White-faced darter distribution is associated with coniferous forests in Great Britain

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Abstract. 1. Understanding of dragonfly distributions is often geographically comprehensive but less so in ecological terms.
2. White-faced darter (Leucorhinia dubia) is a lowland peatbog specialist dragonfly which has experienced population declines in Great Britain. White-faced darter is thought to rely on peat-rich pool complexes within woodland, but this has not yet been empirically tested.
3. We used dragonfly recording data collected by volunteers of the British Dragonfly Society from 2005 to 2018 to model habitat preference for white-faced darter using species distribution models across Great Britain and, with a more detailed landcover data set, specifically in the North of Scotland.
4. Across the whole of Great Britain, our models used the proportion of coniferous forest within 1 km as the most important predictor of habitat suitability but were not able to predict all current populations in England.
5. In the North of Scotland, our models were more successful and suggest that habitats characterised by native coniferous forest and areas with high potential evapotranspiration represent the most suitable habitat for white-faced darter.
6. We recommend that future white-faced darter monitoring should be expanded to include areas currently poorly surveyed but with high suitability in the North of Scotland.
7. Our results also suggest that white-faced darter management should concentrate on maintaining Sphagnum rich-pool complexes and the maintenance and restoration of native forests in which these pool complexes occur.

Key words. Conservation, distribution, dragonfly, habitat, SDM.

Introduction

Dragonflies and damselflies (Odonata) are relatively ‘charismatic’ invertebrate species and have received some considerable attention in the scientific literature (Córdoba-Aguilar, 2008; Kalkman et al., 2018; Teermat et al., 2019). Nevertheless, conservation research on Odonata is still in its relative infancy (Clausnitzer et al., 2009; Bried & Samways, 2015) and even in countries where conservation is seen as a social priority, such as the United Kingdom, there is relatively little conservation action specifically focused on this taxon despite 25% of UK dragonfly and damselfly species being included in the Odonata Red Data List for Great Britain (Beynon et al., 2008). The seven obstacles for invertebrate conservation suggested by Cardoso et al. (2011), and in particular the lack of basic research on habitat requirements and distribution, certainly apply to Odonata conservation at both global and regional scales (Clausnitzer et al., 2009). Indeed, priorities highlighted on the UK red list for Odonata for several species (Beynon et al., 2008) include the urgent need to increase monitoring efforts, to establish species distributions and habitat requirements and understand the factors affecting population change, particularly for those species with a current distribution restricted to remote areas.

As for other invertebrates, the multi-stage life-cycle of Odonata species leaves them vulnerable to multiple threats at different life stages (Córdoba-Aguilar, 2008): The aquatic larval stage is vulnerable to aquatic pollution (Monteiro-Júnior et al., 2014), introduced plant species (Samways & Taylor, 2004), predation by introduced fish (Schilling et al., 2009) and land-use changes...
concern (Elo et al., 2012) and adult stages are particularly vulnerable to land-use changes and habitat fragmentation (Saunders et al., 1991; Drinan et al., 2013). Scale is also an important factor in assessing threats to individual populations. Globally, peatland dragonflies tend to be of lower conservation priority (Clausnitzer et al., 2009); however, peatland habitats can be locally threatened and are considered as priority habitats for conservation in the United Kingdom (Whitfield et al., 2011). In these areas, peatland specialist species may thus potentially be of conservation concern (Elo et al., 2015).

