial anurans originating from South America, whose invaded range includes many tropical and subtropical areas globally, including Australia. The physiological constraints on terrestrial amphibians (Tracy 1976), and experimental data on cane toads (e.g., Cohen and Alford 1996), suggest that seasonal variation in activity should be strongly associated with environmental moisture. Wind speed also affects desiccation rates, and activity, of anurans (Henzi et al. 1995), while locomotor performance and behavior are strongly dependent on temperature in ectotherms (Huey and Stevenson 1979, Huey 1982). Finally, positive and negative effects of lunar cycles on amphibian biology have also been observed (Grant et al. 2012). These factors limit activity in other species; for example, several ectothermic species are inactive below certain temperatures (e.g., Lei and Booth 2014). Any combination of these environmental variables may impose a limit on the maximum or minimum activity of cane toads.

Trapping is a common method for measuring animal activity (e.g., Gibbons and Bennett 1974, Price 1977, Rowcliffe et al. 2014) and could be used to measure cane toad activity (Muller and Schwarzkopf 2017). Cane toad traps for adults contain a lure that produces a cane toad advertisement call, and a light that attracts insects as a visual cue (Yeager et al. 2014). Trap efficacy

depends primarily on activity; toads must be active to approach the lure, and enter the trap. Therefore, the number of toads trapped per night provides an estimate of toad activity on that night. However, if captures are low, or if the trap has limited capacity (i.e., the maximum number of animals capturable is constrained by trap size), trapping may result in a very small range of counts, with numerous tied (equal) count values. Indeed, previous studies report mean cane toad capture rates of approximately 1–6 individuals per trap per night, and it is uncommon to exceed 14 captures in a single night (although the maximum number of toads caught in a single trap to date was 31; Muller and Schwarzkopf 2017). In this case, conventional quantile regression analysis creates serious interpretation and inference issues, because the models assume a continuous dependent variable, rather than a discrete dependent variable (Cade and Dong 2008). The quantile count model is a special implementation of conventional quantile regression, whereby the changes in quantiles of counts are estimated by making them continuous random variables and then back-transforming estimates to the discrete response without sacrificing model accuracy (Machado and Santos Silva 2005). Therefore, a quantile count model can be used to analyze trapping data, to examine the entire cane toad activity distribution in response to an environmental variable.

Multiple environmental factors may influence toad activity across various parts of the activity distribution and, thus, quantile regression modeling, as with any regression modeling, may require considering alternative models with various combinations of predictor variables. Model selection using differences in Akaike's information criterion (AIC) is often used to select among alternative candidate models for analyses in ecology (Arnold 2010). Akaike's information criterion is valuable where there are a range of variables that may be associated with a biological variable and the researcher is interested in which are most influential (Symonds and Moussalli 2010). A range of competing models containing various combinations of variables are analyzed simultaneously and AIC ranks these models (Akaike 1974, 1998, Richards et al. 2011). When differences in AIC among models with various combinations of predictor variables are calculated with

respect to a null model with just an intercept, then the comparison of differences in AIC is related to the proportionate reduction in variation of the phenomenon explained by each combination of variables (adjusted by the number of estimated parameters), given what was measured (Richards et al. 2011). Akaike's information criterion is calculated using the number of fitted parameters (including the intercept) in the model and the likelihood associated with the maximum-likelihood estimate. The weighted sums of absolute deviations minimized in conventional quantile regression estimation are maximum-likelihood estimates assuming an asymmetric double exponential distribution, providing the basis for computing AIC and other information criteria on quantile regression models (Koenker and Machado 1999, Yu and Moyeed 2001, Cade et al. 2005). Therefore, model selection on quantile count models can be used to determine which combination of variables affects toad activity across the entire response distribution.

We trapped cane toads over eleven months at one location while simultaneously collecting information on humidity, temperature, rainfall, wind speed, and moon luminosity. We examined the distributions of toad captures using model selection on quantile count models (using every 5th quantile between  $\tau = 0.05$  and  $\tau = 0.95$ ) to examine which environmental variables affected toad activity at different parts of the activity distribution during different seasons. We suggest that model selection on quantile count models is applicable to any trapping regime for which several environmental variables affect the number of individuals captured, especially if those effects occur near the lower or upper tails of the distribution.

## MATERIALS AND METHODS

### Study site

The study occurred on Orpheus Island (18°36'46.0" S, 146°29'25.2" E) from 21 May 2013 to 28 March 2014, with the exception of 16 d in November 2013, 17 d in December 2013, 10 d in January 2014, and 9 d in February 2014. The island is approximately 23 km east of the Australian mainland and 120 km north of Townsville, Queensland. It is approximately 12 km long and is comprised primarily of dry woodlands, with rainforest patches.

### Data collection

To catch toads, we used wire traps (1 × 1 × 0.25 m), equipped with doors that opened easily with pressure from outside, but prevented egress of trapped toads. The trap contained a lure that repeatedly played a cane toad advertisement call at night, and had a small LED black (UV) light that attracted insects. More detail on the trap and methodology is available in Yeager et al. (2014).

