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DETECTION PROBABILITY AND SITE OCCUPANCY OF THE GRANULAR SPINY FROG (*Quasipaa verrucospinosa*) IN THE TROPICAL RAIN FORESTS OF BACH MA NATIONAL PARK, CENTRAL VIETNAM

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Amphibian species are rarely detected with perfect accuracy, regardless of the method employed. A large-scale assessment for *Quasipaa verrucospinosa* occupancy was conducted at 35 sites in the primary forest and 42 sites in the secondary forest of Bach Ma National Park, central Vietnam. Based on the detection data for each site, the distribution of *Q. verrucospinosa* was estimated in different habitat types using occupancy models. From the best model among all performed models, we estimated a site occupancy probability of 0.576 that was higher than the naive occupancy estimate of 0.403 and a 43.1% increase over the site proportion at which *Q. verrucospinosa* was actually observed. The site covariate of the primary forest was an important determinant of site occupancy, which was not associated with the variable of secondary forest. In a combined AIC model weight: the p(temperature), p(humidity), and p(precipitation) models have 47.3, 67.1, and 90.9% of the total, respectively; providing evidence that aforementioned environmental conditions were important sample covariates in modelling detection probabilities of *Q. verrucospinosa*. Our results substantiate the importance of incorporating detection and occupancy probabilities into studies of habitat relationships and suggest that the primary forests associated with weather conditions influence the site occupancy of *Q. verrucospinosa* in Bach Ma National Park, central Vietnam.

Keywords: Detection probability; maximum likelihood; metapopulation; site occupancy; *Quasipaa verrucospinosa*; rainforests; Vietnam.

INTRODUCTION

Tropical amphibian species are rarely detected with perfect accuracy, regardless of the technique used (MacKenzie et al., 2006). Non-detection of the species at a site during a single survey does not necessarily mean that a species of interest was absent unless the detection probability of the species (detectability) was 100% (MacKenzie et al., 2002). Detectability can vary among sampled sites (habitat variables) and may be related to climatic characteristics of a specific survey on a particular day (i.e., air temperature, relative humidity, and other weather conditions), whereas the occupancy of amphibians relates only to site characteristics.

Large-scale monitoring programs for amphibian species (Seber, 1982; Williams et al., 2002; Kaiser, 2008) often relied on remotely sensed data (data on amphibians that has been gathered using biophysical variables derived from remote-sensing instruments on satellites or from moderate resolution imaging spectroradiometers) to depict spatial models in habitat occupancy (Carey et al., 2001; Shive et al., 2010; Bisrat et al., 2012). Ignoring detectability may lead to biased estimations of site occupancy (Tyre et al., 2003; Gu and Swihart, 2004; Weir et al., 2005) and studies of habitat occupancy are often hampered by imperfect detectability for the target species (MacKenzie et al., 2003, 2004; Dorazio et al., 2006; Bailey et al., 2007; Nichols et al., 2007).

Many conservation programs seek to provide inferences about regions that are too large to be completely surveyed. Therefore, smaller areas must be selected to survey, with the selection being conducted in a manner that permits inference to the entire region of interest (Thompson, 1992; Yoccoz et al., 2001; MacKenzie et al., 2002; Pollock et al., 2002). Solely using the count statistic (not allowing for detectability) as an index to abun-