White-faced darter (Leucorrhinia dubia) is a lowland bog specialist dragonfly species (Smallshire & Swash, 2004; Clausnitzer et al., 2009, Cham et al., 2014). Great Britain represents the western extent of their range and they are found as far east as Japan. In Western Europe, their range extends from the Pyrenees north to Scandinavia. They are locally common across the continent and so are classified as Least Concern on the European Red List for Odonata although further research into their range and population trends are recommended (Clausnitzer, 2009; Kalkman et al., 2010). In Great Britain, their distribution is heavily biased towards the Scottish highlands (Cham et al., 2014) and their range is probably contracting (Hickling et al., 2005). There are several populations further south, in England, which have been the focus of conservation attention, including reintroduction programmes (Meredith, 2017). In Scotland, the distribution of white-faced darter stretches from Argyll (56°13'51"N 5°20'37"W) in the South to Ross-shire (57°51'08"N 5°33'54"W) in the North although the bulk of the population is found in the North on both sides of the Great Glen Fault. In the East, they are found in parts of the Cairngorms and Grampians and they can be found on the West coast although they do not reach as far as the Inner Hebrides. The Scottish populations are thought to be declining but currently receive little conservation intervention (Cham et al., 2014). The species is well monitored in some areas, but their patchy distribution across a large landscape means that the species is thought to be under-recorded (Cham et al., 2014). As with many dragonfly species, white-faced darter has not been the subject of quantitative studies regarding habitat associations except at the very local scale (Davies et al., 2018). White-faced darter is generally found in acidic pool complexes associated with pine or birch woodland (Boudot & Kalkman, 2015) In Great Britain, these pools are generally free from num moss, which appears to be an essential requirement for this species (Smallshire & Swash, 2004; Clausnitzer, 2009). White-faced darter has a particularly strong association with sphagnum moss, which appears to be an essential requirement for the habitats inhabited by their larval stage (Henrikson, 1993; Meredith, 2017).

Species distribution models (SDMs) are a useful tool for the planning of future monitoring programmes (Bourke et al., 2012) and for identifying priority areas for conservation action (Nazeri et al., 2012). SDMs are also useful for estimating the distribution of poorly known species (Wilting et al., 2010), or those which are difficult to survey effectively (Nazeri et al., 2012) as well as for species which are well known locally but poorly known over wider areas (Sutton & Puschendorf, 2018). A patchy, heterogeneous distribution of monitoring effort and species records can lead to biases in the estimated distribution of species (Millar et al., 2018). This can be a particularly serious problem for understudied taxa where expertise may be localised or restricted to only a few specialists (Robinson et al., 2018).

Where species are monitored sporadically, only through incidental sightings or are extremely rare, we might only have access to presence records for a species. Similarly, where taxa are monitored using volunteer recording schemes there is a trade-off between the complexity of survey methodologies and the ease with which volunteers can complete records in the field which can result in data with reduced information content (Tweddle et al., 2012). More complex surveys, which result in information-rich data, require more experienced/trained recorders potentially limiting the geographic coverage of the survey. On the other hand, simpler more widespread surveys can introduce issues with data quality due to identification mistakes by inexperienced observers or patchy records (Donnelly et al., 2014). Information-limited data restrict the choice of methods available to investigate species distributions (Elith et al., 2006) and can make it hard to project models onto unknown or under-recorded areas (Owens et al., 2013). This is particularly problematic because, although species presence can be established relatively error-free, there are likely to be few or low-quality records of species absence (if any).

Modelling methods to predict species distributions using data where absences are unavailable or uncertain requires the use of background or pseudo-absence data to differentiate suitable from unsuitable habitat (Elith et al., 2006). One of the most widely used algorithms used to achieve this, MaxEnt (Phillips et al., 2006; Phillips & Dudík, 2008), is a machine-learning implementation of a point process regression, which uses LASSO penalties to prevent overfitting (Renner & Worton, 2013). MaxEnt has been shown to outperform several other presence-only species distribution modelling methods (Huerta & Peterson, 2008; Elith & Graham, 2009) and is widely used in conservation research.

Here, we use MaxEnt models to investigate the habitat requirements of white-faced darter (Leucorrhinia dubia) and map its potential distribution in the whole of Great Britain with a particular focus on its main range in the North of Scotland using records collected by members of the British Dragonfly Society as presence points along with environmental data reflecting tree cover, climate and the presence of bogs. Understanding drivers of white-faced darter presence across large scales can contribute to conservation of this species by informing landscape management and will help to target future surveys for the species.

Methods

Species data

White-faced darter presence records between 2005 and 2018 were obtained from the British Dragonfly Society through the United Kingdom’s National Biodiversity Network. These data have been collected as incidental, presence-only, records rather
than in a standardised stratified recording scheme and records about flying adults, larvae and exuviae are available in the data set. Incidental records such as these are likely to be spatially biased due to unequal distribution of recording effort. This has the potential to create biased distribution models. Our original data set consisted of 980 individual records; 540 of these were in England and Wales along with 440 in Scotland. The records were heavily biased to a series of well-visited sites with 220 of the records from England and Wales coming from just two sites. We used spatial filtering to combine records within 1.5 km of each other to reduce potential issues related to spatially biased sampling (Fourcade et al., 2014). Species records were thinned using the ‘spThin’ package (Aiello-Lammens et al., 2015) in R (R Core Team, 2019) resulting in 77 presence records across the whole of Great Britain of which 61 were in the North of Scotland (Figure 1).

