



# An improved habitat suitability index for the great crested newt *Triturus cristatus*

Emily Seccombe<sup>1,2</sup> & Roberto Salguero-Gómez<sup>2</sup>

<sup>1</sup>School of Geography and the Environment, Oxford University Centre for the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

<sup>2</sup>Department of Biology, 11a Mansfield Rd, Oxford 3SZ OX1, UK

Great crested newts *Triturus cristatus* are a European protected species whose conservation depends on the provision and protection of their breeding habitat. The species is in decline internationally, partly due to loss of suitable breeding habitat (European Environment Agency, 2019). A habitat suitability index (HSI) developed in 2000 is extensively used in great crested newt conservation to assess breeding habitat quality in the UK. Here, we introduce a new HSI with an improved ability to reflect *T. cristatus* presence/absence in UK ponds. This proposed HSI is easier to use, requires less data and predicts *T. cristatus* presence/absence better than the previous index. To inform the new index, we used a dual approach to identify the relative importance of environmental criteria to predict *T. cristatus* presence/absence. Firstly, we conducted a survey of 288 HSI users to assess the perceived strengths and limitations of the existing index. Secondly, we analysed national datasets of *T. cristatus* presence/absence and associated environmental data. Using these findings, we then tested various index modifications. The final modifications of the new HSI include (i) using an arithmetic (instead of geometric) mean, to reduce calculation errors and allow compensation between variables; (ii) excluding water quality and waterfowl impact, as these lacked significant power to predict *T. cristatus* presence/absence and were deemed inaccurate by HSI users; and (iii) changing the scoring relationship for pond area to better reflect current data and provide scores for ponds over 2000m<sup>2</sup>. We compared scores from the new and original HSIs using an independent dataset for validation, showing that the new HSI better reflects *T. cristatus* presence/absence (larger effect sizes and R-squared values) in comparison to the old HSI. Adopting this improved HSI will enable more effective conservation of the protected species via better-informed decision-making and monitoring.

*Keywords:* HSI, monitoring, *Triturus cristatus*, amphibian

## INTRODUCTION

Britain hosts populations of international importance for great crested newts *Triturus cristatus* (Salamandridae, Dunford & Berry, 2013; Haysom et al., 2018). However, populations of this species are in serious decline (Beebee & Griffiths, 2000). The Joint Nature Conservation Committee's report on UK *T. cristatus* status (2013–2018) concluded that there was an insufficient area and quality of occupied and unoccupied habitat for their long-term viability, and that habitat quality was decreasing (JNCC, 2019). The UK status report echoes the reports of other countries (European Environment Agency, 2019). Consequently, quantifying and identifying *T. cristatus* habitat suitability is an important task for their conservation.

Due to their decline and international rarity, *T. cristatus* is protected in the UK under the Wildlife and Countryside Act (UK Government, 1981) and is a European Protected Species (The Council of the European Communities, 1992). Consequently, actions that may harm individuals or their habitat may require a licence, detailing mitigation requirements (English Nature, 2001). However, these mitigation measures are often suboptimally implemented

and monitored (Edgar & Griffiths, 2004; Lewis et al., 2007; 2014b). This mitigation-based approach relies on having sufficient understanding of the species' habitat preferences to ensure the replacement habitat is suitable.

Habitat Suitability Indices (HSIs hereafter) provide a process-based approach to model habitat suitability. For an HSI to be useful, it needs to accurately predict presence/absence of a given species based on limited data (Zajac et al., 2015). HSIs are widely used (e.g. Soniat et al., 2013; Bender et al., 1996), yet there are key concerns over their use. These include an overreliance on variable expert opinion (Johnson & Gillingham, 2004), a lack of output validation (Brooks, 1997) and a lack of suitable frameworks for objective evaluation (Roloff & Kernohan, 1999). Nonetheless, HSIs are often seen as a pragmatic solution for situations requiring management action (Brooks, 1997).

The current method for assessing a site's *T. cristatus* suitability is the HSI developed by Oldham et al. (2000). This index was created as "a simple model for use by the non-specialist, which provides conservationists with an informed view of the value of a site" (Oldham et al., 2000). In this HSI, scores for ten Suitability Indices (SIs hereafter)

*Correspondence:* Emily Seccombe (emily\_rose@btinternet.com)

are calculated then combined by taking their geometric mean, resulting in a score from zero (poor habitat) to one (suitable habitat) - see Table 1 and Oldham et al. (2000) and ARG UK (2010) for full details. The HSI relies upon data from the 1991 National Amphibian Survey (Swan & Oldham, 1993; Oldham et al., 2000), now 30 years outdated. This HSI underwent limited validation - its parameterisation used only 72 ponds, predominantly located in only two of England's 48 counties.

This HSI is used in a variety of key applications. These include site assessments for developments (Natural England, 2015) and assessment of mitigation success (Lewis et al., 2007; 2014a). Importantly, the HSI is used in the UK's statutory reporting on European Protected Species' Favourable Condition Status (Reason, 2013) and in national reporting efforts (Wilkinson & Arnell, 2013). Furthermore, the HSI has been adapted for monitoring schemes in continental Europe too (Jehle et al., 2011; Unglaub et al., 2015; Bełcik et al., 2019).

Despite the extensive applications of Oldham et al.'s (2000) HSI, there are significant concerns over its accuracy (Reason, 2013; O'Brien et al., 2017; Buxton et al., 2021; Priol et al., 2022). Oldham et al. (2000) acknowledged the conjecture in the production of their HSI, noting that the index "can be upgraded easily as knowledge of crested newt habitat requirements improves".

Several studies have assessed the HSI and found a lack of a relationship with *T. cristatus* occupancy. This research includes studies in England (Reason, 2013; Buxton et al., 2021; Lewis et al., 2007), Scotland (O'Brien et al., 2017; Harper et al., 2019a) and in the Mediterranean (Priol et al., 2022). Buxton et al. (2021) found that only waterfowl (SI6) and fish (SI7) indexes in the HSI were significantly correlated with the species' presence/absence. O'Brien et al. (2017) suggested no significant relationship between *T. cristatus* presence/absence and scores for pond area (SI2), waterfowl (SI6), fish (SI7) or pond density (SI8). Priol et al. (2022) suggested the only SI that significantly affected *T. cristatus* occupancy was pond drying (SI3). In contrast, two studies support the use of the HSI: Harper et al. (2019b) suggest that the HSI can predict eDNA-based *T. cristatus* detection in the UK, and Bełcik et al. (2019) propose that *T. cristatus* occurrence could be predicted by HSI scores in central Poland. Bełcik et al. (2019) found that pond area (SI2), water quality (SI4) and fish (SI7) were the most important factors influencing site occupancy.

Despite advances in data availability since its creation, the HSI has remained largely unchanged. In 2007, the HSI was conservatively amended following a user-group workshop (ARG UK, 2010) to improve standardisation and usability. O'Brien et al. (2017) suggest a change to SI1 boundaries in Scotland. Additionally, Buxton & Griffiths (2022) propose a change to how the HSI scores relate to categories. However, the index remains largely as created in 2000.

Motivated by the widespread application of Oldham's HSI, here we develop an improved great crested newt HSI that increases its accuracy and simplicity. To do so, we surveyed HSI users and analysed national ecological datasets to identify the importance of different

**Table 1.** Suitability indices and their corresponding environmental criteria. This is a summary of the information provided in Oldham et al. (2000) and ARG UK (2010).

Suitability Index	Environmental criteria	Details
SI1	Geographic location	3 categories giving scores of 0.01, 0.5 or 1
SI2	Pond area	Graph gives scores for pond areas measured in m <sup>2</sup>
SI3	Pond permanence	4 categories giving scores of 0.1, 0.5, 1 or 0.9
SI4	Water quality	4 categories giving scores 0.01, 0.33, 0.67 or 1, based on invertebrate diversity
SI5	Shoreline shade	Graph gives scores for percentage of shoreline shaded
SI6	Waterfowl	3 categories giving scores of 0.01, 0.67 or 1
SI7	Fish	4 categories giving scores of 0.01, 0.33, 0.67 or 1
SI8	Pond density	Graph gives scores using the number of ponds within 1km divided by $\pi$
SI9	Terrestrial habitat	4 categories giving scores of 0.01, 0.33, 0.67 or 1
SI10	Macrophyte cover	Graph gives scores for percentage of surface area covered by macrophytes

environmental factors in predicting *T. cristatus* presence/absence across the UK. We then tested modifications and cross-validated the proposed HSI against the original HSI using an independent dataset. Our new HSI outperforms the original one as the goodness-of-fit is higher when using the new HSI compared to the original HSI, for both the original dataset and new independent validation dataset. We hope that the adoption of this HSI will allow more accurate estimation of this species' habitat suitability, thereby enabling more effective protection of this endangered species via better informed decision-making and monitoring.

