

# Ghost-busting: patch occupancy and habitat preferences of *Ocyale ghost* (Araneae: Lycosidae), a single site endemic in north-western Madagascar

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## Abstract

Microendemic species are of great conservation concern due to their vulnerability to stochastic events and environmental change. Therefore, understanding the basic ecology of such organisms is integral to future efforts to conserve them. Here, we present the first ecological study of the only known population of *Ocyale ghost* Jocque & Jocqué 2017 – the single species within this genus in Madagascar – located at a small lake shore in the north-west of the island. We aimed to reveal spatial patterns of microhabitat selection and patch occupancy in relation to environmental covariates, including distance to lake edge, topography and sand coverage. We found microhabitat selection to be strong in our occupancy models, with plots closer to the lake edge and with a higher proportion of sand showing the highest estimated occupancy. We suggest decreases in prey availability and changes in the physical characteristics of the substrate in relation to the distance from lake shore and sand availability (important for burrowing and temperature regulation), respectively, as potential factors behind occupancy. We discuss our findings in the context of the proportional underrepresentation of invertebrates in conservation research, which threatens the persistence of endemic and microendemic invertebrates in the face of significant global and local environmental change.

## Key words

burrowing, conservation, microendemic, occupancy modelling.

## INTRODUCTION

There is a profound lack of ecological knowledge on invertebrates, hampering conservation efforts (Gerlach 2008; Cardoso *et al.* 2011). Many are thought to go extinct before being studied (Platnick & Raven 2013), let alone being assessed against IUCN Red List criteria (Régnier *et al.* 2015). Indeed, extinction risk has been assessed for 66.7% of 69 788 described mammal species, yet only 1.9% of 1 159 365 described invertebrate species (IUCN 2018). Invertebrates fulfil crucial functions within ecosystems (Weisser & Siemann 2008) and they are, therefore, essential for not only the natural world but also human livelihoods, health and wellbeing (Gallai *et al.* 2009; Beynon *et al.* 2015). However, studies on invertebrates are proportionally lacking compared to other taxa, and calls for population and range studies are widespread throughout the literature (Balmford *et al.* 2005; Butchart *et al.* 2007; Cardoso *et al.* 2011).

Endemism has long been used as a means of identifying areas for conservation prioritisation (e.g. Freitag & van Jaarsveld 1997), and endemic invertebrate species may have narrow-range sizes and niche breadth, with a closer relationship with the environment than more widespread species (Rabitsch *et al.* 2016). In this sense, Madagascar's levels of endemism are especially pronounced in a global context, its biota having long been recognised as exceptional (Mittermeier *et al.* 1998; Kremen *et al.* 2008; Vences *et al.* 2009) alongside 24 other global biodiver-

sity hotspots (Myers *et al.* 2000). Endemism, proportionate to land area, is unparalleled (Mittermeier *et al.* 2011): 100% of native amphibians, 86% of macro-invertebrates and over 90% of vascular plants are endemic (Wilmé *et al.* 2012). Historical biodiversity estimates for Malagasy fauna are also proving to be underestimates (Vieites *et al.* 2009).

Microendemism is common in the country, with species often restricted to utilising habitat at fine spatial scales, especially in forests (Goodman & Benstead 2005) and areas surrounding low elevation river catchments (Wilmé *et al.* 2006). Many invertebrates in Madagascar exhibit small populations and restricted ranges, with isolated habitats potentially harbouring microendemic species (Irwin *et al.* 2010).