### Environmental variables

#### Great Britain model.

Land cover data to parameterise our species distribution models was obtained from the CEH LCM2015 landcover data set (Rowland et al., 2017) The variables chosen were based on those described in the United Kingdom (Cham et al., 2014) and European (Boudot & Kalkman, 2015) dragonfly atlases which specify wet, bogy areas within a woodland complex. We calculated the proportion of coniferous woodland, deciduous woodland, standing water and bogs within 1 km of each 100 m × 100 m square in Great Britain using the ‘focal’ function in the ‘raster’ package (Hijmans & van Etten, 2012) in R. Additionally, we used data from the Centre for Ecology and Hydrology (CHESS) data set (Robinson et al., 2016) to represent potential evapotranspiration (PET), indicating the ‘wetness’ of the habitat, and BIOCLIM layers from WorldClim. The BIOCLIM layers were highly correlated with each other so we chose four variables which were ecologically relevant [Annual Mean Temperature (BIO1), Annual temperature range (BIO7), Annual precipitation (BIO12) and Precipitation Seasonality (BIO15)] and highly correlated with a number of the other variables but not each other (rs > 0.7 with 5, 7, 9 and 10 variables, respectively) at our presence locations. We then reduced this to two BIOCLIM variables (Annual Temperature and Annual temperature range) as the two precipitation variables were both highly correlated (rs > 0.77) with the PET layer at our presence points. In this case, we retained the PET layer due to its more accurate resolution. These three layers were resampled to match the resolution of our landcover data using the ‘raster’ package in R.

#### North of Scotland model.

Environmental variables used to predict the distribution of white-faced darter were downloaded from the European Nature Information System (EUNIS) landcover classification for Scotland. This data set is more detailed than the CEH LCM2015 data set and allows us the investigate the influence of more detailed habitat types such as bog woodland and native pine forest. We used established EUNIS classes (Davies et al., 2004) to produce variables representing Scots pine (Pinus sylvestris) forest, coniferous forest (including native pine

![Figure 1](https://wileyonlinelibrary.com) Location of presence records for white-faced darter (in red; n = 77) in Great Britain. [Color figure can be viewed at wileyonlinelibrary.com]

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**Table 1.** Comparison of all MaxEnt models with ΔAICc <2 predicting white-faced darter distribution in the Scottish highlands. Models were tested with linear, quadratic and product responses to predictors along with combinations of these and regularisation values between 0 and 3 at 0.5 increments. Please see Electronic Supplementary Material for the results of all candidate models.

| Features            | Regularisation multiplier | Training AUC | Testing AUC | AICc   | ΔAICc |
|---------------------|---------------------------|--------------|-------------|--------|-------|
| Linear and quadratic| 1                         | 0.89         | 0.81        | 6242.71| 0     |
| Linear and quadratic| 1.5                      | 0.89         | 0.8         | 6243.23| 0.52  |
| Linear and quadratic| 2                        | 0.89         | 0.81        | 6243.45| 0.74  |
| Linear and quadratic| 2.5                      | 0.89         | 0.81        | 6243.67| 0.97  |
| Linear and quadratic| 3                        | 0.89         | 0.81        | 6243.9 | 1.19  |

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forest and plantation forestry), moorland, bogs, bog woodland and standing water. Other potential variables such as mixed woodland or ancient woodland measures (e.g. from the National Forest Inventory Scotland) were not used in our analyses due to issues with collinearity. Instead, we retained only the variables, which we can hypothesise to have an ecological connection with white-faced darter presence based on what is known in the available literature (Dormann et al., 2012). We converted our environmental variables to the proportion of each variable within a 1 km buffer around each pixel at a 10 m resolution from the original categorical landcover maps using the ‘raster’ package (Hijmans & van Etten, 2012) in R. These values were then aggregated to maps at a resolution of 250 m × 250 m retaining the mean value. PET, annual mean temperature and annual temperature range were used in the same way as for the Great Britain model.

Species distribution models. Distribution models were fitted using MaxEnt version 3.3.3 k through the ‘dismo’

Figure 2. Percentage importance for each variable, calculated from the contribution of each variable to regularised gain, used to predict white-faced darter presence across Great Britain ±Standard Error (dotted lines).