## MATERIALS & METHODS

All statistical analyses were performed with RStudio (v. 1.2.5001, R version 3.6.1, R Core Team, 2017) with the 'tidyverse' (Wickham et al., 2019) and 'modeest' (Poncet, 2019) packages for data preparation and description. The code used and a copy of the data with confidential information removed can be found at <https://osf.io/2yt6r/>.

### User survey

We ran a survey targeting users of Oldham et al.'s HSI to assess perceptions of HSI recording accuracy, to elicit suggestions to improve the HSI, and to identify the extent of user support for the existing HSI. Firstly, we conducted a pilot survey (Supplementary material 1) to identify the required minimum sample size and check the survey design

viability, after which minor formatting changes were made. The final survey (Supplementary material 2), published on SurveyMonkey, was sent to 139 UK-based conservation organisations whose members are likely to use the HSI, such as ecology consultancies, biological record centres and conservation organisations. Quantitative questions asked for ratings of accuracy of records of the suitability indexes (SIs) and the HSI itself. Ten qualitative questions asked for information on limitations that reduced accuracy of SI records. Two further qualitative questions asked about additional factors for inclusion and other suggestions for improving the HSI.

The survey was completed by 288 respondents. Most respondents (86%) were professional ecologists. There was a good level of response from experienced users (median of 14 years of HSI experience,  $\pm 0.56$  S.E.). Additionally, there was a reasonably high frequency of HSI use amongst the respondents, with 50.4% using it over ten times per year. Neither years of experience ( $\chi^2_{df=2} = 1.386$ ,  $P = 0.500$ ) nor frequency of use of the index ( $\chi^2_{df=4} = 1.748$ ,  $P = 0.782$ ) significantly impacted scores of HSI accuracy.

We analysed the numeric questions through chi-square tests using the `chisq.posthoc.test` package (Ebbert, 2019). We applied content analysis in NVivo (QSR International Pty Ltd. 2018) to systematically examine the qualitative sections. We coded all answers, then joined codes together into themes based on frequency and similarity, following the practice set out in Bryman (2012). We used open coding rather than a pre-specified coding manual because of the exploratory nature of the survey (Bryman, 2012).

### Statistical analysis of ecological datasets

Next, we conducted a series of statistical analyses on UK ecological datasets of environmental correlates of *T. cristatus* population presence/absence. We sourced three datasets containing sites with data on *T. cristatus* presence/absence and HSI information, see Table 2. An additional dataset from NatureSpace was used for verification of the new model. Prior to analysis, we performed data merging, homogenisation and cleaning, using the R packages 'EnvStats' (Millard, 2019) and 'lubridate' (Grolemund & Wickham, 2011). For sites with multiple survey records over time, we chose the most recent record only, to avoid

unequal representation of sites in the combined dataset. We checked for independence between the datasets by searching the data for duplicate geographic information. The verification dataset contained no duplicated locations from the original dataset.

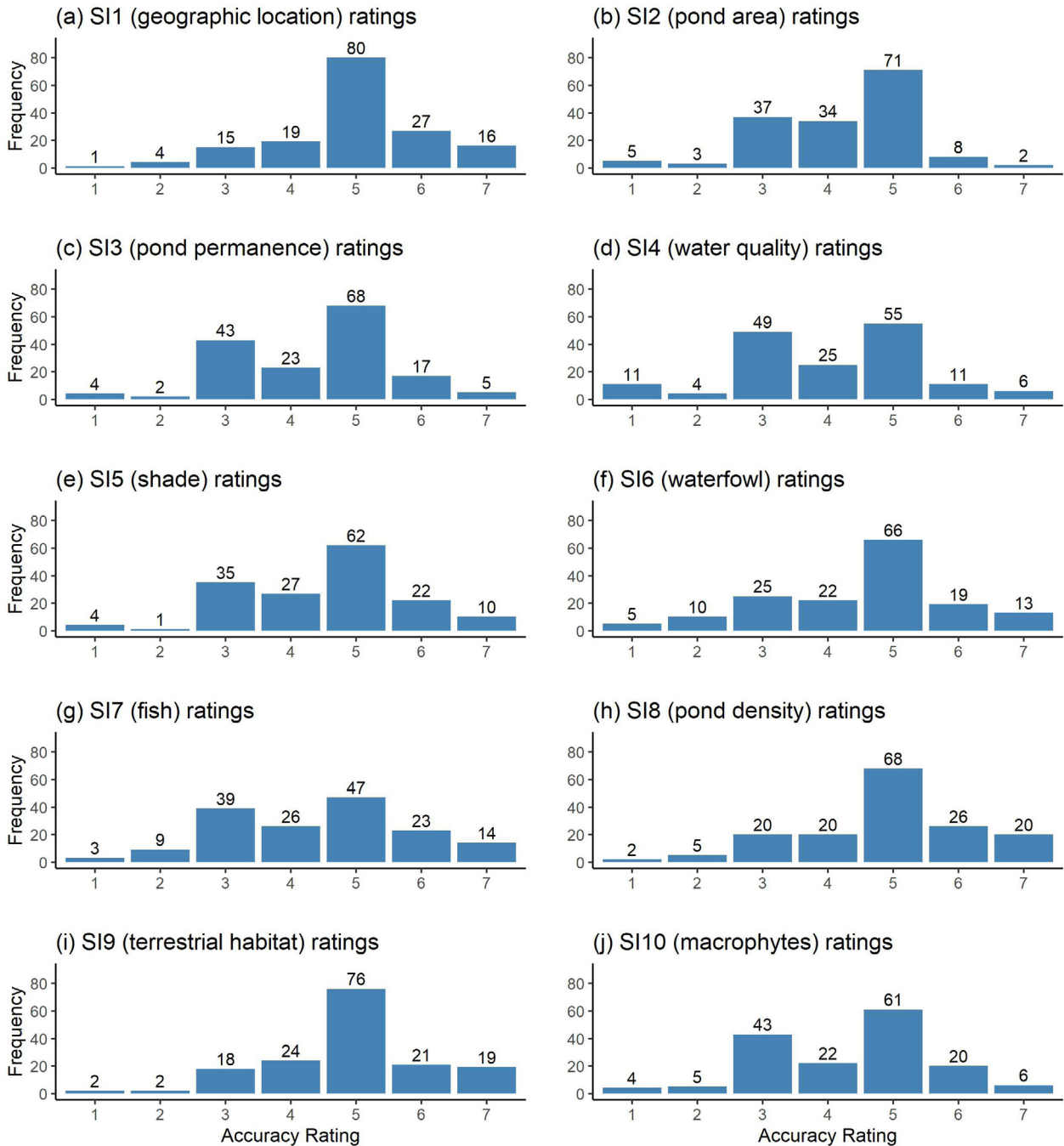
We performed a range of tests to identify statistically significant relationships between individual environmental variables and *T. cristatus* presence/absence. We first fitted logistic regressions in a generalised linear model framework (R package 'glmm', Knudson, 2020) to test the relationship between each of the continuous variables (e.g. pond area, macrophyte cover) and *T. cristatus* presence/absence (Skei et al., 2006). Next, we used chi-square tests to test the relationship between each of the categorical variables (e.g. waterfowl impact, fish presence) and *T. cristatus* presence/absence. We used a Fisher's test in place of chi-square test for location due to imbalanced data (most samples being from 'Area A'). For those variables that were significantly correlated with *T. cristatus* presence/absence ( $P < 0.001$ ), we then performed post-hoc tests of pairwise comparisons using the Bonferroni method (R package 'chisq.posthoc.test'; Ebbert, 2019). Additional statistical details from the post-hoc tests are provided in Supplementary material 3.

### Combining and testing modifications to the HSI

By combining the results of the survey and the statistical analyses regarding the environmental correlates of *T. cristatus* presence/absence, we produced a list of candidate modifications to Oldham et al.'s HSI. We tested some of these modifications where sufficient data were available to explore potential improvements in the HSI's predictive ability. When considering the final modifications to test, our primary aim was to create an improved HSI that would be most useful to land managers, ecologists and policy makers while remaining statistically grounded, rather than to just create a model that best explains the great crested newt presence/absence data, but would be of limited usability by our target users. Accordingly, we considered the findings of the survey in conjunction with the ecological data analyses, to inform the modifications to test, such as which SIs to exclude. 37.78% of records had at least one SI value recorded as 'NA', which reduced the

**Table 2.** Information on the datasets used in this study. All datasets contain information on *T. cristatus* presence/absence or abundance and environmental variables, including HSI scores.