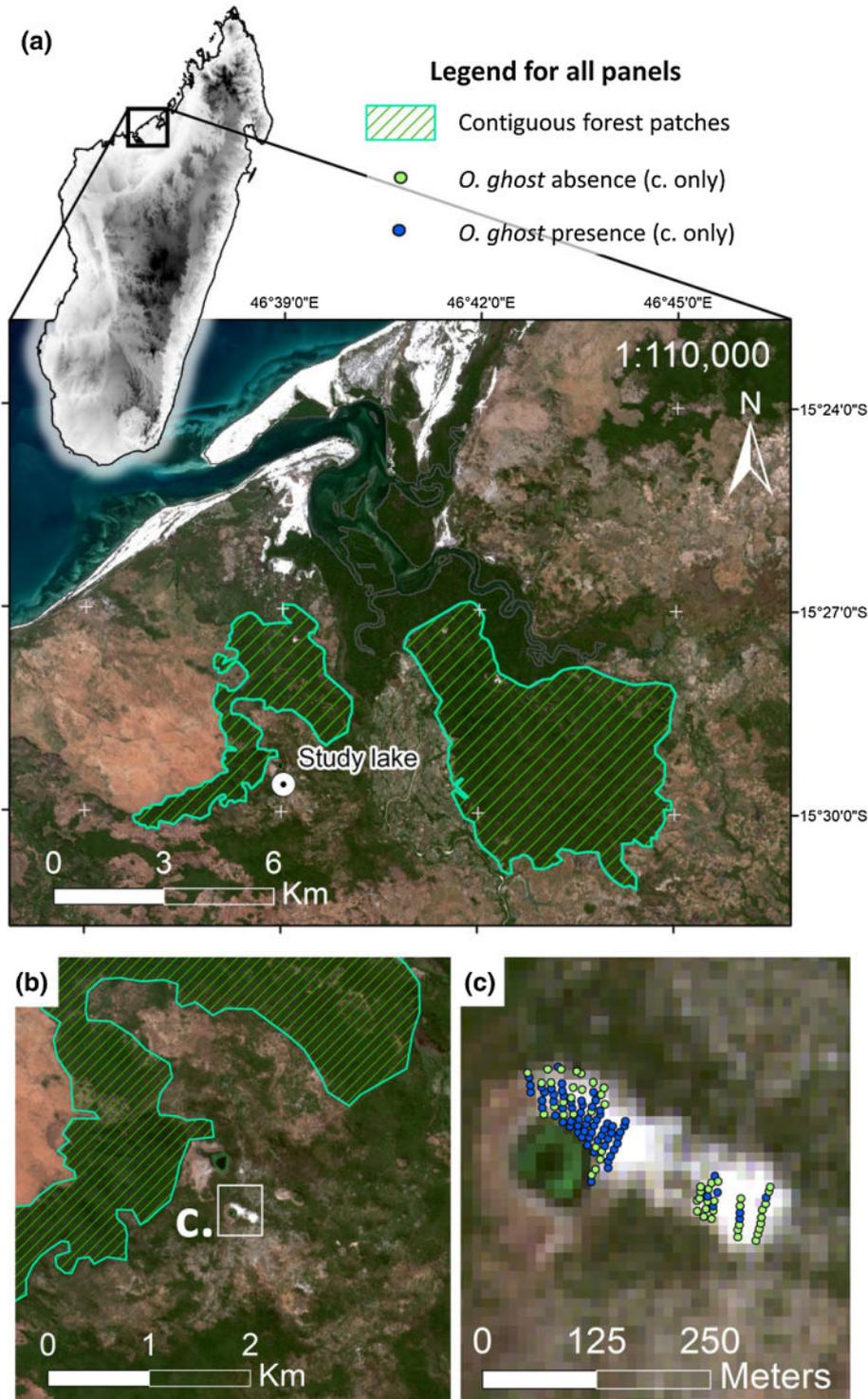
Distribution patterns of specialist invertebrates have been shown to be particularly influenced by habitat quality (Poniatowki *et al.* 2018). Indeed, patch size and connectivity significantly increased patch occupancy in five threatened invertebrate species in Europe (Maes & Bonte 2006). Meanwhile, the distribution of short-range endemic grasshoppers in South Africa was most affected by vegetation type (Adu-Acheampong *et al.* 2017). The role of fine-scale habitat characteristics is therefore emerging as an important general factor for invertebrate distributions.

Spiders have been shown to select living sites based on increased foraging efficiency; i.e. web building (Ruch *et al.* 2011), reduced predation (Rypstra *et al.* 2007) and the presence of beneficial species in the microhabitat (Sinclair *et al.* 2001). A specialist is more likely to survive and thrive in its optimal habitat because of a competitive advantage; however, dispersal may be

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restricted (Bonte *et al.* 2006). For example, specialist *Carabus* species show reduced dispersal compared to sympatric generalists (Brouat *et al.* 2003), whilst increased habitat specificity is negatively associated with propensity for aerial dispersal in spiders (Bonte *et al.* 2003b) due to the increased chances of landing

in an unfavourable habitat. This trade-off is significant when considering psammophilous Lycosidae because their range is likely to be limited by specific environmental conditions that define its niche, and it is therefore difficult to disperse across unsuitable areas that present environmental barriers (Bonte *et al.* 2006).



**Fig. 1.** (a) The study's location in the north-western dry forest within Madagascar, also showing elevation (max = 2744 m); (b) our study lake within the landscape, also showing nearby lakes to the north and north-east; and (c) our study lake in isolation, showing sampled points on the sandy northern/north-eastern shore and a connected sandy area to the east, where blue indicates a presence and light green an absence. All satellite imagery is from SENTINEL (<https://www.copernicus.eu/en>), July 2018, and the elevation data in (a) are from WorldClim (Hijmans *et al.* 2005).

*Ocyale ghost* Jocque & Jocqué, 2017, is found on a very small habitat island, a sandy patch of less than 2 ha, adjacent to a lake in Madagascar's north-western dry deciduous forest. The genus contains large and striking species, yet a dearth of ecological and biological knowledge surrounding *Ocyale* exists (Jocque *et al.* 2017). *Ocyale ghost* is currently awaiting formal Red List assessment (BLP, unpubl. data). At present, only this single population is known to exist.

The use of occupancy models, developed by MacKenzie *et al.* (2006), has been shown to enable efficient monitoring of wildlife populations. Multiple taxa have been studied using these models: e.g. birds (Nichols *et al.* 2007; Martin *et al.* 2009), mammals (MacKenzie *et al.* 2005; Hines *et al.* 2010) and amphibians (MacKenzie *et al.* 2005; Kroll *et al.* 2008). Occupancy models that have been fit to invertebrate data sets are rarer. MacKenzie *et al.* (2005) provide one such example, demonstrating that occupancy models can be used over short time frames to study habitat characteristics for the giant weta *Deinacrida mahoenui* Gibbs 1999 (Anostostomatidae), a nationally threatened insect in New Zealand.

