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# Dragonfly distributional predictive models in Japan: relevance of land cover and climatic variables

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# ABSTRACT

We constructed dragonfly distributional models (logistic regression models) based on occurrence records collected in the national recording scheme of Japan. Such occurrence records have several shortcomings in that they only record what is present and not what is absent, and sampling efforts are highly variable among recording grid-squares (about 10x10 km). Moreover, the accuracy of logistic regression models is strongly influenced by the presence/absence prevalence. We developed two data screening methods to select 'reliable' species presence/absence data sets from presenceonly species assemblage records: exclusion of grid-squares without enough survey efforts, and exclusion of grid-squares out of temperature range in each species. Then we tried to find out landcover-occurrence relationships within the temperature range based on logistic regression models. We obtained statistically significant models for 98 species among all dragonflies inhabiting the main four islands of Japan (128 species). Goodness-offit tests showed that some landcover types significantly affected the occurrence of each species. Area of broad-leaved forests within a grid-square (10x10 km) had positive effects on the occurrence of 57 species, indicating that at least 50% of dragonflies depend on forests. Our analysis also showed that landcover heterogeneity (Shannon-Wiener's H') had positive effects on the occurrence of most species (73 among 98 species). We showed three examples of habitat maps generated by the logistic model together with actual occurrence records. We discussed how the model performance might change in relevance to the data screenings we applied.

# INTRODUCTION

A crucial step in conservation is determining where animals and plant species occur. This applies to any wildlife including dragonflies. However, conducting complete field inventories of animal occurrences is generally infeasible. Then, animal-habitat models based on environmental surrogate measures are often used to predict species occurrence, absence, or relative abundance (review in Guisan and Zimmermann, 2000; Samways 2004). The first step for generating animal-habitat models is to detect a correlation between a species' distribution and the attributes common to the habitats that might constitute ecological requirements. Although our knowledge of dragonfly habitat use is limited, our experience to date indicates that species respond to the features of their habitats in a hierarchical manner, from the biotope (e.g., woodland, marsh), through the larval habitat (e.g., pond, stream), to the oviposition site (living macrophytes, rotting wood) (Wildermuth, 1994). Therefore, processes underlying habitat selection of a given species are rather complex (Corbet, 1999). The main purpose of our analyses is to detect correlations between landcover characteristics and the occurrence of a given species in 10 km grid-squares. Therefore, our analysis may reflect mainly biotope level habitat preference of the species.

We used dragonfly occurrence records collected in the national recording scheme (National Survey on the Natural Environment). Records reported by the network of volunteer recorders provided, to some extent, comprehensive coverage of the country. These are immensely valuable for determining how well or not species are doing over time, as well as the extent of the geographical ranges of species. The outcome has been the production of an atlas (Japan Integrated Biodiversity Information System), which provides an immediate visual overview of present geographical ranges. These types of maps, based on information in about 10x10 km squares (about 100 km<sup>2</sup>), have been used to analyze gross range changes of butterflies of Britain, for example, and to predict future ranges (Hill et al, 2002), as well to determine other landscape effects (Warren et al. 2001). However, there are shortcomings with these "record maps". Firstly, the records are accumulated in an ad hoc manner, resulting in geographically biased records (Dennis and Hardy, 1999). Secondly the data only record what is present and not what is absent. Thirdly, they do not recognize recorder effort that can bias results (Dennis et al., 1999). Fourthly, abundance is neglected though it gives important survival implications for populations.

We report here our recent efforts to overcome these shortcomings inherent to the national recording schemes. We have developed a method to obtain species presence/absence data sets from presence-only species assemblage records. Based on the data sets we tried to find out suitable surrogate measures for the dragonfly-habitat models for all species. The results were used to categorize the diversity of habitat selection in dragonflies and to generate potential habitat maps of each species.

# DATA SOURCES

# **Dragonfly records**

Historical occurrence records of dragonflies in Japanese national recording scheme between 1900 and 1999 consist of 107,717 records, which include 205 (sub) species, though most of the records (>90%) were collected after 1980 (Biodiversity center of Japan, 2002). Each dragonfly record includes information of species, grid code, year and month of collection or sighting. We limited our analysis to the four main islands (Hokkaido, Honshu, Shikoku and Kyushu) in order to avoid island effects (effects of small land area and distance from mainland). The number of 10x10 km gridsquares covering Japan's mainland is 3.961 and the number of grid-squares in which at least 1 species is recorded is 3,083. Therefore, one fourth of grids have no records. The number of records at each grid-square ranges from 0 to 1400 with an average of 18, and the number of species ranges from 1 to 70 with an average of 7. These figures suggest that occurrence records provide incomplete species lists for most grids, though some of them may provide almost complete lists of species, particularly when the number of occurrence records is large.

