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Pett, Brogan L. ORCID logoORCID:
<https://orcid.org/0000-0002-0461-3715> and Bailey, Joseph J.
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1 **GHOST-BUSTING: Patch occupancy and habitat preferences of *Ocyale ghost* Jocque &**
2 **Jocqué 2017 (Araneae: Lycosidae), a single site endemic in north-western Madagascar**

3

4 **Brogan L. Pett** ^{1,3} **Joseph J. Bailey** ^{2, 3}.

5 ¹ Biodiversity Inventory for Conservation, Brussels, Belgium; ² Geography Department, York St. John
6 University, York, United Kingdom; ³ Operation Wallacea, Lincolnshire, United Kingdom.

7 Correspondence: Brogan L. Pett, ORCID: 0000-0002-0461-3715. Email: brogan.pett@outlook.com

8 brogan@paralatierra.org

9

10 **Abstract**

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

25

26 **Key words:** Burrowing, Conservation, Microendemic, Lycosidae, Madagascar, Microendemic,
27 Occupancy modelling, Patch occupancy

28 **Introduction**

29 There is a profound lack of ecological knowledge on invertebrates, hampering conservation efforts
30 (Cardoso *et al.* 2011; Gerlach, 2008). Many are thought to go extinct before being studied (Platnick and
31 Raven 2013), let alone being assessed against IUCN Red List criteria (Regnier *et al.* 2015). Indeed,

1 extinction risk has been assessed for 66.7% of 69,788 described mammal species, yet only 1.9% of
2 1,159,365 described invertebrate species (IUCN 2018). Invertebrates fulfil crucial functions within
3 ecosystems (Weisser and Siemann 2008) and they are, therefore, essential for not only the natural world,
4 but also human livelihoods, health, and wellbeing (Beynon *et al.* 2015; Gallai *et al.* 2009). However,
5 studies on invertebrates are proportionally lacking compared to other taxa and calls for population and
6 range studies are widespread throughout the literature (Balmford *et al.* 2005; Butchart *et al.* 2007;
7 Cardoso *et al.* 2011).

8 Endemism has long been used as a means of identifying areas for conservation prioritisation (e.g.
9 Freitag and van Jaarsveld 1997) and endemic invertebrate species may have narrow range sizes and
10 niche breadth, with a closer relationship with the environment than more widespread species (Rabitsch
11 *et al.* 2016). In this sense, Madagascar's levels of endemism are especially pronounced in a global
12 context, its biota having long been recognised as exceptional (Mittermeier *et al.* 1998; Kremen *et al.*
13 2008; Vences *et al.* 2009) alongside 24 other global biodiversity hotspots (Myers *et al.* 2000).
14 Endemism, proportionate to land area, is unparalleled (Mittermeier *et al.* 2011): 100% of native
15 amphibians, 86% of macro-invertebrates, and over 90% of vascular plants are endemic (Wilme *et al.*
16 2012). Historical biodiversity estimates for Malagasy fauna are also proving to be underestimates
17 (Vietes *et al.* 2009).

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

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

29 Spiders have been shown to select living sites based on increased foraging efficiency; i.e. web building
30 (Ruch *et al.* 2011), reduced predation (Rypstra *et al.* 2007), and the presence of beneficial species in
31 the microhabitat (Sinclair *et al.* 2001). A specialist is more likely to survive and thrive in its optimal
32 habitat because of a competitive advantage, however dispersal may be restricted (Bonte *et al.* 2006).
33 For example, specialist *Carabus* species show reduced dispersal compared to sympatric generalists
34 (Brouat *et al.* 2003) whilst increased habitat specificity is negatively associated with propensity for
35 aerial dispersal in spiders (Bonte *et al.* 2003) due to the increased chances of landing in an unfavourable

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

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

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

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

21 **Materials and Methods**

22 *Study region*

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

1 ***Data collection***

2 Surveys assessing the presence or absence of *O. ghost* were carried out in plots of 9m² (3x3m). In total,
3 122 plots were sampled across the sandy site, separated by a minimum of 5m to ensure each quadrat
4 could be counted as an independent sample. We chose to survey at a fine scale (9m²) in order to increase
5 our spatial data resolution on habitat changes across the small site (<2ha). Lines of plots were set in a
6 systemic array, from points on the sandy patch, following a northerly direction as much as logistically
7 possible, to allow an observable gradient of habitat variables leading away from the lake. Lines ranged
8 from three to eleven quadrats in length depending on logistical considerations.