We used two traps for the study, at two trapping sites. Both trapping sites were located in open, grassy areas and had similar ambient light ( $\bar{x} = 0.051$  lx) and environmental noise ( $\bar{x} = 32.5$  dB) levels. We measured light and noise levels at each site on 15 randomly selected nights, at 22:00 hours, using a lux meter (ATP DT-1300), and a C-weighted Lutron sound level meter (model: SL-4013). We placed the traps 400 m apart, such that the acoustic lure at one site could not be heard by toads at the other site (Muller et al. 2016). We removed, counted, and sexed trapped toads daily by visual inspection of coloration and skin texture (females are dark brown with a smooth bumpy dorsum, whereas males are lighter with a rough sandpaper-like dorsum). We placed a water bowl and PVC pipe for shelter in each trap. Toads were euthanized immediately after their removal from the traps, using an overdose (350 ppm) of buffered tricaine methanesulfonate (MS-222), and exposure was via submersion in water containing a sodium bicarbonate-buffered solution. Euthanizing toads after capture may have reduced the number of toads available for capture on subsequent nights, but there was never a decrease in toad numbers that was not easily explained by weather (e.g., there were no consistent patterns in which nightly captures were low following a large capture event). Toads move nomadically (Schwarzkopf and Alford 2002), and the size of the toad population, and the island, facilitated constant immigration into the study area, and therefore, the number of toads available to local trapping was likely approximately constant.

We collected humidity, minimum temperature, and mean wind speed (recorded every half hour), and recorded total nightly rainfall, from the Australian Institute of Marine Science weather station on Orpheus Island (located approximately 300 m from the study site) for

every night during the trapping period. We averaged half-hourly recordings across the 12-h period from 18:00 hours to 6:00 hours to calculate nightly averages. We characterized moon luminosity as the percent of the moon illuminated on each night (as measured from Townsville; approximately 79 km from the study site) during the trapping period (obtained from [www.timeanddate.com](http://www.timeanddate.com)).

### Statistical methods

We divided the trapping period into four seasons: the dry season (June–August), the pre-wet season (September–November), the wet season (December–February), and the post-wet season (March–May).

We used captures for each trap from each night as replicates so each night had two measures of toad activity which were counts of captured toads. We used the quantile count model of Machado and Santos Silva (2005), where the discrete count response ( $y$ ) is transformed to the continuous scale (jittered) for quantile estimates by adding a random uniform number between 0 and 1 to each count,  $z = y + U[0, 1]$ . We used an exponential count model,  $Q_z(\tau|\mathbf{X}) = \tau + \exp(\mathbf{X}\boldsymbol{\beta}(\tau))$ , estimated in its linear form by taking logarithms, for  $\log(z - \tau)$  the  $Q_{\log(z - \tau)}(\tau|\mathbf{X}) = \mathbf{X}\boldsymbol{\beta}(\tau)$ , where  $\mathbf{X}$  is the matrix of predictor variables and a column of 1's for the intercept. Estimates in the artificial continuous scale are then back-transformed with a ceiling function,  $Q_y(\tau|\mathbf{X}) = \lceil \tau + \exp(\mathbf{X}\hat{\boldsymbol{\beta}}(\tau)) - 1 \rceil$ , to recover the quantile estimates in the discrete random variable scale (counts  $y$ ). Our quantile count model had the typical multiplicative exponential form used with other parametric count models (Cade and Dong 2008) that ensures that all estimates are greater than or equal to zero. For each season, we estimated five candidate quantile count models with environmental predictors (humidity, minimum temperature, rainfall, wind speed, and moon luminosity) and one null quantile count model with just an intercept. Estimates were implemented with the `rq()` function in the `quantreg` package for the R environment for statistical computing and graphics (Koenker 2012; Appendix S1). Models were estimated for  $\tau \in \{0.05, 0.10, 0.15, \dots, 0.95\}$ . To integrate out the artificial noise introduced by jittering toad counts to a continuous variable ( $z = y + U[0, 1]$ ), we estimated

each model  $m = 500$  times, using  $m$  random samples between 0 and 1 ( $U[0, 1]$ ) and averaged the estimates (Machado and Santos Silva 2005, Cade and Dong 2008).

We calculated the AIC for each model, including a null model with just an intercept, for each of the  $m = 500$  replications at every quantile for which models were estimated ( $n = 9500$  AIC estimates across the entire distribution per candidate model). To calculate  $\Delta$ AICs for each candidate model, we subtracted the AICs of each candidate model from the AICs of the null model for each of the  $m = 500$  replications at every quantile for which models were estimated (Cade et al. 2017). Therefore, models with higher  $\Delta$ AIC are better supported because the null model had no significant relationship with any predictor variable. We averaged across  $m = 500$  replications by quantile to compute the average  $\Delta$ AIC of each candidate model at  $\tau \in \{0.05, 0.10, 0.15, \dots, 0.95\}$ . This calculation disclosed the strength of the relationship between toad captures and each predictor variable across the entirety of the distribution in the continuous log-transformed scale of toad counts. We performed model selection for strong predictor variables by identifying models that had the highest  $\Delta$ AIC at any quantile or were within 2  $\Delta$ AIC of the strongest model at any quantile (Burnham and Anderson 2004). Often, different models were strongest at different parts of the distribution. We then considered candidate models that included all possible combinations of the strong predictor variables, and a null model containing only an intercept to which candidate models were compared. We once again identified which models had high average  $\Delta$ AICs across the entirety of the distribution and selected the strongest model for further analysis.

After deciding on a reasonable set of predictor variables to include in our seasonal models, we estimated the models again incorporating the count of toads on the previous night as an additional predictor variable to account for first-order temporal autocorrelation in our estimates. We compared models with and without the lagged toad counts across quantiles with AIC, as before, to determine whether the first-order temporal autocorrelation improved our quantile estimates. Estimates of the first-order

temporal autocorrelation parameter were also examined to determine whether they were sufficiently different from zero to justify their inclusion in the seasonal models.