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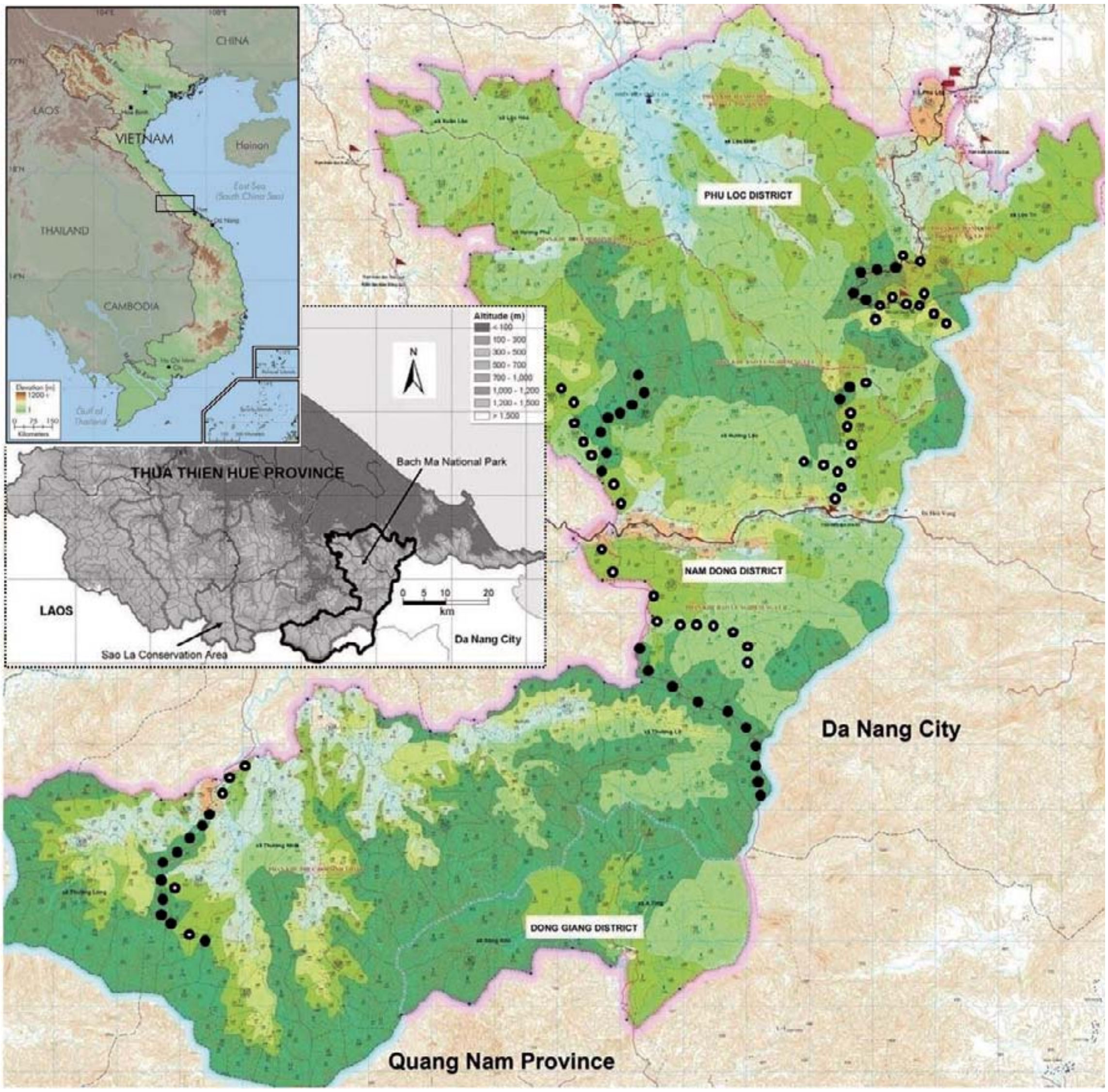

Fig. 1. Location of survey sites on a map of Bach Ma National Park, Thua Thien-Hue Province, central Vietnam, showing 35 plots in primary forests (filled circles) and 42 plots in secondary forests (open circles), where *Quasipaa verrucospinosa* was monitored during the breeding season (from September to December).

dance is unwise (e.g., Seber, 1982; Williams et al., 2002). Thus, inferences regarding the influences of site characteristics on occupancy will be difficult or impossible to discern reliably (e.g., Gu and Swihart, 2004).

Currently, the populations of *Quasipaa verrucospinosa* in Bach Ma National Park are decreasing due to environmental degradation, loss of forest and stream habitats, as a result of logging, and overexploitation for food consumption. Significant regions of appropriate habitat types appear to be covered by the collective protected regions of Viet Nam and Laos, but logging is still an important problem in these regions (van Dijk and Swan, 2004). However, little is known about population status and ecological characteristics of *Q. verrucospinosa* in central Vietnam. Information on the site occupancy of *Q. verrucospinosa* in the primary and secondary forests of Bach Ma National Park is lacking. It is especially critical as these terrestrial habitats have been identified as important to conservation programs (Lehtinen and Galatowitsch, 2001; Weyrauch and Grubb, 2004; Reilly et al., 2007; Vitt and Caldwell, 2009; Nguyen et al., 2013).