In this study, we aimed to (1) assess the habitat characteristics associated with the distribution of *O. ghost*; (2) estimate the area occupied by *O. ghost*; and (3) estimate the probability of detecting *O. ghost* in a given survey plot. Our null hypothesis was that *O. ghost*'s distribution and occupancy would be random across the site. We hypothesised that the relative area of sand across a plot would be a significant factor explaining the presence of *O. ghost*.

## MATERIALS AND METHODS

### Study region

Our study centred around one of three sacred lakes at Matsedroy (15°49'S, 46°65'E) in Boeny region, north-western Madagascar. The study site is within the Matsedroy forest fragment (15°29'23"S, 46°38'25"E), a community managed area without official protected status (Fig. 1). The area is subject to illegal burning and logging for a variety of purposes (Evans *et al.* 2013). Our study area is within a previously defined zone of microendemism (Wilmé *et al.* 2006). Temperatures remain relatively constant throughout the year (annual mean of 27.3°C), and mean monthly rainfall is highly variable (1–360 mm) owing to the pronounced dry season from June to August and the height of the wet season from December to February (Rasamison *et al.* 2018). Our study site peaks at around 20 m elevation, with the wider landscape of Mariarano reaching up to approximately 120 m (calculated in GIS).

### Data collection

Surveys assessing the presence or absence of *O. ghost* were carried out in plots of 9 m<sup>2</sup> (3 × 3 m). In total, 122 plots were sampled across the sandy site, separated by a minimum of 5 m to ensure each quadrat could be counted as an independent sample. We chose to survey at a fine scale (9 m<sup>2</sup>) in order to increase our spatial data resolution on habitat changes across the small site

(<2 ha). Lines of plots were set in a systemic array, from points on the sandy patch, following a northerly direction as much as logistically possible, to allow an observable gradient of habitat variables leading away from the lake. Lines ranged from three to 11 quadrats in length depending on logistical considerations.

We conducted two surveys across each of the 122 plots in August 2018 (total number of surveys = 244), between 19:30 and 01:00, at least 2 h after the sun had set. Plots were set up on the morning 3 days before surveys. This allowed sufficient time for the area to return to normal conditions after the initial disturbance caused by the surveyors. The lunar cycle was approximately 1 week from a full moon, and there was no precipitation during the study period. Each plot was surveyed across two consecutive nights to minimise the chance of burrow relocation and reduce long-term disturbance at the location of this species' only known population worldwide. Surveying each plot twice followed an optimum design set out by MacKenzie *et al.* (2005) based on the prior estimated detection and occupancy probabilities being above 0.6.

Each plot-based survey was carried out by a rotation of observer treatments, including a principal investigator, three University of Mahajanga MSc researchers and a local guide. Survey rotation followed a simple pattern whereby when a plot was surveyed by a single observer, the following survey was carried out jointly by two other observers. This eliminated any bias in detection probability arising from experience or effort hours. Quadrats were considered complete as soon as an adult or subadult individual *O. ghost* was found. We defined the minimum size for a subadult as 40 mm legspan from the tip of leg I to the tip of leg IV, thus explicitly excluding spiderlings from our assessment. We used marking cages of 40 mm diameter with a plunger mechanism of equal size to gently press the individual into a flat splayed position, which made it quickly apparent whether or not the individual met our threshold for inclusion or was deemed a spiderling. Individuals were then gently lowered onto bisecting rulers for final confirmation by three other observers. We did not survey for spiderlings in our study as they are often excluded from optimum habitat by larger individuals (Aisenberg *et al.* 2011). Each survey at a given plot took approximately 5 min. Surveys were initially attempted from the border of the quadrat, looking for the eyeshine of an individual within the sample area. If eyeshine was detected from an individual clearly of sufficient size, the quadrat was deemed sampled. If an individual was not clearly an adult (i.e. unable to visually confirm it met our size threshold), it was captured, and size class assessed. If no individuals meeting the threshold were detected, methodical straight-line transects were walked across the plot, looking for burrows (for closer inspection) or individuals at poor angles for tapetum reflection (the main reason for initial detection failure).

Environmental variables were taken for covariate analyses from each plot. The temperature was recorded at the beginning of the survey using a Benetech GM550 infrared thermometer. After all quadrats were gridded out using a 20 m measuring tape, a substrate assessment was carried out at each one. Each of four observers stood at the corners of the quadrat and independently estimated the proportion of area that was covered by (1) bare ground (sand); (2) leaf litter (common around habitat periphery

(forest)); (3) grasses (Appendix I); and (4) low lying shrub. Estimates were averaged between the four values obtained from each observer, for each variable. Prior to analysis, all plot substrate proportions were arcsine transformed.

Topographic metrics (elevation, aspect and slope) were derived from the Japan Aerospace Exploration Agency (©JAXA; Takaku & Tadono 2017) 30 m global digital surface model in ArcGIS 10.3. Aspect was measured in degrees, converted to radians and then a cosine (for north–south) and sine (for east–west) transformation was applied prior to analysis, to represent north and east as high values (1) and south and west as low values (−1).