Confidence intervals for parameter estimates made in the continuous log scale were estimated by integrating out the artificial noise introduced by the  $m = 500$  random jitters to the continuous scale. We averaged estimates of confidence interval end points for parameters in the strongest model based on the quantile rank score test inversion approach in `rq()`, with weights based on a local bandwidth of quantiles to account for heterogeneity (Koenker and Machado 1999, Cade et al. 2005, Cade and Dong 2008). Other approaches to estimating confidence intervals for quantile count models based on estimating the asymptotic variance/covariance from averaging components across  $m$  simulations have been developed (Machado and Santos Silva 2005) and implemented in the `Qtools` package for R (Geraci 2016). However, the quantile rank score test inversion approach usually provides better confidence interval coverage and length at smaller to intermediate sample sizes than procedures based on the variance/covariance estimates as it requires estimating neither the density of observations near the quantile estimate of interest nor the direct computation of variances of parameter estimates. Properties of the quantile rank score test have been investigated in Koenker (1994) and Cade et al. (2006).

The confidence intervals for parameter estimates and AIC model selection statistics were all obtained in the continuous log scale, but interpretation of the model estimates was made in the discrete count scale. We back-transformed quantile estimates of the strongest model from the continuous log scale to the discrete count scale using the ceiling function (Machado and Santos Silva 2005, Cade and Dong 2008). In cases where the strongest model included more than one predictor variable, we calculated quantile estimates for each variable while holding all other variables included in the model at their median values. From these estimates, we examined the proportional changes in counts by calculating, as a percentage, the changes of estimated counts at particular quantiles, across a selected range of values of the predictor variable.

## RESULTS

Traps were open for 91 nights in the dry season, 74 nights in the pre-wet season, 54 nights in the wet season, and 39 nights in the post-wet season (total of 516 effective trap nights, given two traps were open each night throughout the trapping period). We trapped 241 toads in the dry season, 387 toads in the pre-wet season, 490 toads in the wet season, and 167 toads in the post-wet season. Toads were most active in the wet season and were least active in the dry season (Fig. 1).

### Dry season

In the dry season, the model including rainfall consistently had the highest average  $\Delta$ AIC, across all quantiles (Fig. 2A). We did not include any other variables in a combination model with rainfall, because the  $\Delta$ AIC of every other variable was  $<2$  at all quantiles  $\geq 0.15$  (Fig. 2A). The model that included a first-order temporal autocorrelation effect, in combination with rainfall, was slightly better supported across most of the distribution, but was particularly well supported at lower quantiles (Appendix S2: Fig. S1). In this model, rainfall had a positive effect on all quantiles  $\geq 0.10$  of the toad counts; the estimated partial effect was strongest near the minimum of the distribution (Fig. 3). The proportional changes in counts at quantiles  $\geq 0.75$  increased 60–67% as

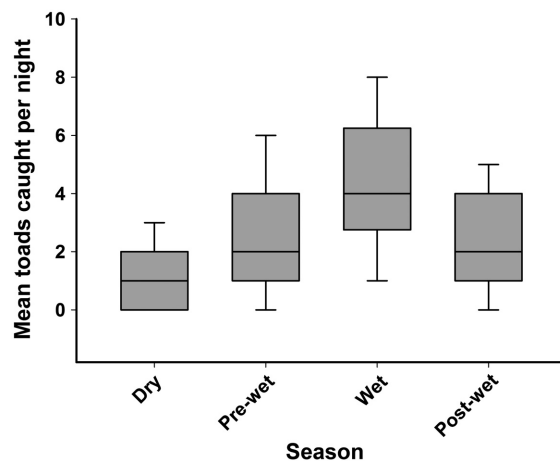


Fig. 1. Seasonal variation in mean nightly cane toad captures on Orpheus Island, from 21 May 2013 to 28 March 2014.