Figure 3. Response curves for each of the three most important predictors, calculated from regularised gain, in Maxent models predicting white-faced darter presence for the whole of Great Britain. For (a) coniferous forest and (b) mean annual temperature and (c) Potential evapotranspiration during the emergence period is represented in mm/day. Y-axes represent the relative suitability for white-faced darter from models using each variable in isolation. Mean response from 10 cross-validated replicate models in shown in black with 95% confidence intervals in red. [Color figure can be viewed at wileyonlinelibrary.com]
MaxEnt has been shown to perform consistently well in cases where few occurrence points are available (Hernandez et al., 2006) and has been shown to maintain consistency of performance across sampling scenarios (Grimmett et al., 2020). We used the variance inflation factor through the ‘vif’ function in the R package ‘usdm’ (Naimi et al., 2014) to check for collinearity between predictor variables and in all cases these were less than the correlation threshold of 0.7. We used the ‘ENMVal’ R package (Muscarella et al., 2014) to find the ‘best’ combination of potential relationships with variables and the optimum regularisation parameter for Maxent models based on Northern Scotland. Using only Northern Scotland, the spatially smaller model, reduced the necessary computational time for model optimisation. We tested linear, quadratic and product features along with combinations of these. We used regularisation values between 0 and 2.5 at 0.5 increments. The optimum model was assessed by comparing AICc across models (Warren & Seifert, 2011). Models with \( \Delta \text{AICc} < 2 \) were considered equivalent (Burnham & Anderson, 1998). Once selected, we fitted the ‘best’ model using 10-fold cross-validated replicates (Merow et al., 2013) for both Great Britain and the North of Scotland. Models were evaluated based on ecological realism (Zurell et al., 2020) and using the area under the receiver operating characteristic curve (AUC; Fielding & Bell, 1997) as well as the True Skill Statistic (Allouche et al., 2006). We used Moran’s I statistic to check for autocorrelation in the residuals (Dormann et al., 2007; Václavík et al., 2012).

**Results**

**Model**

Model selection indicated that the ‘best’ combination of parameters for our model was to use only linear and quadratic features with a beta multiplier of one (Table 1 and Electronic Supplementary Material).

The model for the whole of Great Britain has reasonable predictive power (AUC = 0.78; TSS = 0.47). The most important variable in this model was the proportion of coniferous forest within 1 km (53.4% variable contribution; Figure 2) followed by potential evapotranspiration (14.9%), mean annual temperature (11.5%) and annual temperature range (9.6%). The proportion of bogs, standing water and broadleaved woodland all had importance values of less than 5%. Relative habitat suitability for white-faced darter increased with increasing proportions of coniferous woodland (Fig. 3a) and with decreasing mean annual temperature (Fig. 3b) and decreasing potential evapotranspiration (Fig. 3c). The model showed significant spatial autocorrelation in model residuals (Moran’s I = 0.69, \( P = 0.0001 \)).

Projecting this model onto environmental layers for Great Britain (Fig. 4) shows a predicted distribution which largely represents uplands in Great Britain. The areas of highest predicted

![Figure 4](image-url). Predicted relative habitat suitability for white-faced darter across Great Britain obtained from a MaxEnt Species Distribution model. [Color figure can be viewed at wileyonlinelibrary.com]

![Figure 5](image-url). Percentage importance for each variable, calculated from the contribution of each variable to regularised gain, used to predict white-faced darter presence across the North of Scotland ±Standard Error (dotted lines).

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suitability correspond to important strongholds in the Scottish Highlands such as Abernethy forest but also predict a number of areas with no records for this species in Scotland, Wales and the South of England. The model is unable to predict important sites such as Fenn’s and Whixall Moss on the border between England and Wales but successfully predicts sites in Cumbria and the white-faced darter reintroduction site in Delamere Forest, Cheshire.