### Statistical analysis and model selection

We used single-season occupancy models described in MacKenzie *et al.* 2006, which use binary detection/non-detection data to assess the support for competing hypotheses about the distribution of species. Occupancy models also incorporate the possibility of false absences in data sets by using detection probabilities (notation ‘ $p$ ’), using them to make robust inferences about wider occupancy probabilities. When unaccounted for, imperfect detection can alter occupancy estimates to a large degree (MacKenzie *et al.* 2006).

One of the key considerations in single-season occupancy models is meeting the assumption of population closure during the study period. We believe that the closure assumption can be reliably assumed because (1) our surveys took place on consecutive nights and (2) our observation that disturbed individuals often retreated back to a visible or previously invisible (to the observer) burrow. Three sexually mature adult males did not retreat to an active burrow once released (*BLP personal observation*), but analysing this (currently) statistically negligible transience behaviour in reproductive state males is beyond the scope of this study. Burrow construction in sand-dwelling spiders is energetically expensive (De Simone *et al.* 2015), and thus the probability of an individual changing burrow site over 24 h is assumed to be very low.

Each set of observations at a plot generates a detection history for the target species. For example, in a hypothetical study, the binary notation 101 denotes that the target species was detected on the first and third sampling occasions, but not on the second. Thus, the probability statement for this detection history can be expressed mathematically as

$$Pr(\mathbf{h}_1 = 101) = \Psi p_1 (1 - p_2) p_3,$$

where ‘ $Pr(\mathbf{h}_1)$ ’ is the probability of observing the detection history gathered, in the above case 101. Detection is represented by the true occupancy ( $\Psi$ ) multiplied by detection probability at the first ( $p_1$ ). Non-detection is represented as  $1 - p_2$  (1 – probability of detection at occasion two). Another example, the detection history 001 would signify a detection only on the last of three sample occasions, expressed as

$$Pr(\mathbf{h}_1 = 001) = \Psi (1 - p_1) (1 - p_2) p_3.$$

We used a logit link function to estimate the magnitude of influence that ecological covariates (Table 1) had on the parameters

of interest ( $\Psi$  and  $p$ ). Logit link functions serve to take a linear combination of covariate values and convert them to a scale of probability (MacKenzie *et al.* 2006). Occupancy probability can be modelled with a logit link function as

$$\text{logit } \Psi_i = \hat{\theta}_0 + \hat{\theta}_{1x_1} + \hat{\theta}_{2x_2} \dots + \hat{\theta}_{n x_n},$$

where  $\hat{\theta}_0$  is the intercept value and  $\hat{\theta}_1$  is the effect size of covariate  $x_1$ .

Model selection was made using Akaike’s information criterion (AIC) (Akaike 1973), which can be expressed mathematically as

$$\text{AIC} = -2\ln[L(\theta|\mathbf{x})] + 2\delta,$$

where  $\delta$  is the number of parameters estimated in the model. The penalisation of assessing an increased number of parameters encourages parsimony (i.e. the simplest model with the highest explanatory power). AIC is a robust method of statistical inference, used widely in ecological studies. Aho *et al.* (2014) found that 84% of ecology studies between 1993 and 2013 that used multi-model inferences evaluated using AIC as opposed to other methods of evaluation. Models are evaluated by using calculated Delta AIC ( $\Delta_i$ ) values, which can be expressed mathematically as

$$\text{Delta AIC}_i = \Delta_i = \text{AIC}_i - \text{min AIC},$$

where  $\text{AIC}_i$  is the AIC value for model  $i$ , and min AIC is the AIC value of the model with the strongest support. The highest ranking candidate models are considered with a  $\Delta\text{AIC}$  value  $< 2$  models with  $\Delta\text{AIC} > 7$  are disregarded as having virtually no support, and those in between receiving moderate support (Burnham & Anderson 2002).

We fitted occupancy models using the ‘occu’ function in package ‘unmarked’ (Fiske & Chandler 2011) in R version 3.5.2 (R Core Team 2013). We assessed model fit between our top-ranked model and the reference distributions by comparing the Chisq statistic, using the ‘MacKenzie and Bailey goodness of fit test’. The function ‘mb.gof.test’ in the package ‘AICcmodavg’ (Mazerolle 2019), with 1000 simulations, showed that there was no indication of a lack of fit ( $P > 0.05$ ). MacKenzie *et al.* (2006) note that occupancy modelling without adequate tests of model fit risk weak inferences.

Collinearity between plot-specific variables was generally negligible (Appendix III). In particular, our key variables in the final models were largely independent of one another, and aspect and slope were only weakly correlated or had no significant correlation. For example, collinearity was low between distance to lake edge and east–west aspect ( $r = 0.21$ ;  $P < 0.05$ ) and bare ground ( $r = -0.06$ ;  $P > 0.05$ ). All such variables were therefore analysed as separate factors. However, as expected, the proportion of short grass showed high collinearity with proportion of bare ground ( $r = -0.785$ ;  $P < 0.05$ ), which was considered when interpreting the results.