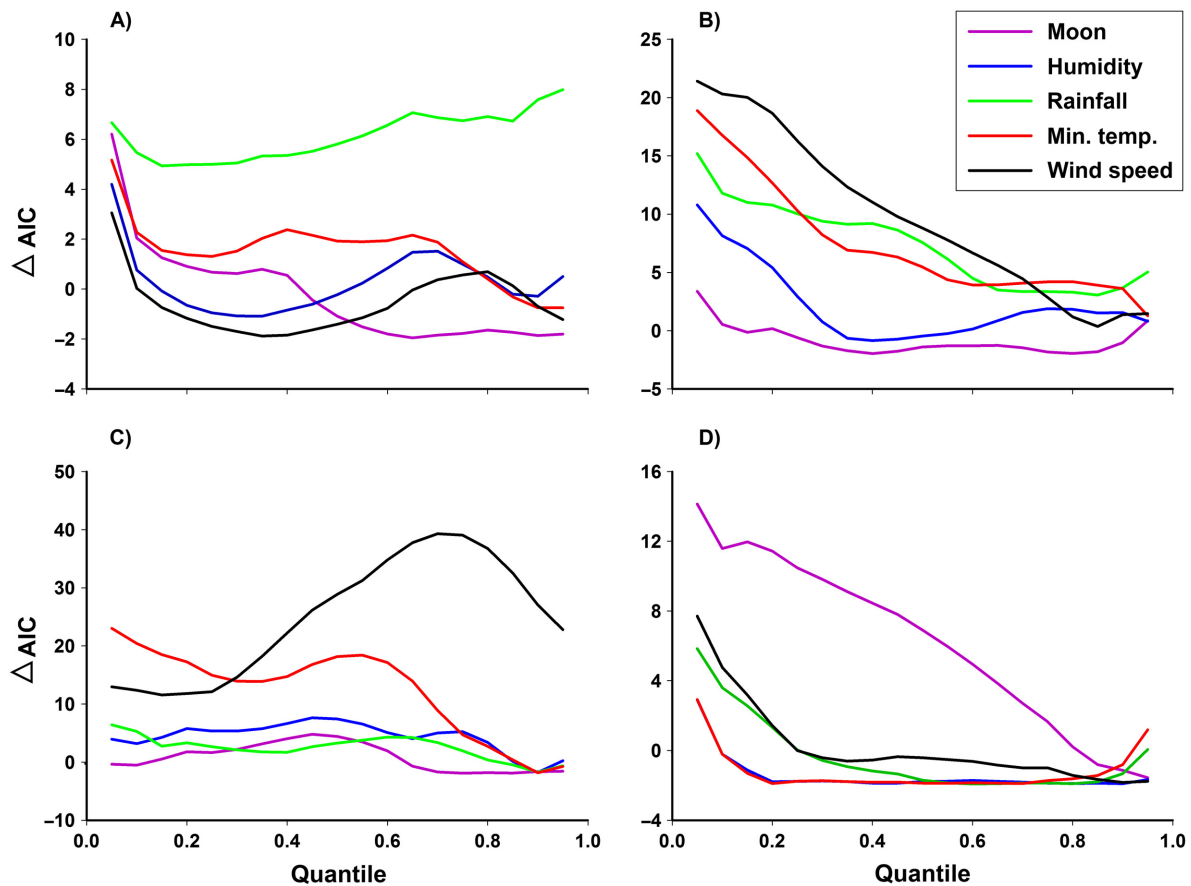


Fig. 2. Change in average  $\Delta$ AICs of candidate variable models in the dry (A), pre-wet (B), wet (C), and post-wet (D) seasons, on Orpheus Island, from 21 May 2013 to 28 March 2014, across  $\tau \in \{0.05, 0.10, 0.15, \dots, 0.95\}$ , for  $m = 500$  replications of  $z = y + U[0, 1)$ . In the dry season (A), rainfall was the strongest predictor variable, at every quantile; therefore, a combination model that included other variables was not estimated. In the pre-wet season (B), wind speed, minimum temperature, and rainfall were all strong predictor variables at different points across the distribution. In the wet season (C), minimum temperature and wind speed were both strong predictors of activity. In the post-wet season (D), moon luminosity was the strongest predictor of activity, especially at lower quantiles. AIC, Akaike's information criterion.

rainfall increased from 20 mm to 33 mm; however, the greatest proportional increases (up to 200%) occurred at quantiles  $\leq 0.25$  as rainfall increased from 20 to 33 mm (Fig. 4). This indicated that rain events were the strongest driver of activity in the dry season. It may also indicate that generally inactive toads (represented by counts at quantiles  $\leq 0.25$ ) were most likely to be trapped during rain events when more than 20 mm fell per night, because the minimum activity (i.e., minimum captures) greatly increased when rainfall was  $>20$  mm.

#### Pre-wet season

In the pre-wet season, wind speed, minimum temperature, and rainfall were all strong predictors of activity, at different points across the distribution (Fig. 2B). Models including various combinations of these variables were of similar strength, especially at higher quantiles (Fig. 5). We selected for further examination a model that included minimum temperature and wind speed, because this model was the strongest at all quantiles  $\geq 0.20$  (Fig. 5). The model that included a first-order temporal autocorrelation