The North of Scotland model shows a good fit to the data (AUC = 0.80, TSS = 0.49). The most important variable in the model (73.9% variable contribution) is the percentage of pine forest (Fig. 5) within 1 km. Other variables are considerably less important with the potential evapotranspiration (11.9%) and mean annual temperature (5.8%) having slightly higher contributions than annual temperature range, percentage of bog woodland, percentage of bogs, percentage of conifer and percentage of moorland within 1 km which all have percentage contributions of less than 5%. Model residuals show significant spatial autocorrelation (Moran’s I = 0.05, P = 0.0005). Response curves indicate that increasing proportions of pine forest within 1 km result in higher relative suitability for white-faced darter (Fig. 6a). The relative suitability is increases when the mean annual temperature is higher (Fig. 6b) and the potential evapotranspiration is lower (Fig. 6c).

Projecting the model onto the environmental data layer for the whole of Scotland produces maps which accurately predict many current strongholds for white-faced darter (Fig. 7). In particular, our model successfully predicts the presence of white-faced darter in Abernethy forest and Glen Affric. Yet, our model fails to predict a well-known population of white-faced darter at Monadh Mor on the Black Isle.

Discussion

Our models suggest that the strongest drivers of white-faced darter distribution are increasing proportions of coniferous forest, specifically pine forest in the North of Scotland, along with low potential evapotranspiration. These results provide quantitative support for the current descriptions of white-faced darter.

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habitat (Cham et al., 2014) and also agree with local-scale descriptions of habitat associations (Meredith, 2017). Nevertheless, our models differ in the relationship between habitat suitability and annual mean temperature. In the model for the whole of Great Britain, white-faced darter are associated with higher temperature, however, in the North of Scotland model the opposite is true. As white-faced darter is found at both more northerly and southerly latitudes in mainland Europe, it is likely that these relationships are broader than our models are able to identify.

Both of our distribution maps predict strongly in several core areas for white-faced darter such as Abernethy forest and Glen Affric. Yet, in other areas, our predictions are less successful and the inability to predict all known locations along with the potential for records of mobile adults to be in areas of unsuitable habitat when recorded (Ruebel et al., 2010) are two plausible reasons for significant spatial autocorrelation in our model residuals. In fact, we miss some locations entirely as we are unable to successfully predict Fenn’s and Whixall Moss on the English and Welsh border using our Great Britain model and fail to predict the population found at Monadh Mor on the Black Isle using our North of Scotland model. These sites may represent unusual cases for the species, several sites in Southern Britain do not have the level of tree cover associated with white-faced darter habitat further North and are heavily managed landscapes. Our models also only highlight coniferous forest as important and do not include the birch forests suggested by several sources (Cham et al., 2014). We see this as a limitation of our model and the data available for analysis, due to the correlation between the distribution of pine forest and other forest types at a landscape scale, rather than an indication that birch forests are not important. More successfully, our models predict high suitability for white-faced darter presence in areas in which the species was not found until very recently, locations not included in our data (Batty, 2017, 2018).

Our models currently predict a high suitability for several areas where white-faced darter has not been recorded yet. In England and Wales, the majority of these locations are likely to be distant from source populations and therefore unlikely to be occupied but may contain some suitable habitat. Although it is unlikely that white-faced darter is under-recorded in the South of Britain, this is possible in the North of Scotland which has lower recorder-effort and so some ‘suitable’ sites here may contain currently unrecorded populations of white-faced darter. There are a number of areas such as the Grampians, which may offer suitable habitat along with specific locations such as Glen Moriston and areas around Tain in Easter Ross and Banchory in Nairn. Our results suggest that these areas would be good targets for expanding monitoring efforts on this species. Remote areas are often difficult to obtain data for when relying on volunteer recorders. One approach to this in UK bird surveys is to encourage volunteers from elsewhere in the country to adopt remote squares (Gillings et al., 2019). This method may be particularly applicable to dragonfly recorders who are fewer in number than those who contribute bird records. Two larger areas of habitat are predicted by our model based around Abernethy forest and Glen Affric. These two sites are well-known locations for the species and our models suggest they may be important sites for the white-faced darter conservation. Large areas of contiguous habitat are likely to hold larger populations. White-faced darter should continue to be considered in management plans for these two sites with the maintenance of bog pool systems within woodland as a conservation focus.

Current management recommendations for white-faced darter suggest maintaining lowland peat pool complexes within woodland using scrub control and maintaining water quality (Cham et al., 2014). Our results confirm that these current recommendations should be maintained and prioritised. The most important variable along with woodland cover in both of our models was potential evapotranspiration. This suggests that white-faced darter is likely to be impacted by drainage as part of woodland management and this should be avoided where this species is present. This also adds support to management operations put in place as part of the white-faced darter reintroduction project in Delamere forest, England where areas are being re-wetted to provide more suitable habitat for the reintroduced population (Meredith, 2017).