Historically, 148 species have been recorded within the main islands of Japan. Among them, we used 128 inhabitants for the analysis excluding seasonal migrants and apparent vagrants.

# Climate data

Temperature data were obtained from "Mesh Climate Data 2000" (Japan Meteorological Business Support Center, 2002) that was released from the Japan Meteorological Agency. This dataset includes 1x1 km grid-square temperature data covering the whole of Japan, which was averaged for 30 years between 1970 and 1999. We calculated the average temperature for each 10x10 km mesh and used it for analysis.

## Landcover data

We used a vegetation data set derived from the National Survey on the Natural Environment (Biodiversity Center of Japan, 1999). In this dataset, area of vegetation and land use types (about  $358,200 \text{ km}^2$ ) are described with vector data (polygon-shaped), and categorized into 326 types mainly based on the plant community structures within each polygon. In order to simplify our analysis, however, we re-categorized them into 9 landcover types: broad leaved forests including evergreen and deciduous forests (BLF), coniferous forests including cypress and cedar plantations (CF), grassy land (GL), wetland vegetation (WL), bamboo or sasaplant vegetation (BS), paddy field (PF), agricultural land use other than paddy field (AF), urban area including residential area, factories and architecture (UR), and others. Table 1 shows the area and the proportion of each landcover types of main lands and that of selected 361 grids (see below). In addition, we used Shannon-Wiener's H as a measure of landcover heterogeneity,

$$H' = -\Sigma P_i \ (\log_2 P_i),$$

where  $\boldsymbol{P}_i$  is a proportion of a given land cover type within a given square-grid.

Table 1. Proportion of landcover types in Japan's main four islands and selected gridsquares for analysis (see text). Contingency table analysis showed that the composition of landcover types of selected grid-squares are significantly different to that of Japan's main four islands (G=6730.5, P<0.001). Higher proportion of UR in selected grids probably reflects that it is easy to approach, and lower proportions of CF and BS reflects that recorders usually take little interest in such landcover types.

Land cover type	Area in main islands	%	Area in selected 361 grids	%
BLF	123,397	31.6	10,054	29.0
CF	106,639	27.3	6,860	19.8
GL	$23,\!130$	5.9	1,339	3.9
WL	3,396	0.9	404	1.2
BS	$21,\!174$	5.4	488	1.4
PF	$42,\!345$	10.8	5,848	16.9
AF	28,007	7.1	3,048	8.8
UR	20,841	5.3	5,281	15.2
others	$21,\!850$	5.6	1,383	4.0
Total	$390,779   { m km^2}$	100.0	$34,704 \text{ km}^2$	100.0

Abbreviations: BLF, broad leaved forests including evergreen and deciduous forests; CF, coniferous forests including cypress and cedar plantations; GL, grassy land; WL, wetland vegetation; BS, bamboo or sasa-plant vegetation; AF, agricultural land use other than paddy field; PF, paddy field; UR, urban area including residential area, factories and architecture

## ANALYTICAL PROCEDURE

### Temperature range of each species

At a broad scale, the main controlling factors of species' geographic ranges are probably climatic conditions (temperature). It is not meaningful to analyze the relationship between landcover types and species occurrence where temperature conditions are not suitable. Therefore, we estimated temperature limits of a given species based on the annual average temperatures of all grid-squares where the species was recorded. As a rule, the temperature range of each species was defined as the range where 95% of grids are included. Therefore, minimum and maximum temperature were at 2.5% and 97.5% points respectively. This procedure is probably effective in excluding latitudinal and altitudinal outliers of the distribution. In cases where the target species occurs further south from the main islands, maximum temperature was defined separately as the highest temperature within the main islands (17.8°C). The results of temperature range estimation are shown in Appendix Table 1. It should be noted that the occurrence probability might vary even within the temperature range of each species.