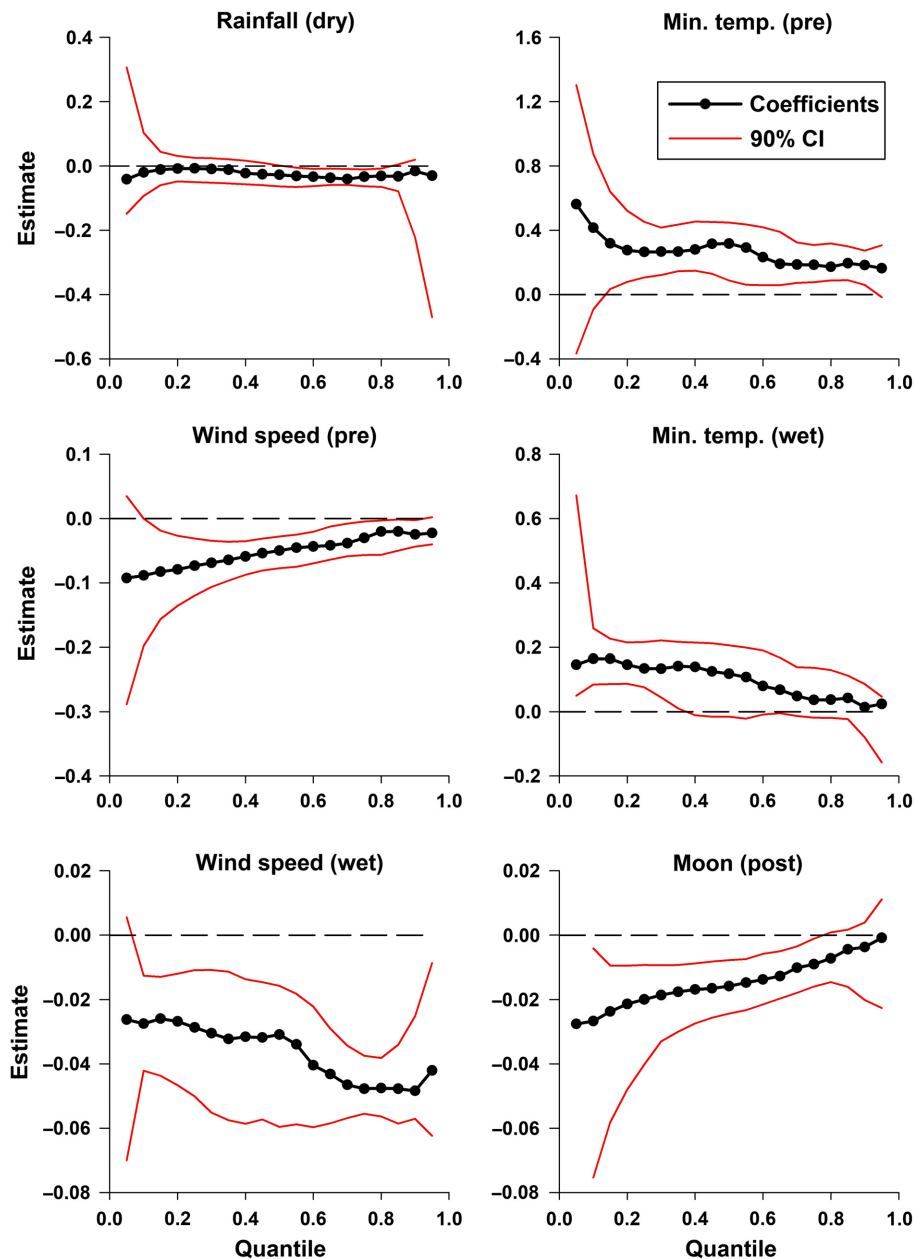


Fig. 3. Average of  $m = 500$  parameter estimates of 90% confidence intervals (rank score test inversion) for quantile count models of trapped cane toads on Orpheus Island, from 21 May 2013 to 28 March 2014, where  $z = y + U$  [0, 1) was randomized  $m$  times for the estimate of strongest model chosen from a selection of models containing various combinations of environmental variables. Shown are the rates of change of the number of toads trapped with the strongest environmental predictor variable(s) in each season, as identified by the quantile count model.

effect, in combination with minimum temperature and wind speed, was well supported, especially at lower quantiles (Appendix S2: Fig. S2). In this model, minimum temperature had a

positive effect on all quantiles  $\geq 0.10$  of the toad counts, when wind speed and lagged toad counts were fixed at their respective median values (Figs. 3, 6A). Proportional increases in toad

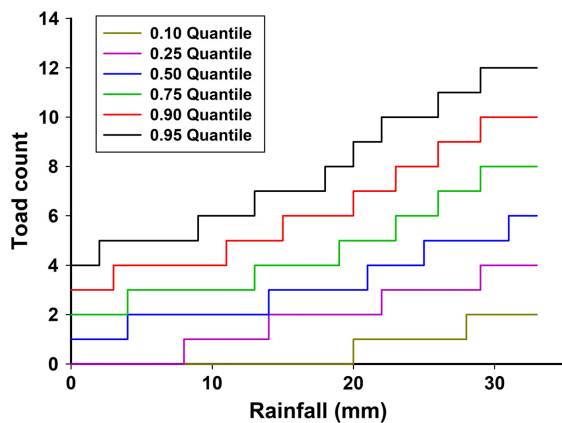


Fig. 4. Estimated quantile count model for cane toad captures ( $n = 182$ ) on Orpheus Island in the dry season (June–August 2013), as a function of rainfall and a first-order autocorrelation effect, estimated using a ceiling function. An average of estimates for  $m = 500$  random jitterings for cane toad counts was used.

counts were largest (57–200%) at quantiles  $\geq 0.50$ , when the minimum temperature increased from 22° to 26°C. Proportional increases in toad counts when minimum temperature increased from 19° to 22°C were considerably smaller, and only occurred at quantiles  $\geq 0.75$ . This may indicate that many toads were inactive when the temperature was below 22°C; the highest chance of capture for these individuals was when temperatures were 22° to 26°C. Conversely, wind speed had a negative effect on all quantiles  $\geq 0.10$  of the toad counts when minimum temperature was fixed at its median value (Figs. 3, 6B). Proportional changes in toad counts were largest when wind speed was below 25 km/h; counts at quantiles  $\geq 0.50$  decreased 38–67% when wind speed increased from 5 to 25 km/h, and toad counts at quantiles  $\leq 0.25$  decreased to zero. The negative effect of wind tapered off when speed exceeded 25 km/h. The combination model suggests that toads are most active in the pre-wet season when the minimum temperature was above 22°C and wind speed was low.

#### Wet season

In the wet season, minimum temperature and wind speed were the two candidate variable models that had the highest average  $\Delta$ AIC, across all quantiles (Fig. 2C). Minimum temperature was

the strongest predictor variable at quantiles  $\leq 0.25$ , while wind speed was the strongest predictor near the middle and upper limits of the distribution. A model including both variables had considerable support across all of the distribution, especially at lower limits (Fig. 7). The model that included a first-order temporal autocorrelation, in combination with minimum temperature and wind speed, was never within 2  $\Delta$ AIC units of the selected model at any quantile, and was not considered further. Minimum temperature had a positive effect on all quantiles  $\geq 0.10$  of the toad counts, when wind speed was fixed at its median value; however, this effect was considerably stronger at lower quantiles (Fig. 3). The proportional changes in counts increased 67–200% at quantiles  $\leq 0.5$  when temperature increased from 24° to 28°C; however, proportional changes in counts at higher quantiles were comparatively lower, across the same temperature range (Fig. 8A). The obvious interpretation is that even the lowest minimum temperatures in the wet season were warm enough to allow toad activity, however when temperatures were higher, the minimum activity (i.e., minimum captures) greatly increased. Wind