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

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

1 walked across the plot, looking for burrows (for closer inspection) or individuals at poor angles for
2 tapetum reflection (the main reason for initial detection failure).

3 Environmental variables were taken for covariate analyses from each plot. The temperature was
4 recorded at the beginning of the survey using a Benetech GM550 infrared thermometer. After all
5 quadrats were gridded out using a 20m measuring tape, a substrate assessment was carried out at each
6 one. Each of four observers stood at the corners of the quadrat and independently estimated the
7 proportion of area that was covered by: (1) bare ground (sand); (2) leaf litter (common around habitat
8 periphery (forest)); (3) grasses (see Appendix 1); and (4) low lying shrub. Estimates were averaged
9 between the four values obtained from each observer, for each variable. Prior to analysis, all plot
10 substrate proportions were arcsine transformed.

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

16 ***Statistical analysis and model selection***

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

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

32 Each set of observations at a plot generates a detection history for the target species. For example, in a
33 hypothetical study, the binary notation 101 denotes the target species was detected on the first and third

1 sampling occasions, but not on the second. Thus, the probability statement for this detection history can
 2 be expressed mathematically as:

$$3 \quad \Pr(\mathbf{h}_1=101) = \Psi p_1(1-p_2)p_3$$

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

$$9 \quad \Pr(\mathbf{h}_1=001) = \Psi(1-p_1)(1-p_2)p_3$$

10 We used a logit link function to estimate the magnitude of influence that ecological covariates (Table
 11 1) had on the parameters of interest (Ψ and p). Logit link functions serve to take a linear combination
 12 of covariate values and convert them to a scale of probability (MacKenzie *et al.* 2006). Occupancy
 13 probability can be modelled with a logit link function as:

$$14 \quad \text{logit } \Psi_i = \delta_0 + \delta_1 x_1 + \delta_2 x_2 \dots + \delta_n x_n$$

15
 16 Where δ_0 is the intercept value and δ_1 is the effect size of covariate x_1

17 Model selection was made using Akaike’s Information Criterion (AIC) (Akaike 1973), which can be
 18 expressed mathematically as:

$$19 \quad \text{AIC} = -2\ln[L(\Theta|\mathbf{x})] + 2 \delta$$

20 Where δ is the number of parameters estimated in the model. The penalisation of assessing an increased
 21 number of parameters encourages parsimony (i.e. the simplest model with the highest explanatory
 22 power). AIC is a robust method of statistical inference, used widely in ecological studies. Aho *et al.*
 23 (2014) found that 84% of ecology studies between 1993-2013 that used multi-model inferences
 24 evaluated using AIC as opposed to other methods of evaluation. Models are evaluated by using
 25 calculated Delta AIC (Δ_i) values, which can be expressed mathematically as:

$$26 \quad \text{Delta AIC}_i = \Delta_i = \text{AIC}_i - \min \text{AIC}$$

27 Where AIC_i is the AIC value for model i , and $\min \text{AIC}$ is the AIC value of the model with the strongest
 28 support. The highest-ranking candidate models are considered with an ΔAIC value <2 models with
 29 $\Delta\text{AIC} >7$ are disregarded as having virtually no support, and those in between receiving moderate
 30 support (Burnham and Anderson, 2002).

31 We fitted occupancy models using the ‘occu’ function in package ‘unmarked’ (Fiske and Chandler
 32 2011) in R version 3.5.2 (R Core Team, 2013). We assessed model fit between our top ranked model

1 and the reference distributions by comparing the Chisq statistic, using the ‘MacKenzie and Bailey
2 goodness of fit test’. The function ‘mb.gof.test’ in the package ‘AICcmodavg’ (Mazerolle, 2019), with
3 1000 simulations, showed there was no indication of a lack of fit ($P > 0.05$). MacKenzie *et al.* (2006)
4 note that occupancy modelling without adequate tests of model fit risk weak inferences.

5 Collinearity between plot-specific variables was generally negligible (Appendix 3). In particular, our
6 key variables in the final models were largely independent of one another and aspect and slope were
7 only weakly correlated or had no significant correlation. For example, collinearity was low between
8 distance to lake edge and east-west aspect ($r = 0.21$; $p < 0.05$) and bare ground ($r = -0.06$; $p > 0.05$).
9 All such variables were therefore analysed as separate factors. However, as expected, the proportion of
10 short grass showed high collinearity with proportion of bare ground ($r = -0.785$; $p < 0.05$), which was
11 considered when interpreting the results.