In this study, we estimated detection probabilities and site occupancy of *Q. verrucospinosa* in Bach Ma National Park, Thua Thien Hue Province, central Vietnam, to (1) compare detection and occupancy probabilities for two specific habitat types (primary and secondary forests); (2) to obtain an overall estimate of site occupancy for the entire national park; and (3) to assess the habitat type of *Q. verrucospinosa* frogs using occupancy models. We examined the effects of site covariates, including air temperature, relative humidity, and precipitation, on the detection and occupancy of *Q. verrucospinosa* frogs, and tested the hypothesis that differences between two habitat types result in different levels of detection.

MATERIAL AND METHODS

Study sites. The fieldwork took place in the tropical rain forests of Bach Ma National Park (15°59′12″ – 16°16′09″ N 107°37′06″ – 107°54′14″ E, approximately 37,487 ha in size according to the Prime Minister of Vietnam's decision 2008; unpublished data), central Vietnam (Fig. 1). The study area is dominated by montane rain forests at elevations of 700 – 1400 m a.s.l. and cloud forests from about 1400 m a.s.l. up to summits at 1712 m a.s.l. (Nguyen et al., 2004, 2013; Ngo et al., 2014). Seasonal monsoons and a tropical climate characterize this study area, with annual temperatures (over the last 10 years) averaging 22.6 ± 0.26°C (ranging from 16.9 ± 0.39°C in January to 26.6 ± 0.36°C in June) and an annual mean precipitation of 3492 ± 229 mm. Most of the rainfall is concentrated in the main rainy season from September to December (monthly mean: 629.2 ± 44.1 mm) and the little rainy season (monthly mean: 149.2 ± 14.5 mm) from May to August, whereas the period from January to April is relatively dry, with a monthly mean rainfall of 94.6 ± 12.8 mm (Data obtained from the monographs and climatic-hydrology characters of Thua Thien Hue Province over the last 10 years; Nguyen et al., 2004, 2013).

Sampling. The study area comprised two habitat types, primary forests (ca. 32.2%; the canopy is not fragmented) and secondary and restored forests (54.0%; fragmented canopy) (Hoang et al., 2012; Nguyen et al., 2013). We conducted seven surveys from September to December 2016 during the breeding season of *Q. verrucospinosa* (Ngo et al., 2013) in primary and secondary forests. We set up 77 sampling plots of 20 × 50 m (1000 m^2 each plot) in size, comprising 35 plots in the primary forest and 42 plots in the secondary forest (Fig. 1). Sample plots were set up along forest streams or marsh, in a distance of about 300 m apart from each other to ensure independence among plots.

We visited and sampled each plot every 2 weeks, at the same time of the day. At each site, two people walked slowly along the plot for 10 – 20 min, and visually searched for frogs using spotlights from 7:00 pm to 02:00 am. We searched for *Q. verrucospinosa* in the water where it was visible and reachable, on land up to 10 m away from the stream or the marsh, or on tree trunks and vegetation.

Data analyses and model selection. The encountered specimen was coded as 1 if detected or 0 if not detected. Using field observations of forest canopy gathered prior to this study, we determined the level of the secondary forest variable at each plot, and a covariate was coded as 1 for the secondary forest and 0 for the primary forest. At each plot, we also recorded ambient temperature (temp) and relative humidity (humid) using a WISEWIND thermometer (Taiwan) for each visit. The covariate of rainfall (rain) was defined as 1 if it was rain and 0 if it was sunny or clouded during the daytime. These variables were considered sample covariates to estimate detection probability. When an individual was detected, we recorded the position of the specimen (e.g., underwater, on land or on the tree).

We used program PRESENCE (Version 12.10) and single-season occupancy models to estimate detection and occupancy probabilities. This model assumes that sites or plots/patches were closed to changes in occupancy between the first and last surveys of a given sampling season (i.e., no colonization, emigration or immigration within the sampling season), and detection of the target species at a site is independent of detecting the species at other sites (MacKenzie et al., 2002, 2003). We used the following parameters of interest for the present study: ψ is the probability of a site being occupied by *Q. verrucospinosa* and p_j is the probability of detecting the species during the jth survey given that it is present.