Dataset	Cofnod great crested newt project	National amphibian and reptile recording scheme	Natural England eDNA research project	Natural England evidence enhancement project	NatureSpace south Midlands district level licencing
Records	574	852	5866	3137	153
Geographic Spread	Wales	UK	England	6 pilot areas across England	South Midlands, England
Years	2011–2019	2013–2019	2017–2019	2013	2021
Surveyors	Professionals and citizen scientists	Citizen scientists	Professionals and citizen scientists	Professionals	Professionals
Newt survey method	Mixed	Mixed. See Wilkinson & Arnell (2013)	Mixed. See Natural England Open Data (2019)	eDNA. See Natural England Open Data (2017)	eDNA



**Figure 1.** The perceived accuracy of suitability index (SI) records by survey respondents varies across all ten categories (Table 1). Bar charts show the frequency of our sampled 288 respondents selecting each rating option (from 1 to 7, where 1 is the lowest) in answer to the questions on the accuracy of records of SIs 1–10 (a–j).

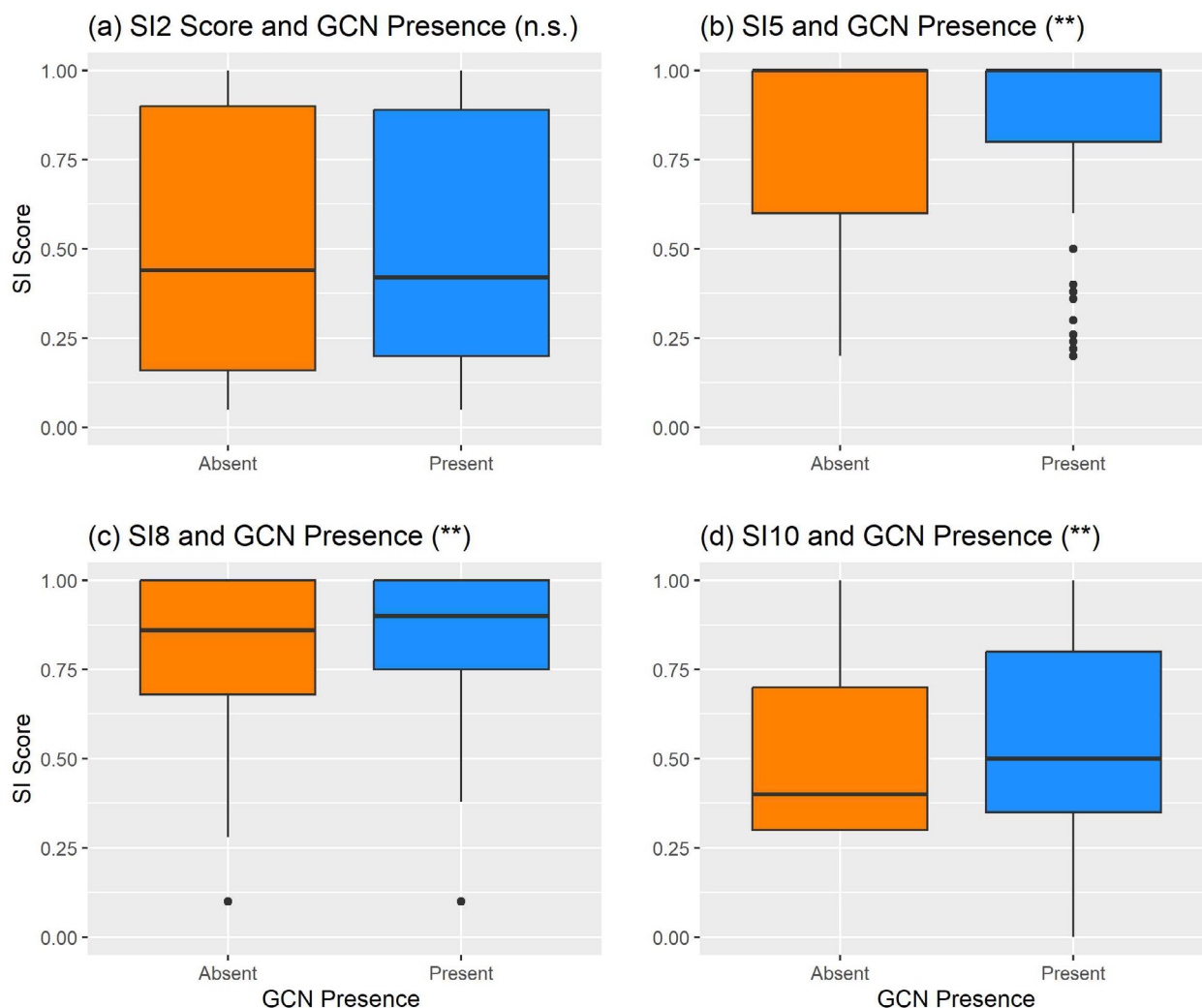
validity of conducting stepwise regressions to determine which SIs to include.

We then quantitatively assessed the potential improvement of the modifications on the HSI by adopting the approach implemented by Buxton et al. (2021). This involved comparing the distribution of *T. cristatus* presence and absence amongst the five habitat suitability categories (Poor, Below Average, Average, Good, Excellent) using the new and modified HSIs. We used chi-square tests and the pertinent post-hoc tests of significant models on the frequency tables of HSI category and *T. cristatus* presence/absence to identify if modified HSIs were more accurate in differentiating habitat quality than Oldham et al.’s HSI. For

these tests, we used the R packages ‘dplyr’ (Wickham et al., 2020), ‘EnvStats’ (Millard, 2019), ‘forcats’ (Wickham, 2023) and ‘chisq.posthoc.test’ (Ebbert, 2019).

**Index cross-validation**

To compare the original and new HSIs, we used the independent dataset (provided by NatureSpace, as noted above). The new HSI scores were calculated for each pond. We fitted logistic regressions in a generalised linear model framework (R package ‘glm’; Knudson, 2020) to test the relationship between the original HSI scores and *T. cristatus* presence/absence. Next, we used chi-square tests and post-hoc tests to test the relationship between



**Figure 2.** Great crested newt (GCN) presence/absence and continuous suitability index (SI) scores. Minimal differences in scores of continuous suitability indexes (SIs) are apparent between sites with great crested newt absent (orange) or present (blue). Box and whisker plots show (a) SI2: pond area, (b) SI5: shade, (c) SI8: pond density, and (d) SI10: macrophyte scores for sites with *T. cristatus* present or absent. “n.s.” indicates statistically non-significant differences between SI scores in ponds with *T. cristatus* absent or present; “\*\*” indicates statistically significant differences at  $P < 0.001$  between SI scores in ponds with *T. cristatus* absent or present.

original HSI category scores (Poor to Excellent) and *T. cristatus* presence/absence, also using the Bonferroni method as above (R package ‘chisq.posthoc.test’; Ebbert, 2019). We then repeated both methods using the new HSI scores.