12 Results

13 We found that microhabitat selection was strong in *O. ghost*. The most important and significant plot-
14 scale covariate predicting occupancy was distance to water, with plots closer to the lake’s edge
15 exhibiting markedly higher occupancy. The proportion of bare sand in a plot was also a significant
16 predictor, with the effect inverted; plots with little sandy substrate had significantly lower occupancy
17 probabilities. Detection was not related to the temperature at the time of survey, however temperature
18 variation during our survey period was relatively low.

19 *Probability of occupancy in relation to habitat covariates*

20 The most parsimonious model based on AIC weights was model “ $\Psi (DW+BGr+AspEW) P (.)$ ” ($w =$
21 0.65 , Table 2). This model indicated that occupancy of *O. ghost* was related to the plot’s distance to the
22 water’s edge, the proportion of bare ground (sand), and the east-west aspect (increased occurrence on
23 west-facing slopes) of the plot. Our second most highly ranked model was structured the same but for
24 the removal of ‘*AspEW*’ as a covariate “ $\Psi (DW+BGr) P (.)$ ” ($w = 0.19$). We included the null model “ Ψ
25 $(.) P (.)$ ” in our final table of results for comparison, receiving no statistical support ($w = <0.0001$); we
26 can firmly reject the null hypothesis that habitat covariates within plots do not influence *O. ghost*
27 distribution.

28 Using the coefficient values estimated from our top model (Table 3), we show that distance to water
29 source (‘*DW*’ in model notation) has a strong negative contribution to the probability of occupancy (Z
30 value = -3.80 , $P < 0.001$) (Figure 2). Our hypothesis that the proportion of bare ground would have a
31 strong positive relationship with *O. ghost* occupancy was supported by our results, (Z value = 2.41 , P
32 = 0.016), although this effect was somewhat weaker than distance to water.

1 Our models were chosen to represent a diversity of plausible scenarios that could affect *O. ghost*
 2 occupancy and ascertain which covariates or covariate pairs influenced occupancy. To avoid data
 3 dredging (Burnham and Anderson, 2002), we chose eleven models *a priori*. Our final top ranked
 4 model was constructed as a 12th due to its anticipated explanatory power based on initial results. This
 5 final model's residuals showed very low spatial autocorrelation (Moran's I = 0.118; $p > 0.05$),
 6 supporting covariate selection.

7 ***Probability of occupancy***

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

13 ***Probability of detection***

14 We initially wanted to evaluate any effect of temperature on the detection probability of *O. ghost*.
 15 However, when modelled, models with detection held constant $\{P(\cdot)\}$ were substantially more
 16 supported than any individual model where constant detection was substituted for temperature $\{P$
 17 $(temp)\}$ or time variation $\{P(t)\}$. Thus, we excluded these models from our final analysis. The model
 18 averaged detection estimate was 0.74 (SE= 0.05) (Appendix 2), validating our initial assertion during
 19 survey design that detection probability would be above 0.6 (see Methods). However, our observed
 20 detection probability was lower than predicted.

21 **Discussion**

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

1 detecting *O. ghost* in a plot was relatively high (3), but possibly reduced by the lower observed
2 temperatures, which would have influenced spider activity levels.

3 Results were consistent across the models. Those incorporating both distance to the water's edge and
4 the proportion of bare ground within a plot had over 92% support, demonstrating a clear relationship
5 between these variables and *O. ghost* occupancy. Insect biomass can be higher closer to water sources
6 (and therefore at the lower elevation), which has been shown to increase resource utilisation by
7 predators such as Lycosidae spiders (Gratton, Donaldson and Zanden 2008), as well as increase the
8 overall abundance and biomass of spiders (Henschel, Mahsberg and Stumpf, 2001). Alternatively, the
9 area surrounding the lake could support a microclimate that is more stable than those at the periphery
10 of the habitat; for example, it might be less susceptible to weather extremes (Lubin, Henschel and Baker
11 2001).