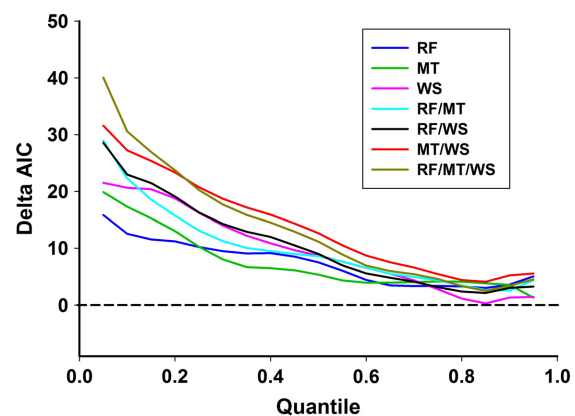


Fig. 5. Change in average  $\Delta$ AICs of models containing various combinations of rainfall, minimum temperature, and wind speed, across  $\tau \in \{0.05, 0.10, 0.15, \dots, 0.95\}$ , for  $m = 500$  replications of  $z = y + U[0, 1)$ , on Orpheus Island, in the pre-wet season (September–November 2013). The relative strength of models containing individual environmental variables in the pre-wet season is shown in Fig. 2B. In the pre-wet season, a combination model containing minimum temperature and wind speed was strongest at all quantiles  $\geq 0.20$ . AIC, Akaike's information criterion.



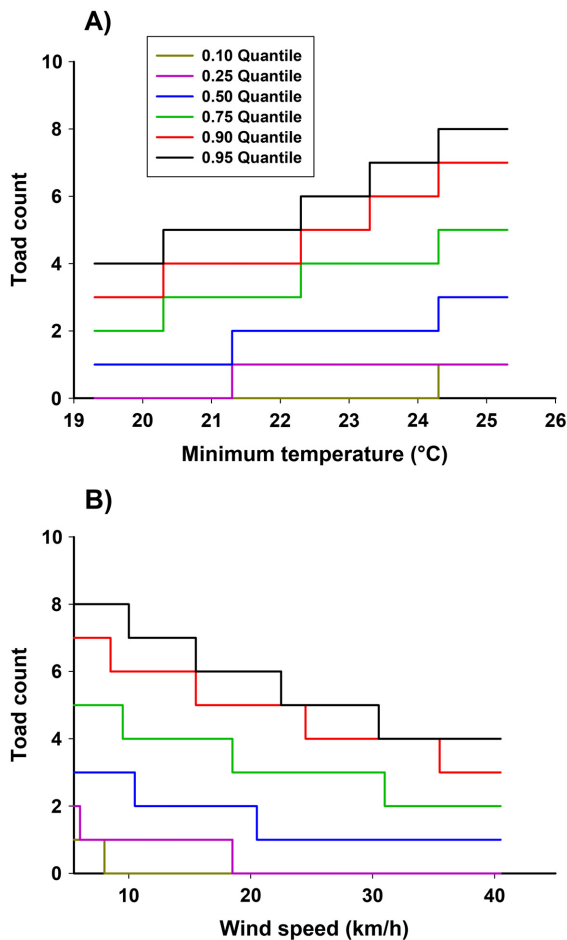


Fig. 6. Estimated quantile count model, including a first-order temporal autocorrelation effect, for cane toad captures ( $n = 148$ ) on Orpheus Island in the pre-wet season (September–November 2013), as a function of minimum temperature, with wind speed and lagged toad counts fixed at their median values (A), and as a function of wind speed, with minimum temperature and lagged toad counts fixed at their median values (B), estimated using a ceiling function. An average of estimates for  $m = 500$  random jitterings for cane toad counts was used.

speed had a negative effect on all quantiles  $\geq 0.10$  of the toad counts, when minimum temperature was fixed at its median value (Fig. 3). When  $\tau \geq 0.75$ , the proportional changes in counts decreased 42–45% as wind speed increased from 5 to 20 km/h (Fig. 8B). This indicated that wind may have limited toad activity in the wet season, given that the rate of change of toad counts was

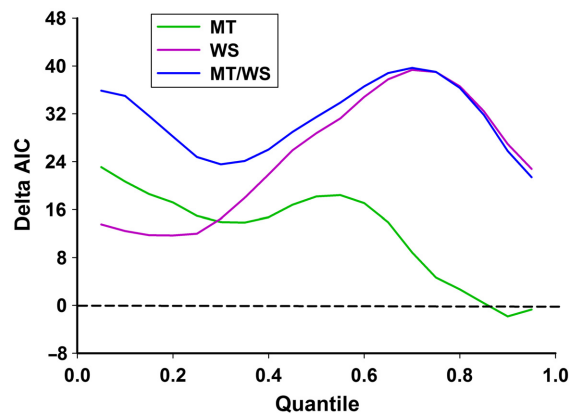


Fig. 7. Change in average  $\Delta$ AICs of models containing minimum temperature, wind speed, and a combination of both variables, across  $\tau \in \{0.05, 0.10, 0.15, \dots, 0.95\}$ , for  $m = 500$  replications of  $z = y + U[0, 1]$ , on Orpheus Island, in the wet season (December 2013–February 2014). The relative strength of models containing individual environmental variables in the wet season is shown in Fig. 2C. In the wet season, a combination model containing minimum temperature and wind speed was strongest at quantiles  $\leq 0.70$ , and within 2  $\Delta$ AIC units of the strongest model at upper quantiles. AIC, Akaike's information criterion.

highest at quantiles near the maximum of the distribution. Overall, the model indicated that warm, still nights were most conducive to toad activity. While minimum temperatures were generally warm enough to facilitate high toad activity, wind speed constrained the maximum activity of toads, and may be the primary driver of activity in the wet season.