## RESULTS

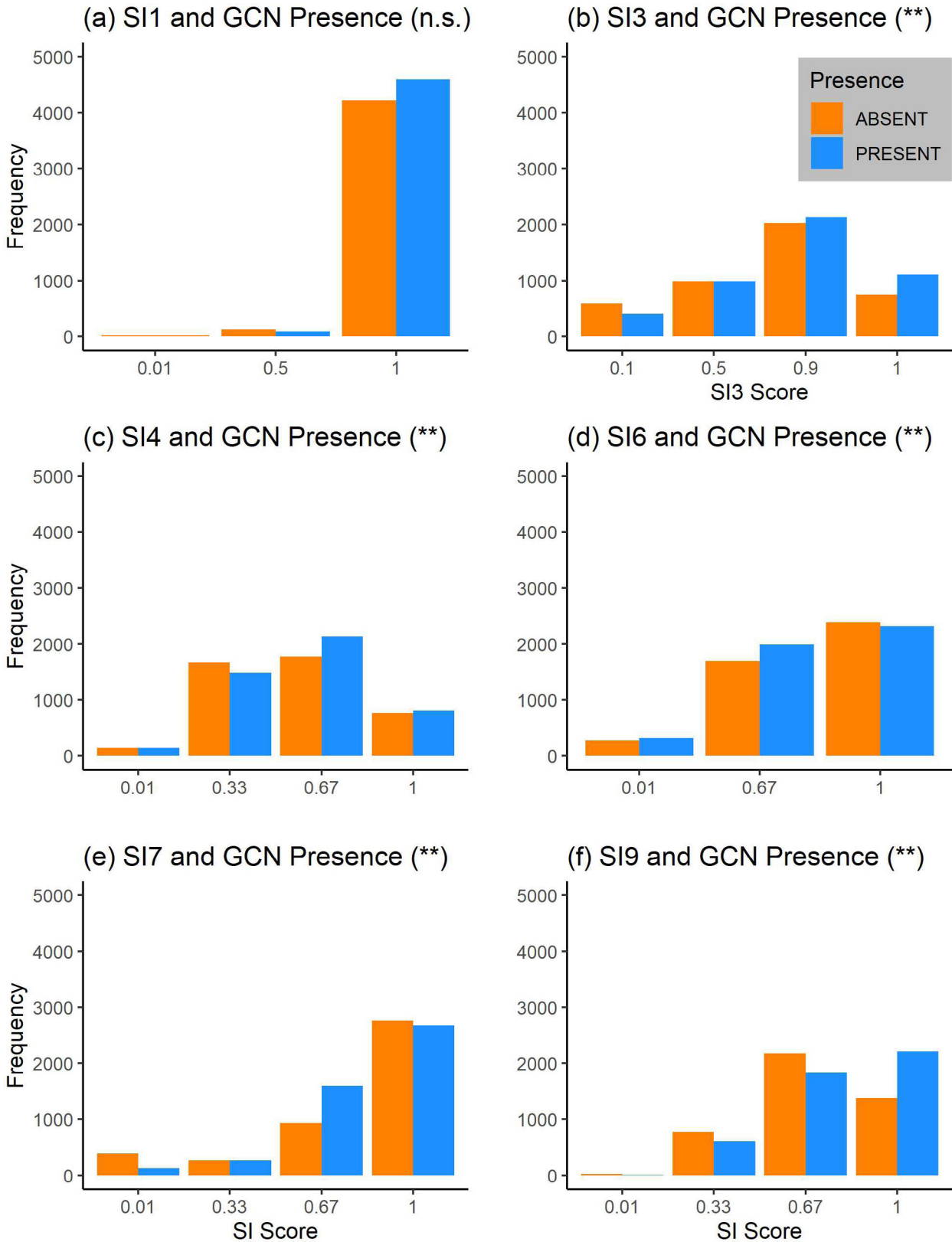
### Survey

The survey’s rating scale section (Supplementary material 2) on perceived SI recording accuracy revealed much variation between SIs (Fig. 1). The chi-square tests showed that different SIs had significantly different perceived accuracy ratings ( $\chi^2_{df=18} = 77.454$ ,  $P < 0.001$ ). Post-hoc tests showed that SI1 (geographic location) and SI9 (terrestrial habitat) had higher perceived accuracy scores ( $P < 0.001$  and  $P < 0.03$  respectively), and that SI4 (water quality) had lower accuracy scores ( $P < 0.001$ ). The use of the HSI for *T. cristatus* abundance estimations was rated significantly lower than for presence/absence estimations ( $P < 0.001$ ;

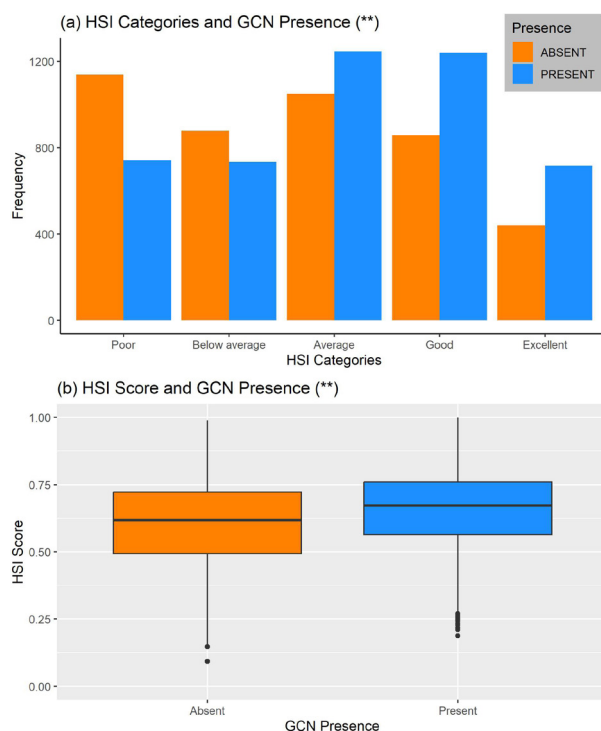
Fig. S1). Overall, a quarter (26%) of respondents rated the HSI as ‘very inaccurate’ for estimating abundance.

Common themes arising from qualitative comments on the limitations of SI1–10 accuracy were identified. These themes included the subjectivity of SI measures, seasonal limitations of the HSI, the difficulty interpreting SI graphs (particularly for SI2 [pond area] and SI8 [pond density]) and criticism of surveyor skills. Respondents also suggested a range of additional factors of potential importance for *T. cristatus* habitat suitability that are not in the current HSI. The most frequent suggestions (with 17 comments each) were proximity to local *T. cristatus* populations, chemical water tests and disturbance/predation (predominantly in relation to dogs or people).

The respondents provided diverse suggestions for improvement of the HSI. These responses were grouped into themes which included improving guidance to reduce subjectivity, making the HSI easier to use, using HSI results more appropriately and adapting the HSI to fit other circumstances (e.g. to apply to ditches). Many comments



**Figure 3.** Great crested newt (GCN) presence/absence and categorical suitability index (SI) scores. Most categorical SIs (Table 1) show marginally higher frequency of ponds with *T. cristatus* present (blue) for higher score categories, and lower frequency of ponds with *T. cristatus* absent (orange) for lower score categories. This pattern is not apparent for waterfowl (SI6), and is hard to assess for pond location (SI1) due to the predominance of a score of 1. Bar charts show the frequency of score levels for sites with *T. cristatus* present or absent for (a) SI1: geographic location, (b) SI3: pond permanence, (c) SI4: water quality, (d) SI6: waterfowl, (e) SI7: fish, and (f) SI9: terrestrial habitat. “n.s.” indicates statistically non-significant differences between SI scores in ponds with great crested newts absent or present, “\*\*” indicates the statistically significant differences at  $P < 0.001$  between SI scores in ponds with *T. cristatus* absent or present.



**Figure 4.** Great crested newt (GCN) presence/absence and habitat suitability index (HSI) scores. HSI scores for great crested newts are higher in ponds where the species is present. HSI (a) categories and (b) scores are shown for sites with (orange) or without (blue) great crested newts. (a) The bar chart shows higher frequencies of ponds with *T. cristatus* present and lower frequencies of ponds with *T. cristatus* absent for the higher HSI categories (Average, Good and Excellent). The panel also shows lower frequencies of ponds with *T. cristatus* present and higher frequencies of ponds with *T. cristatus* absent for the lower HSI categories (Poor and Below Average). (b) Box and whisker plot of scores showing higher HSI scores for sites where *T. cristatus* are present.

suggested misuse of the HSI, such as application outside of the recommended season and incorrect geometric mean calculation. Hierarchy plots of the qualitative question responses are given in Supplementary material 4.

#### Ecological determinants of *T. cristatus* presence

Scores of continuous SIs were significantly higher in sites with *T. cristatus* present than sites with *T. cristatus* absent for SI5 (shade), SI8 (pond density) and SI10 (macrophytes) (all  $P < 0.001$ ; Fig. 2). Logistic regressions found no significant difference in SI2 (pond area) scores for ponds with *T. cristatus* present or absent.

Of the categorical SIs, significant differences in scores at ponds with *T. cristatus* present or absent were apparent for SI3 (pond permanence), SI4 (water quality), SI6 (waterfowl), SI7 (fish) and SI9 (terrestrial habitat) ( $P < 0.001$ , for full residuals, please see Supplementary material 3a) - see Figure 3. The post-hoc tests showed that these differences were in the directions expected (i.e. higher SI values correlated with presence of the species) for most of these SIs, except for SI6 and SI7.

**Table 3.** Potential modifications to improve the great crested newt suitability indices (SIs) within the habitat suitability index (HSI), inferred from peer-review literature, user survey results and ecological data analysis performed in this research.