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

23 Our results show an association between *O. ghost* occupancy and the aspect of the slope, with a
24 preference for west-facing slopes. Some Lycosidae species have been shown to prefer certain sides and
25 slopes of sand dunes for their burrow site (Aisenberg *et al.* 2011). The same study also showed a clear
26 difference between burrow site location and age class of Lycosidae spiders. Territorial exclusion and
27 intraguild predation have been demonstrated in burrowing Lycosidae species previously (Moya- Laraño
28 *et al.* 2002), and it is a likely cause of age class separation. Sex is known to be a key factor for some
29 wolf spider activity patterns (Framenau, 2005; Cera and Spunģis, 2011). Whilst this was beyond the
30 scope of our present study, it warrants further investigation, given that burrowing Lycosidae may show
31 unusual patterns in relation to sex, such as reversed sex roles (Aisenberg and Costa, 2008).

32 The preference for west-facing slopes may simply be because this is where most of the suitable habitat
33 was in our study area, it may relate to insolation, or be due to the interaction of these factors. West-
34 facing slopes are likely to have higher insolation than east-facing slopes, potentially increasing the
35 average and maximum daily temperature of burrows, depending on local topography. Predatory

1 arthropods living in sand are exposed to higher climate extremes, with hot days and substantially cooler
2 nights (Bonte *and* Maelfait 2001) and these fine-scale temperatures are likely to be affected by east-
3 west aspect. Maintaining a relatively constant burrow temperature may reduce extreme metabolic
4 fluxes, increasing individual survival. Longer burrows offer a buffer to external heat fluctuations in
5 Lycosidae (Aisenberg *et al.* 2011), but we did not measure burrow temperature, and thus our inferences
6 about the role of aspect is speculative.

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

15 We are confident in our data from the few sampling occasions. Utilising such ‘snap-shot’ data has been
16 effectively demonstrated elsewhere, following optimum design set out by MacKenzie *et al.* 2006, e.g.:
17 toads (Bradford *et al.* 2003), hemipterans (Biedermann, 2004); and orthopterans (MacKenzie *et al.*
18 2005). The fact that we were in the field for a single season does pose its own limitations. Temporally,
19 conducting a similar study during the wet season would elucidate whether or not these patterns of spatial
20 distribution are consistent. Curtis and Bloch (2014) showed that microhabitat selection shifted
21 seasonally in an Amblypygid, another terrestrial predatory arthropod. Thus, the question of *O. ghost*'s
22 wet season habits emerges. The observed night-time temperatures during the study period were
23 relatively low (average 19.8°C) and having an equal sampling period during the same season with
24 greater temperature variation could prove insightful. However, due to the low likelihood of regular
25 burrow relocation (see Methods), we believe the temperature had minimal influence on the observed
26 distribution of *O. ghost*. Temperature could influence the activity patterns and hence detection
27 probabilities, though, as demonstrated in other ectothermic invertebrates (Høy and Forchhammer
28 2008), including spiders (Pruitt, Demes and Dittrich- Reed 2011).

29 Goodman and Benstead (2005) showed that of 5,808 species of non-marine invertebrate in Madagascar,
30 4,976 (86%) of species are endemic. They also classified the spider fauna as ‘relatively well known’ at
31 459 species (pp. 74). However, in the years since, numerous publications have described dozens of new
32 species at a time (e.g. Álvarez- Padilla *et al.* 2012; Wood 2008; Wood and Scharff 2018). Some research
33 even includes currently undescribed species (e.g.: Henrard and Jocque, 2016; Bauer *et al.* 2018). Such
34 is the complexity of Madagascar’s spider fauna.

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

11 Only 238 of 47,904 described spider species have been assessed against IUCN Red List criteria (IUCN
12 2018; World Spider Catalog 2018), with the description of new species showing no signs of slowing
13 (Platnick and Raven 2013). A growing body of work demonstrates the paucity of invertebrate
14 conservation research compared to other organisms (Clark 2002), including the megadiverse order of
15 Araneae. Indeed, when species richness is corrected for, arthropods are heavily selected *against* as
16 research study organisms (Rosenthal *et al.* 2017). Cardoso *et al.* (2011), note that basic science and
17 funding is lacking for invertebrates, a key factor impeding invertebrate conservation. Consequently, a
18 lack of knowledge is one of the key factors threatening invertebrates, their associated ecosystem
19 functions, and species that depend upon them.