Our models, particularly the model for the North of Scotland, suggest that suitable white-faced darter habitat is patchy within the landscape and that populations may be fragmented at some distance from each other. Within sites, white-faced darter favours pool complexes and may use different areas in different years (Kharitonov & Popova, 2011). These two features of white-faced darter populations suggest that connectivity at

![Figure 7. Predicted relative habitat suitability for white-faced darter across the North of Scotland obtained from a Maxent species distribution model. [Color figure can be viewed at wileyonlinelibrary.com]](image-url)
multiple scales may be important in terms of population persistence. White-faced darter has the potential to travel relatively long distances (Johansson et al., 2017), but it is particularly reliant on sphagnum filled pools within their preferred habitat (Henriksson, 1993). The ability to move across a landscape matrix can be influenced by structural features in the landscape such as forest cover and type (Chin & Taylor, 2009). It would be extremely valuable for informing conservation efforts for white-faced darter in the United Kingdom, to assess how populations are connected at both large and small distances and how habitat and landscape features might influence this connectivity. Although some tracking studies have been performed on Odonata (e.g. Wikelski et al., 2006) the numbers of animals which would be possible to involve is likely to be very low. Equally, mark-recapture studies, although they have been successfully used to estimate white-faced darter local population sizes (Dolný et al., 2018), generally have low recapture rates in Odonata (Cordero-Rivera & Stoks, 2008) making them unsuitable for studies on population connectivity. Genetic methods are therefore likely to hold the most value in investigating this issue (Keller et al., 2010; Dolný et al., 2018).

Our models currently only use presence records to investigate distribution. However, records of species presence not only depend on the distribution of that species but also on the detectability of the species (Lahoz-Monfort et al., 2014). Presence-only methods like MaxEnt cannot disentangle the detection probability (i.e. the probability a species is detected if present) from the probability a site is occupied, generally underestimating the true occupancy and thus potentially providing biased predictions of the distribution (Lahoz Monfort et al., 2014) or population status (Bried et al., 2012). We are confident that the impact of imperfect detection is limited in our model because these presence records are part of a wider dataset of dragonfly records where the presence of other species indicates at least some searching effort by dragonfly enthusiasts. However, in future, we recommend that data are collected in a way which facilitates the incorporation of detectability into models of dragonfly distributions. This would involve making repeated visits to sites (MacKenzie et al., 2002) and indicating when a complete list of all species present has been provided to the national recording scheme (Isaac & Pocock, 2015).

Despite the inherent limitations of relatively information-poor data, presence-only modelling can still be an extremely valuable tool in mapping and understanding the distribution of important species allowing to use and obtain conservation relevant information from incidental records, often collected in the past, and for which repeated visits are not available (Elith et al., 2006). This kind of data, often collected over extended periods of time (years if not decades) and over extended ranges, incidentally by volunteers like those of the British Dragonfly Society, can provide large-scale information on temporal and spatial changes in species distribution happened in the past which would not be possible to obtain with methods taking into account imperfect detection, simply because we cannot go back in time to collect the necessary data with these approaches. Here, we have demonstrated that at broad scales, the distribution of suitable habitat for white-faced darter is dependent on wet areas in coniferous woodland and that pine forest, in particular, is an important habitat in Scotland. Our specific predictions can be useful to landmanagers who are looking to develop landscapes for this species and also to conservation organisations designing surveys for this species. In future, it would be beneficial to investigate the drivers of white-faced darter distribution at finer scales as well as population connectivity across landscapes. Our research supports, with quantitative evidence, the importance of protecting wet habitats within coniferous woodlands in order to manage landscapes for this species.

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Authors Contribution

M.G. originally formulated the idea, M.G. and A.v.H. developed methodology, analysed the data and wrote the manuscript.

Data availability statement

The white-faced darter presence data used in the current study are available from the British Dragonfly Society on reasonable request or through the UK’s National Biodiversity Network.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Electronic Supplementary Material. Comparison of all MaxEnt models predicting white-faced darter distribution in the Scottish highlands. Models were tested with linear, quadratic and product responses to predictors along with combinations of these and regularisation values between 0 and 3 at 0.5 increments.

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