Aspect of the HSI	Potential modifications to HSI or associated guidance
SI1	Increase the number of zones, use more up-to-date data and better define borders Include new map with new Scotland zones (O'Brien et al., 2017) Make an easier-to-read map or an online look-up system
SI2	Create SI2 scores for ponds over 2,000 m <sup>2</sup> Removing or rescoring SI2 based on underlying environmental data (Denoel & Ficetola, 2008)
SI3	Test relationship between great crested newts presence/absence and desiccation (Griffiths & Williams, 2000)
SI4	Remove SI4 from HSI Replace with chemical testing of water
SI6	Remove SI6 from HSI
SI7	Test importance of fish presence for great crested newts; try removing from HSI
SI8	Trial excluding SI8 from HSI if HSI < 0.75 (Oldham et al., 2000) Ensure SI8 scores correctly divided pond numbers by pi; create new graph to avoid need to divide by pi Test importance of pond density for great crested newts Remove from HSI
SI10	Change focus from living plant material to any egg-laying material

Surprisingly, the post-hoc test for SI6 showed that ponds with *T. cristatus* absent had significantly more scores of 1 (indicating waterfowl absence) and fewer 0.67 scores (indicating minor waterfowl impact) and vice versa for ponds with *T. cristatus* present ( $P < 0.001$ ). The post-hoc test for SI7 also showed an unexpected pattern; ponds with *T. cristatus* absent had more 0.01 scores (indicating major fish impact), more 1 scores (indicating fish absence) and fewer 0.67 scores (indicating possible fish impact) and vice versa ( $P < 0.001$ ). No significant difference was found for SI1 scores (geographic location) at ponds with *T. cristatus* present than ponds with the species recorded as absent.

Logistic regression found a significant relationship (slope = 0.703, d.f. = 9,046,  $P < 0.001$ ) between HSI scores and *T. cristatus* presence/absence (Fig. 4). We found significant differences in the HSI category frequencies for ponds with *T. cristatus* present or absent ( $\chi^2_{df=4} = 245.04$ ,  $P < 0.001$ ). As expected, post-hoc tests showed that ponds without *T. cristatus* had more Below average and Poor scores and fewer Excellent and Good scores than ponds with *T. cristatus* ( $P < 0.001$  in all cases). This reflects the patterns shown in Figure 4a.

#### HSI improvements

Informed by the previous results, a list of potential modifications is presented in Tables 3 & 4. Some of these

**Table 4.** Potential modifications to improve the great crested newt habitat suitability index (HSI), inferred from peer-review literature, user survey results, and ecological data analysis performed in this research.

Improve guidance to reduce subjectivity and emphasise appropriate use (not as substitute for population survey) (Buxton et al., 2021)
Weight SIs according to importance (Oldham et al., 2000)
Add measures of uncertainty to output (Bender et al., 1996; Burgman et al., 2001; Zajac et al., 2015; Biggs et al., 2014)
Test predictive ability of HSI scores on great crested newt presence/absence, abundance and breeding success (Reason, 2013; Buxton et al., 2021; Lewis et al., 2007)
Create clearer graphs and provide formulae for the relationship between the SI score and the underlying environmental variable shown in the graph
Check if HSI scores provided correctly uses the geometric mean of SIs; try arithmetic mean or cumulative score of SIs to reduce mistakes of miscalculation (U.S. Fish and Wildlife Service, 1981; Burgman et al., 2001)
Increase the number of categories for categorical SIs
Investigate additional factors for potential inclusion (Langton et al., 2001; Skei et al., 2006; Marklund et al., 2002; Denoel & Ficetola, 2008; Gustafson et al., 2011; Cresswell & Whitworth, 2004; JNCC, 2019; Dunford & Berry, 2013)
Provide greater clarity on detailed, reproducible methods for recording SIs

modifications require additional data or involve changes to the written guidance. The modifications that could be tested with the data available for this study were explored and results presented below. Additionally, new graphs were produced to aid reading of continuous SIs (see Figs. S4–S6), and formulae are provided in Supplementary material 5.

Two of the datasets were found to have incorrect HSI calculations due to not adjusting the exponent in the geometric mean calculation to take account of the number of SIs recorded. To overcome this issue, new HSI scores were calculated using the arithmetic mean. The distribution of HSI score categories remained significantly different between sites with *T. cristatus* present or absent ( $\chi^2_{df=4} = 261.85$ ,  $P < 0.001$ ), see Supplementary material 3b for residuals from the post-hoc test. Therefore, the arithmetic mean-based HSI is comparable in terms of reflecting *T. cristatus* presence/absence, but avoids the likelihood of calculation mistakes as it is simpler to calculate.

SI8 (pond density) scores were not calculated correctly in the NARRS dataset (SI8 scores were not divided by  $\pi$ , resulting in no sites scoring between 0.1 and 0.7). The risk of error by forgetting to divide by  $\pi$  was also noted by survey respondents. To prevent these errors, a modified graph was produced (Fig. S5) that avoids the need for division by  $\pi$ .

New HSI scores were created by excluding the SIs that received low accuracy ratings in the survey. Independent

**Table 5.** Habitat suitability index (HSI) categories (left column) and corresponding values (centre column) under the original habitat suitability index (ARG UK, 2010) and with the new modified habitat suitability index (right column).

Category	HSI value cut-offs for original HSI, as given in ARG (2010)	HSI value (x) cut-offs for new HSI combining useful modifications
Poor	< 0.5	$x < 0.70$
Below average	0.5–0.59	$0.70 \geq x < 0.77$
Average	0.6–0.69	$0.77 \geq x < 0.80$
Good	0.7–0.79	$0.80 \geq x < 0.87$
Excellent	>0.8	$x \geq 0.87$

exclusion of SI4 (water quality) and SI6 (waterfowl) were found to be beneficial (see Supplementary material 3c & 3d), so these SIs were then excluded simultaneously. The distribution of sites between HSI categories remained different for ponds with *T. cristatus* present or absent ( $\chi^2_{df=4} = 369.83$ ,  $P < 0.001$ ). The post-hoc test showed the modified HSI was better than the original (larger residuals) for distinguishing Excellent and Poor ponds, and comparable for other categories (Supplementary material 3e).

A new scoring method for SI2 (pond area) was created by plotting new data to create a new scoring graph (see Figs. S2 & S3). HSI scores were recalculated with the new SI2 scores. The distribution of sites between HSI categories remained different for ponds with *T. cristatus* present or absent with the new SI2 scores ( $\chi^2_{df=4} = 297.51$ ,  $P < 0.001$ ). The post-hoc test showed the modified HSI was better at distinguishing between ponds in the Below Average, Excellent and Good categories, although very slightly worse for the Poor category (see residuals in Supplementary material 3f) in comparison to the original HSI.

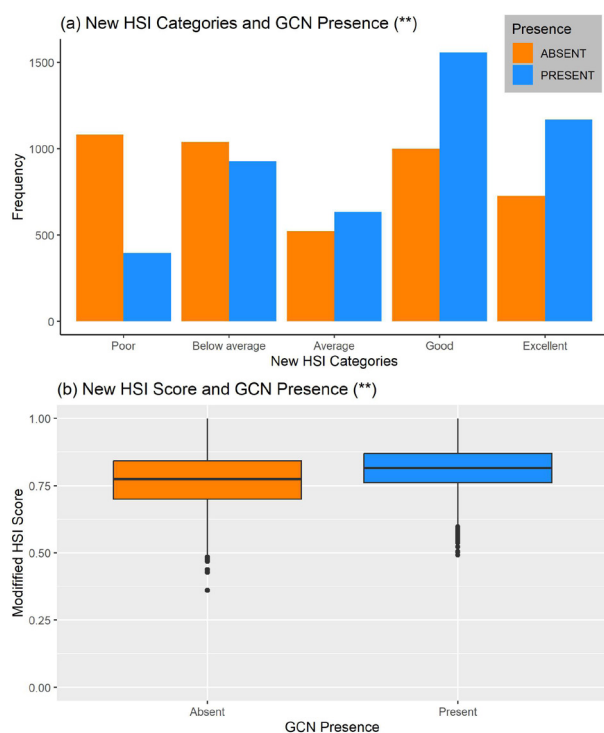
The modifications detailed above were then combined and new HSI scores were calculated using these modifications. The scores were grouped in categories with new boundaries to create more equal splits to facilitate interpretation (Table 5). The new scores and category frequencies are shown in Figure 5, which can be compared to the original HSI scores and category frequencies in Figure 4.

The chi-square test of the new HSI categories and *T. cristatus* presence/absence showed strong significance ( $\chi^2_{df=4} = 533.11$ ,  $P < 0.001$ ). The residuals for all categories are larger than for the original HSI (see Supplementary material 3g for residuals).