20 Habitat destruction, fragmentation, and degradation are key drivers of species endangerment in
21 Madagascar, and indeed globally (Harper *et al.* 2007). Many of the spider species assessed as
22 endangered or critically endangered cite these factors as a cause; e.g. *Anapistula ataecina* (Cardoso
23 2010), *Hogna ingens* (Cardoso 2014), *Mariblemma pandani* (Gerlach 2014). In the case of *Ocyale*
24 *ghost*, its sandy habitat is relatively safe from the more common forms of habitat loss because the area
25 is a designated sacred lake by the Sakalava people living in neighbouring villages. However, the
26 stability of sand dynamics (the stability of the habitat) could be affected by deforestation. For example,
27 deforestation in the surrounding area decreases soil quality (Islam and Weil 2000), which reduces soil
28 stability, and could allow an increase in sand dynamics. The area is also susceptible to increasing
29 disturbance as the human population in the surrounding villages increases, with livestock utilising the
30 nearby lake daily in this dry landscape (*pers. obs.*). Increased cattle grazing decreases occupancy of
31 sand dwelling invertebrates (Bonte and Maes 2008). Although, cattle grazing reduces vegetation cover
32 significantly, which has been shown to alter the spider community by way of suppressing guilds and
33 species that utilise vegetation (Warui 2004). Therefore, in a relatively unique biological case, the overall
34 net impact of cattle grazing and deforestation on *O. ghost* is unknown. Unfortunately, however, due to
35 the very small habitat area, stochastic vulnerability to extinction is likely to be high for this species.

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

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

21 **Conclusion**

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

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1 Tables

2

3 **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 (see Appendix 1).
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.

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

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	AIC	Δ AIC	AIC weight	Cumulative Weight	K*
Model					
Ψ (DW+BGr+AspEW) P (.)	260.26	0.00	0.65	0.65	5
Ψ (DW+BGr) P (.)	262.65	2.39	0.19	0.84	4
Ψ (DW+BGr+Slp) P (.)	264.46	4.20	0.08	0.92	5
Ψ (DW+L.Shr) P (.)	264.85	4.59	0.07	0.99	4
Ψ (.) P (.)	298.12	37.85	<0.0001	<0.0001	2

9 Notes: K= number of parameters, DW= Distance to water (m), BGr= Bare ground, AspEW= Aspect
10 East/West, Slp= Slope, L.Shr= Low shrubs, (.) denotes a parameter held constant. See methods section
11 for treatment of covariates and statistical summaries.

12

13 **Table.3** Coefficients for our top ranked model “ Ψ (DW+BGr+AspEW) P (.)” (see table 2)

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

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4 **Table.4** Occupancy estimates for each model from Table 1