## RESULTS

We found that microhabitat selection was strong in *O. ghost*. The most important and significant plot-scale covariate predicting

**Table 1** Predictors (and abbreviations) used in the modelling

Predictors used in logit link (abbreviation)	Description
Bare ground (BGr)	Bare sand substrate without stones, leaf litter or other objects.
Distance to water (DW)	Distance between centroid of plot and the nearest edge of the adjacent lake.
Short grass (ShGr)	Below knee-height grass that grows in concentrated patches at site (Appendix I).
Leaf litter (LeLit)	Leaf litter often at the periphery of the site, blown from nearby forest. Also included patches of broken branches that created an inconsistent substrate area.
Low shrub (L.Shr)	Areas of dry shrubby vegetation (not grasses) that generally appear as sporadic and sparse.
Elevation (Elev)	Metres above sea level.
Slope (Slp)	Topographic slope in degrees. Calculated in ArcGIS.
Aspect EW (AspEW)	The degree to which the slope faces east or west. Calculated in ArcGIS.
Aspect NS (AspNS)	The degree to which the slope faces north or south. Calculated in ArcGIS.

occupancy was distance to water, with plots closer to the lake's edge exhibiting markedly higher occupancy. The proportion of bare sand in a plot was also a significant predictor, with the effect inverted; plots with little sandy substrate had significantly lower occupancy probabilities. Detection was not related to the temperature at the time of survey; however, temperature variation during our survey period was relatively low.

### Probability of occupancy in relation to habitat covariates

The most parsimonious model based on AIC weights was model ' $\Psi$  ( $DW + BGr + AspEW$ )  $P$  ( $\cdot$ )' ( $w = 0.65$ , Table 2). This model indicated that occupancy of *O. ghost* was related to the plot's distance to the water's edge, the proportion of bare ground (sand) and the east–west aspect (increased occurrence on west-facing slopes) of the plot. Our second most highly ranked model was structured the same but for the removal of ' $AspEW$ ' as a covariate ' $\Psi$  ( $DW + BGr$ )  $P$  ( $\cdot$ )' ( $w = 0.19$ ). We included the null model ' $\Psi$  ( $\cdot$ )  $P$  ( $\cdot$ )' in our final table of results for comparison, receiving no statistical support ( $w \leq 0.0001$ ); we can firmly reject the null hypothesis that habitat covariates within plots do not influence *O. ghost* distribution.

Using the coefficient values estimated from our top model (Table 3), we show that distance to water source (' $DW$ ' in model notation) has a strong negative contribution to the probability of occupancy ( $Z$  value =  $-3.80$ ,  $P < 0.001$ ) (Fig. 2). Our hypothesis that the proportion of bare ground would have a strong positive relationship with *O. ghost* occupancy was supported by our results, ( $Z$  value =  $2.41$ ,  $P = 0.016$ ), although this effect was somewhat weaker than distance to water.

Our models were chosen to represent a diversity of plausible scenarios that could affect *O. ghost* occupancy and ascertain

**Table 3** Coefficients for our top-ranked model ' $\Psi$  ( $DW + BGr + AspEW$ )  $P$  ( $\cdot$ )' (Table 2)

	Estimate	SE	Z-value	P
(Intercept)	-1.36	1.04	-1.31	0.19
DW	-0.03	0.01	-3.80	<0.001**
AspEW	-1.14	0.59	-1.91	0.056
BGr	2.72	1.13	2.41	0.016*

*AspEW*, aspect east/west; *BGr*, bare ground; *DW*, distance to water (m).

which covariates or covariate pairs influenced occupancy. To avoid data dredging (Burnham & Anderson 2002), we chose 11 models a priori. Our final top-ranked model was constructed as a 12th due to its anticipated explanatory power based on initial results. This final model's residuals showed very low spatial autocorrelation (Moran's  $I = 0.118$ ;  $P > 0.05$ ), supporting covariate selection.

### Probability of occupancy

Traditional presence–absence methods (naïve occupancy) would estimate the survey site as having 55% of plots occupied (67/121). However, using model averaged estimates of true occupancy, by estimating the detection parameter, we estimate that 63% (SE 7%, Table 4) of plots were occupied (76/121). This suggests that nine plots were occupied by target sized individuals of *O. ghost* and not detected by observers.

### Probability of detection

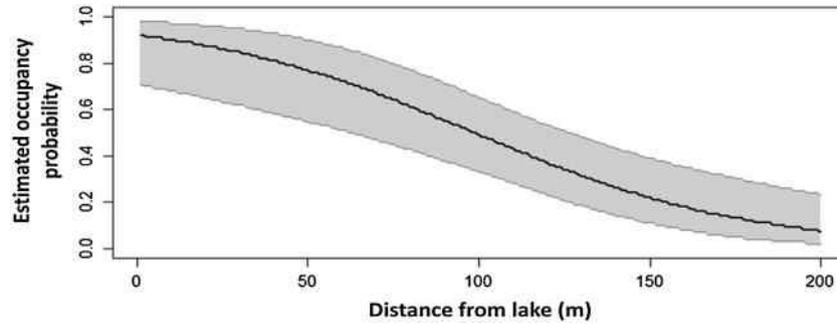
We initially wanted to evaluate any effect of temperature on the detection probability of *O. ghost*. However, when modelled, models with detection held constant ( $\{P(\cdot)\}$ ) were substantially

**Table 2** Model comparisons to identify ecological patch covariates that influence ghost spider occupancy using single-season survey design