We used 16 candidate models without considering interactions between factors (Table 1) to assess detection and occupancy probabilities in two habitat types, including two essential models for the present study. The first model that assumes that detection and occupancy probabilities with respect to *Q. verrucospinosa* are constant across sites and surveys [denoted $\psi(\cdot)p(\cdot)$]. The second model assumes constant occupancy among sites, but detection probabilities are allowed to vary among seven survey occasions [denoted $\psi(\cdot)p(\text{survey})$]. Previous studies suggest that the detection probability ≥0.15 in the model $\psi(\cdot)p(\cdot)$ is needed for unbiased occupancy modelling (Bailey et al., 2004; O'Connell et al., 2006). Our model $\psi(\cdot)p(\cdot)$ with a detection probability of 0.3298 (SE = 0.0354) is appropriate to pursue inference and to estimate the details of the parsimonious process of model selection. In the present study, detectability was either constant across all survey occasions and sites $p(\cdot)$ or varied in three possible ways: among seven survey occasions p(survey), or across sites according to weather conditions p(temp, humid, rain).

We used the Akaike Information Criterion for small sample size (AIC$_c$) and referred to Burnham and Anderson (2002) and Mazerolle (2006) to make inferences. All models with AIC differences of <2.0 have a substantial level of empirical support and should be considered when making statistical inferences or reporting parameter estimates of the best models. We also estimated an overdispersion parameter (c) from 10,000 bootstrap samples using the PRESENCE software for the global model (the most general model in the model set or the model with the most parameters) from the candidate models. All data are presented as mean ± 1 SE (unless otherwise noted) with a 95% confidence interval (CI).

RESULTS

The Granular Spiny Frog was detected at least once at 31 of the 77 plots (eight plots in secondary forests and 23 plots in primary forests), yielding an overall naïve occupancy estimate of 0.403, clearly indicating that detection probability of the species in the tropical rain forests of Bach Ma National Park is less than one. However, we believed that *Q. verrucospinosa* frogs may be more likely to occupy undisturbed plots in primary forests compared to disturbed plots in secondary forests. There might conceivably be a number of locations where *Q. verrucospinosa* was present but simply never detected during the seven surveys. Our detection-corrected occupancy estimates by the site in primary and secondary forests of the national park ranged from 0.143 – 0.714 (an average naïve occupancy = 0.351 ± 0.032). The proportion of sites occupied by *Q. verrucospinosa* from the constant model $\psi(\cdot)p(\cdot)$ was 0.433 ± 0.0612 (CI = 0.319 – 0.554). The second model assumes that all sites have the same occupancy probability, but that p can vary among the seven surveys. The proportion of occupied sites based on the second model $\psi(\cdot)p$(survey) was 0.433 ± 0.0611 (CI = 0.319 – 0.554). However, the estimated occupancy in the global model ψ(PF)p(temp, humid, rain) was 0.576 ± 0.1271 (CI = 0.339 – 0.793). Clearly, accounting for detection and occupancy probabilities have increased the evaluated level of site occupancy of *Q. verrucospinosa* after combined with affected factors.

The estimated occupancy probability is the same in the two basic models (0.433 and 0.433 from the first and secondary models). When estimating occupancy probabilities including only two models [($\psi(\cdot)p(\cdot)$ and $\psi(\cdot)p$(survey)], both models gave the same results, and both were about 8% larger than the naïve occupancy estimate. It is suggested that *Q. verrucospinosa* was never detected at one in every seven surveys. However, in terms of detection probability and site occupancy, we believe that the relative abundance of *Q. verrucospinosa* frogs in primary forests was higher than that in secondary forests (Table 1).

Testing the global model (the model included six parameters with AIC differences of <2.0 units) from the candidate set (Table 1), the model [ψ(PF)p(temp, humid, rain)], does not show any evidence of overdispersion ($\chi^2 = 207.87$, P-value = 0.911, weighted $\hat{c} = 0.436$), indicating insufficient evidence of the poor model fit using 10,000 bootstrap iterations. The adjustment has been made to the model selection procedure (AIC) and parameter assessments to estimate the details of this parsimonious process of model selection. Detectability varied among surveys and possibly among sites with previously disturbed and undisturbed histories of habitat types for *Q. verrucospinosa* frogs (Fig. 2).