#### Cross-validation

Both the original and new HSIs lacked predictive power for *T. cristatus* presence/absence at high significance values with the independent dataset. However, the new HSI had higher effect sizes and lower residuals from the logistic regression than the original HSI scores (see Fig. 6 and Supplementary material 3h for full residuals). Following chi-square tests to look at HSI category scores, post-hoc





**Figure 5.** Distribution of **(a)** HSI categories and **(b)** HSI scores for sites with great crested newts (GCNs) present or absent under the newly proposed habitat suitability index (HSI). HSI scores are statistically higher in ponds with *T. cristatus* present ( $P < 0.001$ ) - see Supplementary material 3g. **(a)** Bar chart showing higher frequencies of ponds with *T. cristatus* present and lower frequencies of ponds with *T. cristatus* present for the higher HSI categories (Average, Good and Excellent). This panel shows lower frequencies of ponds with *T. cristatus* present and higher frequencies of ponds with *T. cristatus* absent for the lower HSI categories (Poor, Below Average). **(b)** Box and whisker plot of the newly proposed HSI scores showing higher HSI scores for sites with *T. cristatus* present ( $P < 0.001$ ) - see Supplementary material 3h. The interquartile range of modified HSI scores in Figure 5b is higher and more compact than that of Oldham's HSI shown in Figure 4b, necessitating the new category divisions proposed in Table 5.

tests were carried out, but no significant differences in *T. cristatus* presence/absence between HSI categories were found (see Supplementary material 3i).

## DISCUSSION & CONCLUSION

We examined potential improvements to the existing habitat suitability index (HSI) for the great crested newt proposed by Oldham et al. (2000), as adapted by ARG UK (2010). Through a combined approach using a HSI-user survey and robust statistical analyses of presence/absence and environmental data across the UK, we found that the HSI could be improved by removing the indices for SI4 (water quality) and SI6 (waterfowl), combining the index values with an arithmetic (rather than geometric) mean, and creating a new scoring scheme for SI2 (pond area). Thus, we introduce an improved HSI for great crested newts in the UK.









This study identified a range of limitations of the original HSI which builds upon a growing evidence base

suggesting the HSI needs improvement. The findings echo wider literature about HSIs, such as concerns about a lack of objectivity (Brooks, 1997). HSIs are intended as applicable management tools and thus their accuracy will pragmatically always be limited (Johnson & Gillingham, 2004). Nonetheless, the limitations to the HSI given in the survey and the criticism in the existing literature justify further work to improve the HSI, particularly given its conservation importance for the species. Indeed, the original HSI paper noted that the HSI "can be upgraded easily as knowledge of crested newt habitat requirements improves" (Oldham et al., 2000), demonstrating the expectation of ongoing modification to the HSI.

Concern over application of the HSI to reflect great crested newt abundance was a key theme arising from the survey. The HSI guidance (NARRS, n.d. & ARG UK, 2010) and Natural England's great crested newt web page (Natural England, 2015) specify that the HSI should not be used as replacement for population surveys or to predict abundance. Our survey found that this practice was continuing despite the guidance, which corroborates concerns raised by Lewis et al. (2007) and Buxton et al. (2021). This finding demonstrates the importance of clearer HSI guidance to ensure practitioners are not misusing the HSI to absolve the need for population surveys.

The ecological data analysis suggested that the original HSI has limited ability to differentiate *T. cristatus* suitability as inferred from presence/absence. Our results showed that many ponds in low HSI categories (Poor or Below Average) have *T. cristatus* present, and many ponds in high HSI categories (Good or Excellent) have *T. cristatus* recorded as absent. This finding echoes the results of Buxton et al. (2021) at a national stage. This demonstrates the need to continue investigating HSIs after their creation - such research is lacking for other species' HSIs too, as highlighted in Brooks (1997). These findings provide clear evidence that the existing HSI should not be overly-relied upon for conservation and mitigation decisions.

A limitation of the HSI identified by the ecological analysis is that only some SIs were significantly correlated with *T. cristatus* presence/absence. This finding corroborates wider evidence, such as that of O'Brien et al. (2017) and Priol et al. (2022). SI1 (location) and SI2 (pond size) were not significantly correlated with *T. cristatus* presence/absence. SI5, SI8, SI9 and SI10 (shade, pond density, terrestrial habitat quality and macrophytes) scores were positively correlated with *T. cristatus* presence. SI3 (pond permanence), SI4 (water quality), SI6 (waterfowl) and SI7 (fish) had less clear results. The lack of clear correlation between SI7 and *T. cristatus* presence/absence in this study reflects the findings of Denoël & Ficetola (2008), who found a negative impact of fish on other newt species, but no significant impact on great crested newts specifically. Wider research suggests that fish do have a negative impact on great crested newts (e.g. Skei et al., 2006; Miró et al., 2017; Harper et al., 2019b; Bełcik et al., 2019), so the lack of significant correlation in our study may be due to the difficulties in determining fish presence as part of the HSI methodology, a challenge noted by survey respondents and in O'Brien et al. (2017).

	Original dataset - old HSI	Original dataset - new HSI	Verification dataset - old HSI	Verification dataset - new HSI
Effect size	**  0.736	**  5.266	 0.7759	 1.411
R <sup>2</sup> (calculated from glm as 1-(residual deviance/nul l deviance)	 0.029	 0.038	 0.041	 0.043
Notes: **: P < 0.001, otherwise P > 0.05. Effect size: direction of arrow reflects direction of effect, length of arrow reflects size of effect. R <sup>2</sup> : Radius of circle reflects size of R <sup>2</sup> value.				

**Figure 6.** Effect sizes and goodness-of-fit for the new and original Habitat Suitability Indexes (HSIs). The newly proposed HSI outperforms the old HSI in terms of effect sizes and goodness-of-fit when *T. cristatus* predicting presence/absence. The length of the arrows is proportional to the effect size for the output of the logistic regression, under the two HSIs, firstly tested on the original dataset and secondly on the independent verification dataset. The circles show the R<sup>2</sup> values - with the new HSI, these values are larger (more so for the original dataset) suggesting a better goodness-of-fit between the new HSI and the *T. cristatus* presence/absence data. The effect sizes are only statistically significant when using the larger, original dataset.

This study also identified errors in HSI calculation. These errors include incorrectly calculating pond density scores (as in the NARRS dataset) or not correctly adjusting the geometric mean calculation for the number of SIs recorded (as in the NARRS dataset and the Natural England eDNA dataset). This finding adds to the need for increased validation of HSIs (Brooks, 1997), to ensure that not only does the HSI provide an accurate reflection of the species' habitat requirements, but that the HSI is easy to calculate correctly.

This study produced a range of potential modifications to improve the HSI (summarised in Tables 3 & 4). Some of these require further ecological data collection and analysis, and so are out of the scope of this study, but provide a starting point for further research. However, additional variables and complex methodologies could make the HSI harder to use. Future research could also investigate how uses and perceptions of the HSI vary across the geographical range in which the HSI is applied, including outside of the UK.

Those modifications which could be tested with the available data and would not add to calculation

complexity were investigated in this study, leading to a new HSI formulation. The proposed HSI has the following modifications: an arithmetic mean is used to combine SIs instead of a geometric mean, a new SI2 (pond size) scoring relationship is provided, SI4 (water quality) and SI6 (waterfowl) are removed, and new graphs are provided for SI calculation. Following the approach of Buxton et al. (2021), the distribution of ponds with *T. cristatus* present or absent between different HSI categories was used to assess HSI accuracy. According to this method, the new HSI is better than the original at distinguishing great crested newt habitat suitability, assuming that suitability can be inferred from presence/absence (Lewis et al., 2007).

The new HSI should be easier to conduct due to simpler calculation and having fewer SIs. The exclusion of SI4 (water quality) and SI6 (waterfowl) avoids the problems in assessing water quality and waterfowl impact noted by survey respondents. The new graphs (Figs. S4–S6) and formulae (Supplementary material 5) also support ease-of-use of the new HSI. By not incorporating any new SIs, the new HSI has backwards compatibility with existing records;

the changes to the HSI would allow the recalculation of scores on existing data, where underlying data (e.g. pond scores not just SI2 scores) are available. This ability is only possible due to not adding any additional SI variables. Although other factors may have significant influences on *T. cristatus* occupancy, we focussed on amendments that would make backwards comparisons possible. The improved HSI presents a way forward for great crested newt habitat monitoring, which could provide more indicative results (better reflection of likely presence/absence), with fewer errors.