Model	AIC	$\Delta$ AIC	AIC weight	Cumulative Weight	K*
<b><math>\Psi</math> (<math>DW + BGr + AspEW</math>) <math>P</math> (<math>\cdot</math>)</b>	<b>260.26</b>	<b>0.00</b>	<b>0.65</b>	<b>0.65</b>	<b>5</b>
$\Psi$ ( $DW + BGr$ ) $P$ ( $\cdot$ )	262.65	2.39	0.19	0.84	4
$\Psi$ ( $DW + BGr + Slp$ ) $P$ ( $\cdot$ )	264.46	4.20	0.08	0.92	5
$\Psi$ ( $DW + L.Shr$ ) $P$ ( $\cdot$ )	264.85	4.59	0.07	0.99	4
$\Psi$ ( $\cdot$ ) $P$ ( $\cdot$ )	298.12	37.85	<0.0001	<0.0001	2

*AspEW*, aspect east/west; *BGr*, bare ground; *DW*, distance to water (m); K, number of parameters; *L.Shr*, low shrubs; *Slp*, slope; ( $\cdot$ ) denotes a parameter held constant. See section for treatment of covariates and statistical summaries.

\*denotes the number of parameters in the model. Top ranked model presented in bold.



**Fig. 2.** Estimated probability of occurrence (grey shading shows upper and lower 95% confidence intervals) in relation to distance from the lake shore.

**Table 4** Occupancy estimates for each model from Table 1 note: model estimates were obtained by fixing covariates at their mean values

Model	$\widehat{\Psi}$	SE
$\Psi (DW + BGr + AspEW) P (.)$	0.69	0.09
$\Psi (DW + BGr) P (.)$	0.62	0.07
$\Psi (DW + BGr + Slp) P (.)$	0.65	0.10
$\Psi (DW + L.Shr) P (.)$	0.61	0.06
$\Psi (.) P (.)$	0.59	0.05
Model averaged	<b>0.63</b>	<b>0.07</b>

model averaged estimates are presented in bold.

more supported than any individual model where constant detection was substituted for temperature  $\{P(temp)\}$  or time variation  $\{P(t)\}$ . Thus, we excluded these models from our final analysis. The model averaged detection estimate was 0.74 (SE = 0.05) (Appendix II), validating our initial assertion during survey design that detection probability would be above 0.6 (Materials and Methods section). However, our observed detection probability was lower than predicted.

## DISCUSSION

We have found a strong evidence that microhabitat selection is a key factor influencing the distribution of *O. ghost*, following our assessment of fine-scale habitat characteristics. Distance to the lake edge and proportion of bare ground appeared to be key factors for this microendemic spider (aim 1). Indeed, occupancy estimates were dramatically reduced at greater distances from the water (i.e. the edge of the lake) (2). Our top-ranking model estimated occupancy at  $\geq 0.85$  for plots within 30 m of the lake edge, dropping to 0.5 at just under 100 m; at  $>150$  m from the lake edge, estimated occupancy reduced substantially to 0.2. Our most parsimonious model ' $\Psi (DW + BGr + AspEW) P (.)$ ' accounted for 0.65 of AICc model weight, with a single variation our second-ranked model accounted for 0.19 model weight (the exclusion of aspect east–west). Our top-ranked model also showed very low spatial autocorrelation in the residuals, suggesting that key facets of the environment were adequately accounted for. Combined, our two best models carry over 80% of AICc weight, the only variation in model structure being the removal

of east–west aspect in the second-favoured model. The probability of detecting *O. ghost* in a plot was relatively high (3) but possibly reduced by the lower observed temperatures, which would have influenced spider activity levels.

Results were consistent across the models. Those incorporating both distance to the water's edge and the proportion of bare ground within a plot had over 92% support, demonstrating a clear relationship between these variables and *O. ghost* occupancy. Insect biomass can be higher closer to water sources (and therefore at the lower elevation), which has been shown to increase resource utilisation by predators such as Lycosidae spiders (Gratton *et al.* 2008), as well as increase the overall abundance and biomass of spiders (Henschel *et al.* 2001). Alternatively, the area surrounding the lake could support a microclimate that is more stable than those at the periphery of the habitat; e.g. it might be less susceptible to weather extremes (Lubin *et al.* 2001).

The proportion of bare ground (sand) in a plot was hypothesised to increase the occupancy of *O. ghost*, chiefly due to the species' psammophilous specialisation. A specialised species will outcompete a generalist in optimal habitat (Bonte *et al.* 2006), corroborating our observations that other Lycosidae species are at very low abundances on the sandy habitat (*BLP personal observation*). Sand is a critical substrate for *O. ghost* burrow construction, it being less energy expensive to construct burrows than in soil (Suter *et al.* 2011). Burrowing Lycosidae species have also been shown to be highly tenacious and venture only short distances from burrows (Suter *et al.* 2011). However, the substrate itself may be influenced by the lake, which may cause moisture gradients that affect individual spiders' ability to burrow and forage. Therefore, the prominence of lake distance in our results may be moderated by its effect on the substrate, but further work on these abiotic factors, and their interaction, is needed.