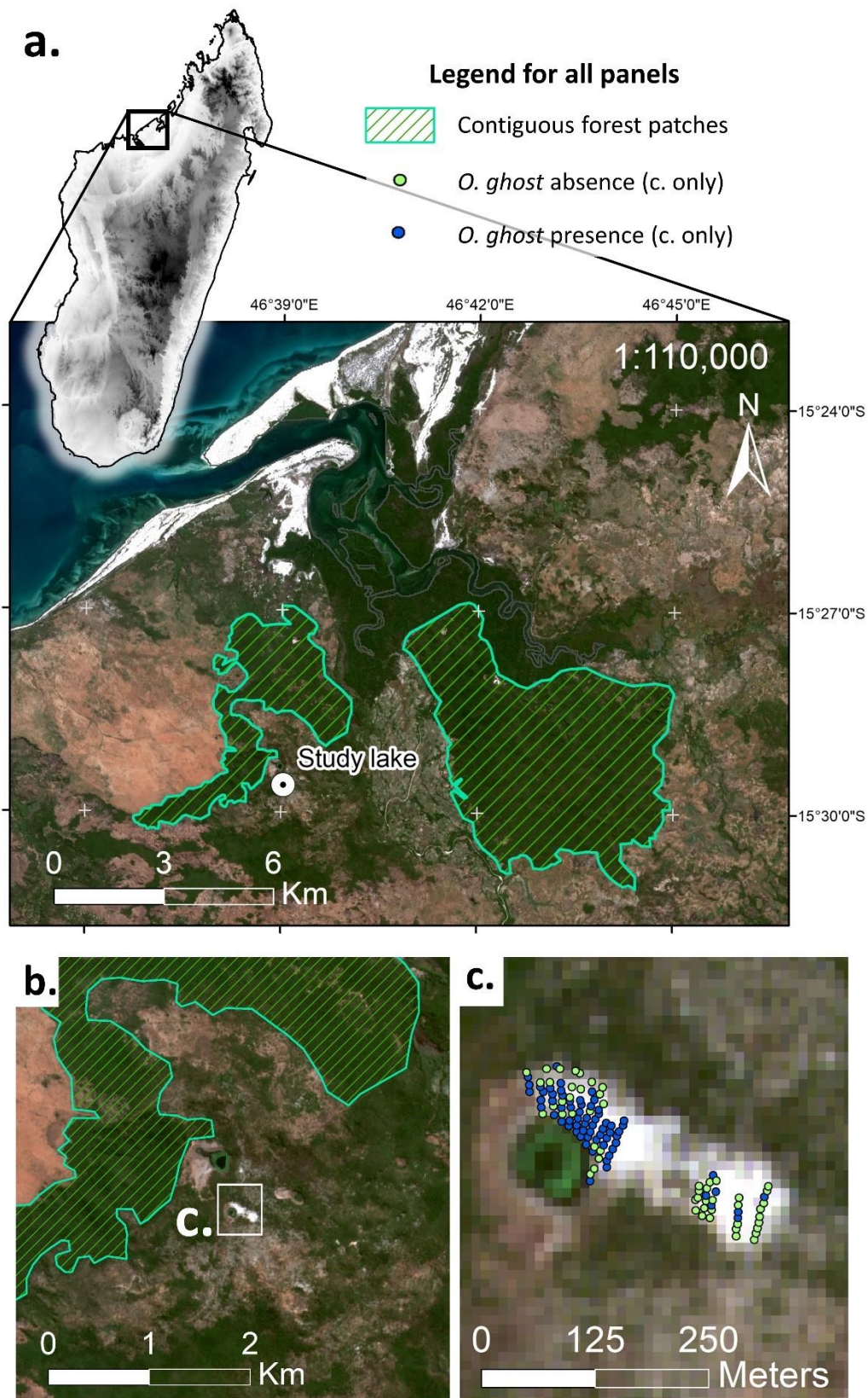
5 note: model estimates were obtained by fixing covariates at their mean values

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

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1 Figures



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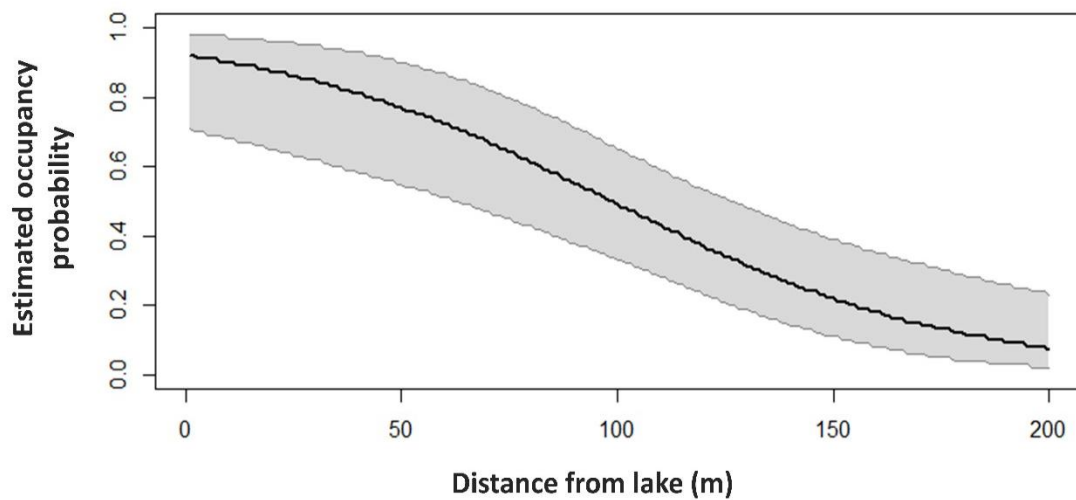
3 **Fig 1** (a) The study's location in the north-western dry forest within Madagascar, also showing elevation
 4 (max = 2744m); (b) Our study lake within the landscape, also showing nearby lakes to the north and

1 north-east; (c) our study lake in isolation, showing sampled points on the sandy northern/north-eastern
2 shore and a connected sandy area to the east, where blue indicates a presence and light green an absence.
3 All satellite imagery is from SENTINEL (<https://www.copernicus.eu/en>), July 2018, and the elevation
4 data in (a) is from WorldClim (Hijmans *et al.* 2005).

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

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