The results of the cross-validation logistic regression using generalised linear models suggests that the new HSI scores better reflect *T. cristatus* presence/absence. Both indexes are limited in predictive power, although the new index has higher effect sizes and  $R^2$  values, whilst importantly using fewer variables. The lack of significance when using either HSI on the verification dataset may be due to the small sample size, or irregularities of the data.

The complex nature of the ecological data used introduces limitations, such as non-random site selection and varied sampling effort. One difficulty comes from the false assumption that populations are in equilibrium with the environment, thereby creating an issue with using presence/absence as a proxy for habitat suitability (Latimer et al., 2006). This assumption is particularly problematic for species with metapopulation dynamics (Kupfer & Kneitz, 2000).

The research presented here provides an evidence-based starting point for adapting the great crested newt HSI and the accompanying guidance. In the context of the international decline in their populations and suitable habitat (European Environment Agency, 2019), the HSI is a crucial tool for monitoring and for determining mitigation requirements, being used in UK status reporting (JNCC, 2019) and relied upon in mitigation practices (Natural England, 2015). Accordingly, the issues with the existing HSI highlighted in this study are of importance to the conservation of this species, as they present a notable barrier to accurate habitat assessment. The modified HSI delivers upon the original HSI creator's intention to update the HSI when improved knowledge was available (Oldham et al., 2000). With the modified HSI and appropriate usage guidance, we believe the assessment of great crested newt habitat can be improved, thereby increasing the potential of conservation and mitigation works to benefit the species.

Our multidisciplinary approach, which combines expert great crested newt elicitation together with robust environmental statistical analyses, shows tangible ways to improve the existing great crested newt HSI. We presented greater insight into the current HSI's limitations, and proposed a modified HSI which better reflects *T. cristatus* presence/absence and is easier to use. Our proposed new HSI has three key modifications: i) using an arithmetic (rather than geometric) mean to combine variables, to reduce calculation errors and allow compensation between variables; ii) excluding water quality and waterfowl impact as these lacked significant power to predict *T. cristatus* presence/absence and

were deemed inaccurate by HSI users; and (iii) changing the scoring relationship for pond area to better reflect current data and provide scores for ponds over 2000m<sup>2</sup>. We argue that the improved HSI developed in this study is better able to inform accurate assessment of the habitat suitability of ponds for great crested newts, and thereby provide more accurate monitoring of habitat trends and guide their conservation and development-mitigation. This research is important due to the extensive use of the HSI in great crested newt conservation and we hope that a new HSI will be implemented as a result of this research.

## ACKNOWLEDGEMENTS

We thank Dr P. Berry (University of Oxford) and Dr J. Wilkinson (Amphibian and Reptile Conservation Trust) for their advice. We thank the Amphibian and Reptile Conservation Trust, Cofnod and NatureSpace for permitting access to their data, and the survey participants. Roberto Salguero-Gómez was supported by a NERC Independent Research Fellowship (NE/M018458/1).

## DATA ACCESSIBILITY

The data, code and supplementary materials can be found here: <https://osf.io/2yt6r/>. The Natural England data can be found at <https://naturalengland-defra.opendata.arcgis.com/> - see references for Natural England Open Data 2017 and 2019.

## REFERENCES

- ARG (Amphibian and Reptile Groups) UK. (2010). ARG UK Advice Note 5: Great Crested Newt Habitat Suitability Index. [www.arguk.org](http://www.arguk.org).
- Beebee, T. & Griffiths, R. (2000). Newts. In *Amphibians and Reptiles: A Natural History of the British Herpetofauna*. HarperCollins. London: UK.
- Belcik, M., Klimaszewski, K., Pełnia-Iwanicka, E. & Zajchowska, J. (2019). Testing the habitat suitability index for great crested newt in central Poland. *Ecological Research* 34(6), 711–717. <https://doi.org/10.1111/1440-1703.12051>.
- Bender, L.C., Roloff, G.J. & Haufler, J.B. (1996). Evaluating confidence intervals for habitat suitability models. *Wildlife Society Bulletin* 24(2), 347–352.
- Bethlehem, J. (2010). Selection bias in web surveys. *International Statistical Review* 78(2), 161–188. <https://doi.org/10.1111/j.1751-5823.2010.00112.x>.
- Biggs, J., Ewald, N., Valentini, A., Gaboriaud, C., Griffiths, R., Foster, J., Wilkinson, J., Arnett, A., Williams, P. & Dunn, F. (2014). Analytical and methodological development for improved surveillance of the great crested newt. Appendix 4. Results of a pilot survey to test the use of eDNA outside of the recommended great crested newt survey window. Defra Project WC1067. Freshwater Habitats Trust: Oxford: UK.
- Brooks, R.P. (1997). Improving habitat suitability index models. *Wildlife Society Bulletin* 25(1), 163–167.
- Bryman, A. (2012). *Social Research Methods* (4th Edition). Oxford University Press.
- Burgman, M.A., Breininger, D.R., Duncan, B.W. & Ferson, S.

- (2001). Setting reliability bounds on habitat suitability indices. *Ecological Applications* 11(1), 70–78.
- Buxton, A., Downs, N. & Tracey, H. (2021). How reliable is the habitat suitability index as a predictor of great crested newt presence or absence? *The Herpetological Journal* 31, 111–117. <https://doi.org/10.33256/31.2.111117>.
- Buxton, A. & Griffiths, R.A. (2022). A revised system for interpreting great crested newt habitat suitability indices. *The Herpetological Journal* 32, 114–119. <https://doi.org/10.33256/32.3.114119>.
- Cresswell, W. & Whitworth, R. (2004). An assessment of the efficiency of capture techniques and the value of different habitats for the great crested newt *Triturus cristatus*. *English Nature Research Reports Number* (Vol. 576).
- Denoël, M. & Ficetola, G.F. (2008). Conservation of newt guilds in an agricultural landscape of Belgium: The importance of aquatic and terrestrial habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18(5), 714–728. <https://doi.org/10.1002/aqc.853>.
- Dunford, R.W. & Berry, P.M. (2013). Climate change modelling of English amphibians and reptiles. Report to Amphibian and Reptile Conservation Trust.
- Ebbert, D. (2019). `chisq.posthoc.test`: A post hoc analysis for Pearson's chi-squared test for count data. R package version 0.1.2. <https://CRAN.R-project.org/package=chisq.posthoc.test>.
- Edgar, P. & Griffiths, R.A. (2004). An evaluation of the effectiveness of great crested newt *Triturus cristatus* mitigation projects in England, 1990–2001. *English Nature Research Reports*, No. 575.
- English Nature. (2001). Great crested newt mitigation guidelines. English Nature.
- European Environment Agency. (2019). Species assessments at EU biogeographical level. Available at <https://nature-art17.eionet.europa.eu/article17/species/summary/?period=5&subject=Triturus%20cristatus>. Accessed on 2 April 2023.
- Griffiths, R.A. & Williams, C. (2000). Modelling population dynamics of great crested newts (*Triturus cristatus*): a population viability analysis. *The Herpetological Journal* 10, 157–163.
- Grolemund, G. & Wickham, H. (2011). Dates and times made easy with `lubridate`. *Journal of Statistical Software* 40(3), 1–25. <http://www.jstatsoft.org/v40/i03/>.
- Gustafson, D.H., Malmgren, J.C. & Mikusiński, G. (2011). Terrestrial habitat predicts use of aquatic habitat for breeding purposes — a study on the great crested newt (*Triturus cristatus*). *Annales Zoologici Fennici* 48(5), 295–307. <https://doi.org/10.5735/086.048.0504>.
- Harper, L.R., Downie, J.R. & McNeill, D.C. (2019a) Assessment of habitat and survey criteria for the great crested newt (*Triturus cristatus*) in Scotland: a case study on a translocated population. *Hydrobiologica* 828(1), 57–71. <https://doi.org/10.1007/s10750-018-3796-4>.
- Harper, L.R., Handley, L.L., Hahn, C., Boonham, N., Rees, H.C., Lewis, E., Adams, I.P., Brotherton, P., Phillips, S. & Hänfling, B. (2019b). Generating and testing ecological hypotheses at the pondscape with environmental DNA metabarcoding: A case study on a threatened amphibian. *Environmental DNA* 2(2), 184–199. <https://doi.org/10.1002/edn3.57>.
- Haysom, K., Driver, D., Cartwright, M., Wilkinson, J. & Foster, J. (2018). Review of the Current Conservation Status (CCS) of the Great Crested Newt in Wales, with specific references to its long term prospects and within its stronghold in North-East Wales. NRW Science Report Series. Report No: 259. [www.naturalresourceswales.gov.uk](http://www.naturalresourceswales.gov.uk).
- Jehle, R., Thiesmeier, B. & Foster, J. (2011). *The crested newt: a dwindling pond dweller*. Laurenti Verlag, Bielefeld: Germany.
- JNCC. (2019). Conservation status assessment for the species: S1166 - Great crested newt (*Triturus cristatus*) Fourth Report by the United Kingdom under Article 17 on the implementation of the Directive from January 2013 to December 2018. <https://doi.org/10.1101/339853>.
- Johnson, C.J. & Gillingham, M.P. (2004). Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. *Journal of Applied Ecology* 41(6), 1032–1041.
- Knudson, C. (2020). `glmm`: Generalized Linear Mixed Models via Monte Carlo Likelihood Approximation. R package version 1.4.2. <https://CRAN.R-project.org/package=glmm>.
- Kupfer, A. & Kneitz, S. (2000). Population ecology of the great crested newt (*Triturus cristatus*) in an agricultural landscape: dynamics, pond fidelity and dispersal. *The Herpetological Journal* 10, 165–171.
- Langton, T., Beckett, C. & Foster, J. (2001). *Great crested newt conservation handbook*. Froglife. Peterborough: UK.
- Latimer, A.M., Wu, S., Gelfand, A.E. & Silander, J.A. (2006). Building statistical models to analyze species distributions. *Ecological Applications* 16(1), 33–50.
- Lewis, B., Griffiths, R.A. & Barrios, Y. (2007). Field assessment of great crested newt *Triturus cristatus* mitigation projects in England. Natural England Research Report NERR001. [www.naturalengland.org.uk](http://www.naturalengland.org.uk).
- Lewis, B., Griffiths, R.A., Wilkinson, J.W. & Arnell, A. (2014a). Examining the fate of local Great crested newt populations following licensed developments. <https://randd.defra.gov.uk/ProjectDetails?ProjectId=17856>.
- Lewis, B., Griffiths, R.A. & Wilkinson, J.W. (2014b). Population status of great crested newts (*Triturus cristatus*) at sites subjected to development mitigation. *The Herpetological Journal* 27(2), 133–142.
- Marklund, O., Sandsten, H., Hansson, L.A. & Blindow, I. (2002). Effects of waterfowl and fish on submerged vegetation and macroinvertebrates. *Freshwater Biology* 47(11), 2049–2059. <https://doi.org/10.1046/j.1365-2427.2002.00949.x>.
- Millard, S.P. (2013). *EnvStats: An R Package for Environmental Statistics*. Springer, New York.
- Miró, A., O'Brien, D., Hall, J. & Jehle, R. (2017). Habitat requirements and conservation needs of peripheral populations: the case of the great crested newt (*Triturus cristatus*) in the Scottish highlands. *Hydrobiologia* 792(1), 169–181. doi:10.1007/s10750-016-3053-7.
- NARRS (n.d.). GCN Habitat Suitability Index Guidance. Available at [www.narrs.org.uk/documents/HSI%20guidance.pdf](http://www.narrs.org.uk/documents/HSI%20guidance.pdf). Accessed on 2 June 2020.
- Natural England. (2015). Great crested newts: surveys and mitigation for development projects. Available at: [www.gov.uk/guidance/great-crested-newts-surveys-and-mitigation-for-development-projects](http://www.gov.uk/guidance/great-crested-newts-surveys-and-mitigation-for-development-projects). Accessed on 3 June 2020.
- Natural England. (2019). New for newts: better for wildlife, business and people. Available at <https://www.gov.uk/government/news/new-for-newts-better-for-wildlife->