Our results show an association between *O. ghost* occupancy and the aspect of the slope, with a preference for west-facing slopes. Some Lycosidae species have been shown to prefer certain sides and slopes of sand dunes for their burrow site (Aisenberg *et al.* 2011). The same study also showed a clear difference between burrow site location and age class of Lycosidae spiders. Territorial exclusion and intraguild predation have been demonstrated in burrowing Lycosidae species previously (Moya-Laraño *et al.* 2002), and it is a likely cause of age class separation. Sex is known to be a key factor for some wolf spider

activity patterns (Framenau 2005; Cera & Spun̄gis 2011). Whilst this was beyond the scope of our present study, it warrants further investigation, given that burrowing Lycosidae may show unusual patterns in relation to sex, such as reversed sex roles (Aisenberg & Costa 2008).

The preference for west-facing slopes may simply be because this is where most of the suitable habitat was in our study area, it may relate to insolation, or be due to the interaction of these factors. West-facing slopes are likely to have higher insolation than east-facing slopes, potentially increasing the average and maximum daily temperature of burrows, depending on local topography. Predatory arthropods living in sand are exposed to higher climate extremes, with hot days and substantially cooler nights (Bonte & Maelfait 2001) and these fine-scale temperatures are likely to be affected by east–west aspect. Maintaining a relatively constant burrow temperature may reduce extreme metabolic fluxes, increasing individual survival. Longer burrows offer a buffer to external heat fluctuations in Lycosidae (Aisenberg *et al.* 2011), but we did not measure burrow temperature, and thus, our inferences about the role of aspect is speculative.

Burrow site selection in a species of Eresidae spider in Namibia was suggested as having been influenced by conspecific cuing (Birkhofer *et al.* 2012), potentially buffering the population against extreme climatic events. Meanwhile, patch quality was a significant predictor of occurrence in another Lycosidae species (Bonte *et al.* 2003a). A species of *Pardosa* (Lycosidae) was shown to select substrate with less variable temperatures in winter (Kraus & Morse 2005), and a web-building Oecobiidae spider was shown to select strongly for substrate during web construction (Voss *et al.* 2007). Despite the dearth of ecological studies on habitat selection in spiders, studies that deal with the topic clearly report consistent results.

We are confident in our data from the few sampling occasions. Utilising such ‘snapshot’ data have been effectively demonstrated elsewhere, following optimum design set out by MacKenzie *et al.* 2006, e.g. toads (Bradford *et al.* 2003), hemipterans (Biedermann 2004), and orthopterans (MacKenzie *et al.* 2005). The fact that we were in the field for a single-season does pose its own limitations. Temporally, conducting a similar study during the wet season would elucidate whether or not these patterns of spatial distribution are consistent. Curtis and Bloch (2014) showed that microhabitat selection shifted seasonally in an Amblypygid, another terrestrial predatory arthropod. Thus, the question of *O. ghost*’s wet season habits emerges. The observed night-time temperatures during the study period were relatively low (average 19.8°C) and having an equal sampling period during the same season with greater temperature variation could prove insightful. However, due to the low likelihood of regular burrow relocation (Materials and Methods section), we believe that the temperature had minimal influence on the observed distribution of *O. ghost*. Temperature could influence the activity patterns and hence detection probabilities, though, as demonstrated in other ectothermic invertebrates (Høye & Forchhammer 2008), including spiders (Pruitt *et al.* 2011).

Goodman and Benstead (2005) showed that of 5808 species of non-marine invertebrate in Madagascar, 4976 (86%) of species are endemic. They also classified the spider fauna as

‘relatively well known’ at 459 species (p. 74). However, in the years since, numerous publications have described dozens of new species at a time (e.g. Wood 2008; Álvarez-Padilla *et al.* 2012; Wood & Scharff 2018). Some research even includes currently undescribed species (e.g. Henrard & Jocqué 2016; Bauer *et al.* 2018). Such is the complexity of Madagascar’s spider fauna.

Madagascar’s biodiversity is exceptional, largely as a result of the endemism and microendemism across multiple taxa (e.g. Wilmé *et al.* 2006). *Neogrosphus* scorpions (Buthidae) contain only three species yet exhibit species ranging from the extreme subarid conditions of the south-west to the subhumid evergreen forests of the north-east (Lourenço *et al.* 2015). Isolated populations of *Neogrosphus griveaudi* (Vachon 1969) exist more than 300 km apart, a likely prequel to allopatry. Species with low dispersal capabilities (e.g. scorpions) in a country characterised by processes capable of fragmenting habitat areas into small isolated islands (see Lourenço *et al.* 2015 for a detailed treatment) are a chief component of the high species richness of Madagascar (Mittermeier *et al.* 2011). Microendemism is not limited to arachnids, however (e.g. *Brookesia* chameleons, Townsend *et al.*, 2009, and Microhylid frogs, Scherz *et al.*, 2019).

Only 238 of 47 904 described spider species have been assessed against IUCN Red List criteria (IUCN 2018; World Spider Catalogue 2018), with the description of new species showing no signs of slowing (Platnick & Raven 2013). A growing body of work demonstrates the paucity of invertebrate conservation research compared to other organisms (Clark 2002), including the megadiverse order of Araneae. Indeed, when species richness is corrected for, arthropods are heavily selected *against* as research study organisms (Rosenthal *et al.* 2017). Cardoso *et al.* (2011) note that basic science and funding is lacking for invertebrates, a key factor impeding invertebrate conservation. Consequently, a lack of knowledge is one of the key factors threatening invertebrates, their associated ecosystem functions and species that depend upon them.