Our candidate set contained the sixteen models that ranked according to AIC and without considering interactions between factors (Table 1). There was no single model that was demonstrably better than the others. The six best models are separated by less than 2.0 AIC units, which means that these models have substantial support and should be considered when reporting parameter estimates or making inferences (Table 1). As such, the AIC model weight (w) is distributed across a number of mod-

TABLE 1. Summary of AIC Model Selection Procedure for *Quasipaa verrucospinosa* from 77 Plots in Bach Ma National Park, Central Vietnam

Models	AIC$_c$	ΔAIC$_c$	w	K	$-2l$
ψ(PF), p(humid, rain)	322.33	0.00	0.242	5	300.33
ψ(PF), p(temp, humid, rain)	322.45	0.12	0.228	6	314.45
ψ(PF), p(temp, rain)	323.39	1.06	0.143	5	313.39
ψ(SF), p(temp, humid, rain)	324.05	1.72	0.102	6	314.05
ψ(SF), p(humid, rain)	324.12	1.79	0.099	5	300.12
ψ(PF), p(rain)	324.19	1.86	0.095	3	300.19
ψ(PF), p(temp, humid)	325.36	3.03	0.053	5	313.36
ψ(SF), p(temp, rain)	326.06	3.73	0.038	5	300.06
ψ(SF), p(temp, humid)	342.75	20.42	0.000	5	332.75
ψ(SF), p(rain)	348.01	25.68	0.000	3	342.01
ψ(PF), p(temp)	368.28	45.95	0.000	3	362.28
ψ(SF), p(temp)	368.28	45.95	0.000	3	362.28
ψ(PF), p(humid)	374.71	52.38	0.000	3	368.71
ψ(SF), p(humid)	377.68	55.35	0.000	3	372.09
$\psi(\cdot)$, $p(\cdot)$	383.14	60.81	0.000	2	379.14
$\psi(\cdot)$, p(survey)	393.13	70.8	0.000	8	377.13

Note. ΔAIC$_c$, the difference in AIC value for a particular model when compared with the top-ranked model; w, the AIC model weight; K, the number of parameters; $-2l$, twice the negative log-likelihood value; PF, primary forest; SF, secondary forest; temp, temperature; humid, relative humidity; rain, precipitation.

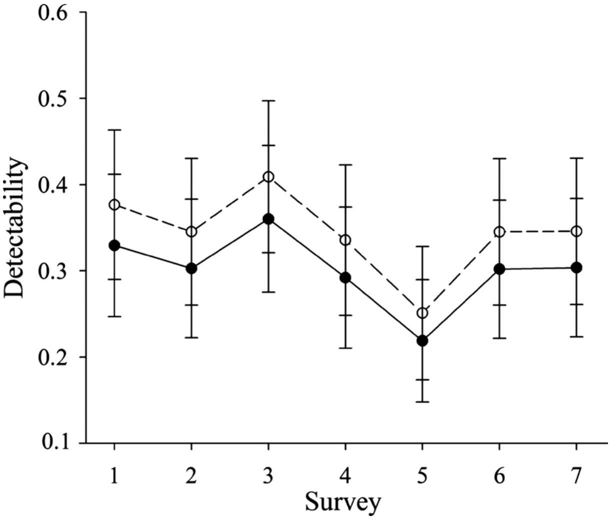

Fig. 2. Estimating the average pattern of detectability across surveys and among sites with different disturbance histories of *Quasipaa verrucospinosa* in Bach Ma National Park, central Vietnam. Undisturbed habitat (broken line, open circles) and disturbed habitat (solid line, filled circles).

els, indicating that a number of models may be reasonable for our collected data. In terms of model weights of sampled covariates, the *p*(temperature), *p*(humidity), and *p*(precipitation) models have 47.3, 67.1, and 90.9% of the total, respectively. Our results provide clear evidence that weather condition is an important factor in terms of accurately modelling detection probabilities. In terms of comparing hypotheses, the hypothesis that the detection probability varied among weather conditions, therefore, has much greater support than the hypothesis that it was constant.

In terms of occupancy probability, based upon rankings and AIC model weights, the combined weight for the ψ(primary forest) model was 70.8%, and the ψ(secondary forest) model was 9.9% (Table 1), indicating a certain evidence that the probability of occupancy is higher in the primary forest plots than those in the secondary forest (evidence ratio [Akaike weight of the ψ(PF) model/Aikaike weight of the ψ(SF) model = 7.15 times). Thus, the secondary forest variable was not strong determinants of *Q. verrucospinosa* occupancy in Bach Ma National Park, central Vietnam.