#### Post-wet season

In the post-wet season, moon luminosity was the strongest predictor of toad activity; the model including moon luminosity had the highest average  $\Delta$ AIC for  $m = 500$  replications of jittered toad counts, across most quantiles (Fig. 2D). This model was strongest at the lower limits of the distribution, and gradually weakened at higher quantiles. The model that included a first-order temporal autocorrelation, in combination with moon luminosity, was never within 2  $\Delta$ AIC units of the selected model at any quantile, and was not considered further. Although the negative effect of moon luminosity on toad activity was strong at quantiles  $\leq 0.50$

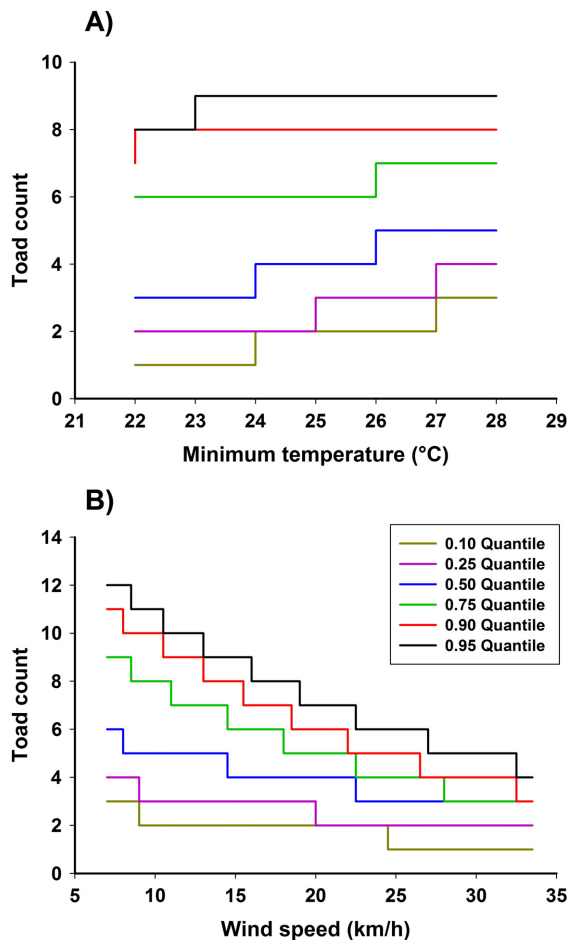


Fig. 8. Estimated quantile count model for cane toad captures ( $n = 108$ ) on Orpheus Island in the wet season (December 2013–February 2014), as a function of minimum temperature, with wind speed fixed at its median value (A), and as a function of wind speed, with minimum temperature fixed at its median value (B), estimated using a ceiling function. An average of estimates for  $m = 500$  random jitterings for cane toad counts was used.

(Figs. 2D, 3), none of the models had an average  $\Delta AIC > 2$  at quantiles  $\geq 0.80$ , indicating that none of the measured variables limited toad activity in the post-wet season. The proportional changes in counts decreased 67–200% (to zero in some cases) at quantiles  $\leq 0.50$  as moon luminosity increased from 0% to 52% (Fig. 9). The decrease in proportional changes in counts was not as rapid at moderate to high moon luminosities ( $\geq 52\%$ ), at quantiles where counts were above

zero. This may indicate that most toads preferred dark conditions in the post-wet season, and were not active when moon luminosity was  $\geq 52\%$ ; however, some toads were always active, regardless of moon luminosity.

## DISCUSSION

Overall, several different variables had synergistic and antagonistic effects on cane toad activity. Using our combination of statistical techniques, we detected the influence of environmental variables on both lower and upper bounds of toad activity. We also found that there was high seasonal variability in cane toad activity; toads were more active in the wet season (December–February) and less active in the dry season (June–August). Furthermore, there was variability in the combinations of environmental variables that influenced toad activity, depending on the time of year. This may be because particular environmental variables were sufficient for minimum activity during certain seasons, but not others.

Results acquired using model selection on quantile count models were consistent with expectations based on the physiological requirements of cane toads. For example, rainfall was the strongest predictor of toad activity in the dry season, across all measured quantiles. Minimum

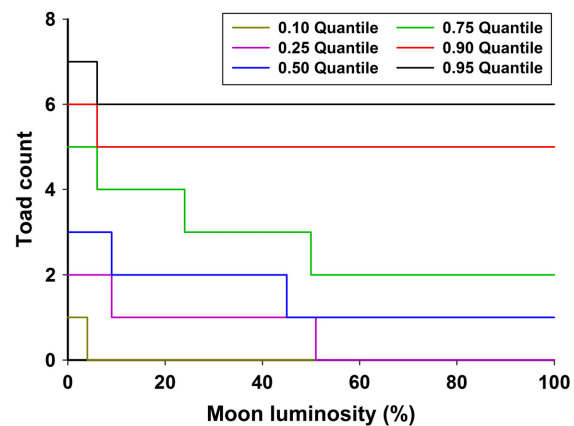


Fig. 9. Estimated quantile count model for cane toad captures ( $n = 78$ ) on Orpheus Island in the post-wet season (May 2013, March 2014), as a function of moon luminosity, estimated using a ceiling function. An average of estimates for  $m = 500$  random jitterings for cane toad counts was used.

toad activity increased up to 200% when rainfall exceeded 20 mm, suggesting that many toads may be generally inactive during the dry season, and only emerge from their burrows, forage, or search for mates, when rainfall is high. Cane toads emerge from their burrows more frequently (Seebacher and Alford 1999), and move longer distances (Schwarzkopf and Alford 2002) when there is more atmospheric and soil moisture, probably because moist conditions limit water loss *via* their permeable skin (Schwarzkopf and Alford 1996). The first-order temporal autocorrelation effect evident in the dry season indicated that activity on a given night partially predicted activity on the subsequent night. This could be interpreted as a lagged effect of rainfall, where soil moisture was comparatively high for several consecutive nights after rain, which created extended periods of favorable conditions for toad activity. Rainfall in the dry season was rare; therefore, the physiological cost of movement was generally high. Toad capture rates increased with rainfall, probably because the cost of movement (i.e., water loss) was lower than in dry periods (Schwarzkopf and Alford 2002).