Habitat destruction, fragmentation and degradation are key drivers of species endangerment in Madagascar, and indeed globally (Harper *et al.* 2007). Many of the spider species assessed as endangered or critically endangered cite these factors as a cause; e.g. *Anapistula ataecina* (Cardoso 2010), *Hogna ingens* (Cardoso 2014) and *Mariblemma pandani* (Gerlach 2014). In the case of *Ocyale ghost*, its sandy habitat is relatively safe from the more common forms of habitat loss because the area is a designated sacred lake by the Sakalava people living in neighbouring villages. However, the stability of sand dynamics (the stability of the habitat) could be affected by deforestation. For example, deforestation in the surrounding area decreases soil quality (Islam & Weil 2000), which reduces soil stability, and could allow an increase in sand dynamics. The area is also susceptible to increasing disturbance as the human population in the surrounding villages increases, with livestock utilising the nearby lake daily in this dry landscape (*pers. obs.*). Increased cattle grazing decreases occupancy of sand-dwelling invertebrates (Bonte & Maes 2008), although cattle grazing reduces vegetation cover significantly, which has been shown to alter the spider community by way of suppressing guilds and species that utilise vegetation (Warui 2004). Therefore, in a relatively unique

biological case, the overall net impact of cattle grazing and deforestation on *O. ghost* is unknown. Unfortunately, however, due to the very small habitat area, stochastic vulnerability to extinction is likely to be high for this species.

Compounding these localised threats, climatic change in the area is likely to create drier, warmer conditions, affecting water availability and ground temperatures (Hannah *et al.* 2008). These factors will undoubtedly increase the frequency of droughts and the severity of fires, which could increase mortality of individual spiders. Insect species have been shown to shift upwards in elevation to combat the increased temperature at lower elevations (Wilson *et al.* 2007). However, this is unlikely in our study species due to its low elevation lake shore habitat and the unsuitable surrounding habitat matrix. *O. ghost* also favoured plots closer to the water source: as the climate dries, the water level of the lake and surrounding water sources is likely to decrease, further augmenting the loss of suitable habitat (if such sandy plots persist at all).

Madagascar is changing dramatically, with land use and climate change predicted to significantly alter habitats for many taxa, as well as overall biodiversity and ecosystem function (Thuiller *et al.* 2006; Schatz *et al.* 2008). Narrow-range endemics and habitat specialists are placed at a substantial evolutionary disadvantage because of their lower dispersal capabilities and inability to move to suitable habitat (assuming it exists and it is accessible to the species). As a result of this, endemic and threatened species are, inherently, at the greatest risk of extinction and of greater conservation concern and public interest (Williams *et al.* 2000). It has also been demonstrated elsewhere that, nationally, areas containing rare and endemic species may highlight areas of higher conservation priority (e.g. Bonn *et al.* 2002). Borders of distinct habitat types also create various degrees of edge habitat, increasing activity of some invertebrates (De Smedt *et al.* 2019) and potentially allowing some species to exist in the 'transition' zone (Brown & Hutchings 1997).

## CONCLUSION

Our single-season occupancy models provided strong evidence that microhabitat selection is strong in *O. ghost*. Our null model was rejected and key habitat covariates were elucidated. The species was not detected at any of 14 other potentially suitable sites in the region (BLP, unpubl. data). Thus, assessing the ability and usage of aeronautic ballooning dispersal, or dispersal of any kind, in *O. ghost* should be central to future study of the species. Without such a mechanism, it is likely that this is indeed the only population of *O. ghost* and, as such, we work towards listing the species in one of the IUCN-threatened categories. This species is the only known representative of its genus in Madagascar and may represent a distinct evolutionary lineage. Building up a knowledge base on the fine-scale ecology of likely threatened species is vital towards future efforts to conserve them. Conservation of this charismatic species would be inexpensive and have benefits for other species; it is therefore crucial to the integrity of conservation efforts in this unique part of the world.

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**APPENDIX I**

Lake and surrounding sandy area home to the only known population of *Ocyale ghost*. Note substrates listed in methods: short grasses, bare ground (sand), leaf litter (mainly at the periphery of the habitat close to the forest line) and low shrub (can be seen in isolated areas throughout the site). Photograph by B. L. P.

**APPENDIX II**

Estimated detection probabilities for each individual model

Model	Det	SE
$\Psi$ (DW + BGr + AspEW) P (.)	0.726	0.049
$\Psi$ (DW + BGr) P (.)	0.742	0.047
$\Psi$ (DW + BGr + Slp) P (.)	0.733	0.056
$\Psi$ (DW + L.Shr) P (.)	0.749	0.046
$\Psi$ (.) P (.)	0.748	0.047

**APPENDIX III**

Collinearity between patch substrate variables

Variable	Short grass	Bare ground	Leaf litter	Low shrub
Short grass	X	-0.785†	-0.236	-0.131
Bare ground	-0.785†	X	-0.348	-0.355
Leaf litter	-0.236	-0.348	X	-0.080
Low shrub	-0.131	-0.355	-0.080	X

†Indicates high collinearity between variables.