DISCUSSION

The occupancy of *Quasipaa verrucospinosa* in Bach Ma National Park forests is not associated with the secondary forest variable. Excluding the two basic models, four models include the secondary forest covariates with the values of $\Delta AIC_c > 20.4$ units and all AIC model weights are zero. These findings were similar to previous studies that showed that *Q. verrucospinosa* frogs were more commonly found in the primary forests of central Vietnam (van Dijk and Swan, 2004, Ngo et al., 2013, 2015). In fact, we sampled in two forest types (42 plots in the secondary forest and 35 plots in the primary forest). However, the specimens of *Q. verrucospinosa* were only found at eight plots with eight individuals in the secondary forests. We speculate that air temperature, relative humidity, and abundant precipitation during our surveys may have lessened the effects of forest types because weather conditions were important covariates for the site occupancy and detectability of *Q. verrucospinosa* in the tropical forests of Bach Ma National Park. The presence of a forest canopy that regulates air temperature and forest soil moisture appears more critical in determining the survival of amphibians and movement models (Porej et al., 2004; Price et al., 2004). Previous studies showed that some anuran species (particularly juveniles) have indicated a preference for habitat types with forested canopies compared with fragmented forests or open-vegetation types (Demaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Ngo, 2015).

The occupancy of *Q. verrucospinosa* relates only to site characteristics, whereas the probability of detecting a species during a single survey can vary with survey characteristics (e.g., temperature and precipitation) and site characteristics (e.g., habitat variables such as forest types) (MacKenzie et al., 2006). An observed absence at a site occurs if either the species was truly absent or not detected; while non-detection of a species does not mean that that species was truly absent unless the detection probability of the species was 100%. That is the reason why previous occupancy studies are often impeded by imperfect detectability (Gu and Swihart, 2004; MacKenzie et al., 2003). From the best model ψ(PF)*p*(temp, humid, rain) in the total candidate models are given in Table 1, with the occupancy estimate of 0.576 comparing to the naïve occupancy estimate of 0.403 was completely reliable. Although we did not consider colonization probabilities, emigration, and immigration, these two variables often influence parameter estimates in long-term monitoring programs of amphibians (Hanski, 1994; Moilanen, 1999; MacKenzie et al., 2003).

Moreover, our parameter estimates have also satisfied normal assumptions of a model of single-species and single-season occupancy (MacKenzie et al., 2006), including (1) the occupancy state of the sites does not change during the survey period, but it can change between survey periods, (2) the detection of the species in each survey occasion of a site is independent of detections within other survey occasions of the site, (3) occupancy probability is the same across sites or differences in habitat occupancy may be explained with site traits (covariates), (4) species detection probability at occupied sites is the same across all sites and surveys, or differences in detection probability can be explained with survey or site traits, and (5) the detection histories observed at each location are independent for a species of interest.

A brief examination of the estimated detection probabilities clearly indicates why the overall level of occupancy is 43.1% larger than the naïve occupancy estimate, the estimation based on the number of sites where *Q. verrucospinosa* frogs were detected during seven surveys. Estimates for detection probabilities for each sampling covariate showed that the rainfall is the most important covariate. There is clearly a reasonable level of substantial differences among sampling covariates (temperature, relative humidity and rainfall). Furthermore, the detection of a species at each plot is indeed indicative of the presence but non-detection of a species is not equivalent to the absence unless the detecting probability of the species was one, and a species can go undetected at a site or some sites even when present. Therefore, non-detection sites of a frog represent a case where the target species was never detected. These sites could either be unoccupied, which mathematically is $(1 - \psi)$, or they could be occupied but we never detected the target species during k survey occasions, which mathematically is $\psi(1 - p_j)^k$. Both of these detectabilities have been included in maximum likelihood methods incorporated in program PRESENCE to obtain estimates of occupancy and detectability (MacKenzie et al., 2002).

Parameter assessments and associated confidence intervals from pattern averaging indicated that the primary forest was an important determinant of *Q. verrucospinosa* occupancy in Bach Ma National Park. The effects of forest types on site occupancy and detectability of amphibians emphasize the importance of conducting longer-term studies for describing critical habitat relationships (Skelly et al., 1999, 2003).

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