In the wet season, wind speed appeared to limit toad activity (Fig. 8B). This may be because evaporative water loss rates increase when wind speed is high (Bentley and Yorio 1979); therefore, toads may reduce activity when wind exceeds a certain speed. High winds may also reduce insect activity (Holyoak et al. 1997), so toads may be less active for feeding, and our insect-attracting UV light lure may also be less attractive when it is windy (McGeachie 1989). Windy conditions may have also increased the excess attenuation of the call used to lure toads, and therefore reduced the distance the call carried (Larom et al. 1997). The strongest predictor model in the wet season also included minimum temperature, the effect of which was strongest at lower quantiles. Toad captures increased a great deal (67–200%) at lower quantiles ( $\leq 0.5$ ), when minimum temperature increased 4°C (from 24° to 28°C), while captures at upper quantiles, across the same temperature range, remained relatively stable. This large increase in toad captures with a relatively small increase in ambient temperature indicates that minimum temperature in the wet season was well above the minimum threshold for toad activity, because many toads were active, regardless of

temperature. The increase in minimum toad activity is consistent with the strong increase in toad locomotor performance from a preferred temperature of 24°C toward a thermal optimum of approximately 30°C (Kearney et al. 2008). The availability of temperatures conducive to high performance may have encouraged activity from even the most inactive toads, and greatly increased their chance of capture.

Our toad activity models included various combinations of rainfall, minimum temperature, and wind speed in most seasons. However, in the post-wet season, moon luminosity appeared to influence toad activity, especially at lower quantiles. Activity in the post-wet season may occur because there is a need to feed after breeding in the wet season (Yasumiba et al. 2016). Toads strongly avoid light (Davis et al. 2015), but will feed under lighted conditions if there is food available (González-Bernal et al. 2011). We suggest some toads limited their activity as ambient light increased; however, bolder (or hungrier) individuals may have continued feeding in spite of the moonlight. Several studies report depressed nocturnal activity in amphibians due to moonlight, probably because amphibians avoid light, which may occur because there is an increase in their detectability to predators in lighter conditions (reviewed in Grant et al. 2012). It was surprising that the moonlight effects were only detectable in one season and that the magnitude of reduction in activity appeared to vary across the moon luminosity spectrum. Possibly, the effects of moonlight were most detectable in this season because, after the wet season, toad activity was most strongly determined by foraging needs. Temperature and humidity were still high enough to encourage activity, so that an otherwise weak effect of moon luminosity, not detectable in other seasons, when other factors (such as reproduction or hydration) were affecting the toad's propensity to be active, then became influential.

One of the main strengths of quantile count models, and the quantile regression approach more generally, is that prediction intervals for future new observations are easily obtainable, without any of the parametric distributional assumptions (e.g., a normal error distribution) required for interpretation of prediction intervals obtained using ordinary least squares regression (Neter et al. 1996, Cade and Noon 2003). In

quantile regression, the interval between 0.10 and 0.90 quantile regression estimated at any specified value of  $X$  is an 80% prediction interval for a single future observation of  $y$  (Cade and Noon 2003). For example, in the dry season, the 80% prediction interval increases from 0–4 toads when rainfall is 10 mm, to 1–8 toads when rainfall is 25 mm (Fig. 4). Conversely, in the wet season, the 80% prediction interval decreases from 2–10 toads when wind speed is 10 km/h to 1–5 toads when wind speed is 25 km/h (Fig. 8B). Our quantile count models characterize the variability of prediction intervals for future toad counts reasonably, in each season, with few assumptions. An additional advantage of the quantile count model over traditional parametric count models is that it avoids having to select from among various parametric distributions (e.g., Poisson, negative binomial, and their zero-inflated counterparts).

Examining rates of change at various points across cane toad capture distribution models, using model selection, enabled us to more effectively examine the influence of several environmental factors across the entire distribution. Our jittered quantile count model is particularly useful when the dependent variable includes many tied values, across a small range of values. Indeed, nightly numbers of toads captured often ranged between 0 and 5 (89% of the toad counts fell within this range). Thus, our jittered quantile count model allowed for interpretation of a discrete count response variable with many tied values, across an extremely limited range of values (Machado and Santos Silva 2005, Cade and Dong 2008). Finally, our model selection procedure allowed us to select strong predictor models at any quantile in the distribution to include in combination models, while simultaneously rejecting weak predictor models that may have otherwise added an uninformative parameter to the combination model (Arnold 2010). This method streamlined the model selection process and reduced the chance of misinterpretation of AIC results (see Arnold 2010).

Model selection on quantile count models was extremely effective at examining, in depth, the effect of environmental variables on cane toad trapping rates, and activity. Our study provides a simple example of this methodology, using only five environmental variables. Future studies

could incorporate a wider range of variables to better approximate the factors effecting activity, and counts. This methodology could also be used for standard quantile regressions, when the range of values is large, with few tied values, using a process similar to generalized linear modeling to obtain slope estimates at various quantiles across the distribution. The independent use of AIC model selection, and quantile count models, is not new; however, we have demonstrated that the use of both methods, simultaneously, can allow us to examine extensively the relationship between environmental variables and rates of capture in trapping and mark–recapture regimes, and also to determine which of these variables affect the study organism's activity.

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