- business-and-people. Accessed on 3 June 2020.
- Natural England Open Data. (2017). Great Crested Newt Evidence Enhancement Project 2013. Available at <https://naturalengland-defra.opendata.arcgis.com/datasets/great-crested-newt-evidence-enhancement-project-2013/explore?location=51.968537%2C-0.808718%2C7.55>. Accessed on 3 June 2020. Data uploaded 22 March 2017.
- Natural England Open Data. (2019). Great Crested Newts eDNA Pond Surveys for District Level Licensing (England). Available at <https://naturalengland-defra.opendata.arcgis.com/datasets/great-crested-newts-edna-pond-surveys-for-district-level-licensing-england/explore?location=52.809139%2C-0.857662%2C6.40>. Accessed on 3 June 2020. Data uploaded 20 November 2019.
- O'Brien, D., Hall, J., Miró, A. & Wilkinson, J. (2017). Testing the validity of a commonly-used habitat suitability index at the edge of a species' range: Great crested newt *Triturus cristatus* in Scotland. *Amphibia Reptilia* 38(3), 265–273. <https://doi.org/10.1163/15685381-00003108>.
- Oldham, R.S., Keeble, J., Swan, M.J.S. & Jeffcote, M. (2000). Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). *The Herpetological Journal* 10(4), 143–155.
- Poncet, P. (2019). modeest: Mode Estimation. R package version 2.4.0. <https://CRAN.R-project.org/package=modeest>.
- Priol, P., Renet, J., Besnard, A., Scher, O. & Bernard, P. (2022). Habitat suitability index is not relevant for great crested newt occupancy at its range margins: a Mediterranean case study. *Hydrobiologica* 850, 591–605. <https://doi.org/10.1007/s10750-022-05109-y>.
- QSR International Pty Ltd. (2018). NVivo (Version 12), <https://www.qsrinternational.com/nvivo-qualitative-data-analysis-software/home>.
- R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.r-project.org/>.
- Reason, P. (2013). Great crested newt evidence enhancement project: Phase 1 Report. Report for Natural England by Hyder Consulting (UK) Limited.
- Roloff, G.J. & Kernohan, B.J. (1999). Evaluating reliability of habitat suitability Index models. *Wildlife Society Bulletin* 27(4), 973–985.
- Skei, J.K., Dolmen, D., Rønning, L. & Ringsby, T.H. (2006). Habitat use during the aquatic phase of the newts *Triturus vulgaris* (L.) and *T. cristatus* (Laurenti) in central Norway: proposition for a conservation and monitoring area. *Amphibia-Reptilia* 27, 309–324.
- Soniati, T.M., Conzelmann, C.P., Byrd, J.D., Roszell, D.P., Bridevaux, J.L., Suir, K.J. & Colley, S.B. (2013). Predicting the effects of proposed Mississippi river diversions on oyster habitat quality; application of an oyster habitat suitability index model. *Journal of Shellfish Research* 32(3), 629–638.
- Swan, M.J.S. & Oldham, R.S. (1993). National Amphibian Survey (English Nature Research Report No. 38). <https://publications.naturalengland.org.uk/file/154309>.
- The Council of the European Committees. (1992). Council Directive 92/43/EEC (The Habitats Directive). <https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:31992L0043&from=EN>.
- UK Government. (1981). Wildlife Countryside Act 1981. Available at <https://www.legislation.gov.uk/ukpga/1981/69/contents>. Accessed on 5 August 2020.
- Unglaub, B., Steinfartz, S., Drechsler, A. & Schmidt, B.R. (2015). Linking habitat suitability to demography in a pond-breeding amphibian. *Frontiers in Zoology* 12(1). <https://doi.org/10.1186/s12983-015-0103-3>.
- U.S. Fish and Wildlife Service. (1981). 103 ESM Standards for the development of habitat suitability index models. Washington, DC: USA.
- Wickham H. (2023). forcats: Tools for working with categorical variables (factors). R package version 1.0.0, <https://github.com/tidyverse/forcats>, <https://forcats.tidyverse.org/>.
- Wickham, H., François, R., Henry, L. & Müller, K. (2020). dplyr: A grammar of data manipulation. R package version 1.0.1. <https://CRAN.R-project.org/package=dplyr>.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Golemund, G., Hayes, A., Henry, L., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software* 4(43), 1686. Doi:10.21105/joss.01686.
- Wilkinson, J.W. & Arnell, A.P. (2013). NARRS Report 2007–2012: Establishing the baseline (HWM Edition). ARC Research Report 13 January.
- Zajac, Z., Stith, B., Bowling, A.C., Langtimm, C.A. & Swain, E.D. (2015). Evaluation of habitat suitability index models by global sensitivity and uncertainty analyses: A case study for submerged aquatic vegetation. *Ecology and Evolution* 5(13), 2503–2517. <https://doi.org/10.1002/ece3.1520>.

Accepted: 6 July 2023

Please note that the Supplementary Material for this article is available online via the Herpetological Journal website: <https://thebhs.org/publications/the-herpetological-journal/volume-34-number-2-april-2024>