#### Selection of grid-squares for analysis

It is expected that the more occurrence records of any species we have within a grid-square, the more its species list will become complete. Let's suppose that we make several inventory efforts over the years within a grid-square. During the first inventory we may obtain a list of some proportion of species living within this grid-square. In the next inventory we may add some new species into this list, but the list of new species is likely to be smaller than the previous one. The list of new species will become gradually smaller as we repeat this procedure (Fig. 1). The relationship is often described using a negative exponential function relating the number of species  $(S_r)$  to the number of records chronologically accumulated (r). This relationship is given by

$$S_{\rm r} = S_{\rm max}[1 - \exp(-br)],$$

where  $S_{\text{max}}$ , the asymptote, is the estimated total number of species in a given grid-square and b is a fitted constant that controls the shape of curve (e.g., Gotelli and Colwell 2001; Lobo & Martin-Peira 2002; Colwell et al. 2004). The curvilinear function was fitted by the quasi-Newton method using Mathematica (v.5.1). We also calculated the 95% confident interval of  $S_r$  and determined the adequacy of records in each grid-square. Where the number of species recorded was within the confidence interval, we assumed that the



Cumulative number of records (r)

Fig. 1. A typical relationship between the cumulative number of dragonfly records and the cumulative number of dragonfly species in a grid. As the species list becomes larger, new species are less likely to be added in the list. Number of species present in the grid was estimated by fitting a negative exponential equation (see text).

records made up an almost complete species list. As a result, we selected 361 grids for analysis.

The selected grids cover about 10% of the whole area, and the proportion of each land cover type in the selected grids was roughly the same as that of whole land area except for UR, CF and BS (Table 1). Contingency table analysis showed that the composition of landcover types of selected gridsquares was significantly different to that of Japan's main four islands (G=7369.4, P<0.001). Higher proportion of UR in selected grids is probably due to the easiness of approaches, and lower proportions of CF and BS reflects that dragonfly recorders usually take little interest in such landcover types. This kind of bias is difficult to avoid when we deal with records reported by the network of volunteer recorders. The ability of the model to detect the effects of UR may be stronger and that of CF or BS may be weaker than other variables. Therefore we should be careful in interpreting the results. However, some preliminary analyses reducing the number of UR-rich gridsquares showed that such effects were not large.

The selection of grids reduced the number of species for statistical analysis, because some species are recorded only once or less among the selected grids. We therefore excluded these species and consequently we analyzed 126 out of 128 species.

## Construction of logistic models and evaluation

Using the selected datasets of 361 grid-squares, we analyzed the effects of landcover type on the occurrence of each dragonfly species using multiple logistic regression models coupled with a stepwise variable selection procedure (JMP v.6.0, SAS). Because logistic regressions results tend to be influenced by extreme prevalence scores, it is necessary to use the same number of presence and absence records. As this condition is not generally satisfied even if we excluded grid-squares out of temperature range, we used weighing methods suggested by King and Zeng (2000) using the prevalence value calculated in the later section.

The discrimination ability of logistic regression models was quantified by calculating statistics from a confusion matrix of predictions and observations (Fig. 2) (e.g., Edwards et al. 1996; Boone and Krohn 1999). A species was predicted to be present or absent at a grid-square based on whether the predicted probability for the grid is higher or lower than a specified threshold probability. We used the relative operating characteristic (ROC) curve (Field-ing and Bell 1997; Manel et al. 1999; Guisan 2002) to find out a suitable threshold probability. An ROC curve is a plot of the specificity and false positive values of sensitivity obtained by considering a large number of threshold probability values. We show the ROC plot of a logistic model for *Calopteryx cornelia* as an example (Fig. 3). For a given threshold, sensitivity is the proportion of a converted probability and false position.

tion of occupied grids correctly classified by the model as occupied. We used sensitivityspecificity sum maximization approach (Cantor et al. 1999, Manel et al. 2001) to determine threshold cut-off to predict distribution. We also calculated overall prediction success rate (OPS) [(a+d)/(a+b+c+d)], sensitivity (a/a+c) and specificity (d/b+d) as accuracy indices of predictions.

		Predi	ction
		Present	Absent
Observation	Present	a	b
Observation	Absent	с	d

Fig. 2. The confusion matrix comparing observed to predicted numbers of present and absent data.



**Fig. 3.** Graphic representation of discrimination performance (ROC curve) of a model for *Calopteryx cornelia*. AUC: area under the ROC curve. We used sensitivity-specificity sum maximization approach to determine threshold cut-off to predict distribution (see text).

A more universal accuracy measure should describe the accuracy of the whole model and not just its performance for a given threshold value. One such measure is the area under the ROC curve. The area under this curve (AUC), expressed as a proportion of the area yielded by a model with perfect accuracy, provides a measure of discrimination ability. This area is equivalent to the Mann-Whitney-Wilcoxon statistic (Hanley and McNeil 1982), and ranges between 0.5 and 1.0, with 0.5 indicating discrimination performances equivalent to a random model and 1.0 indicating complete discrimination for occupied and unoccupied grids.

# RESULTS

## **Prevalence of species**

Among selected grid-squares, we classed them within and out of the range of temperature conditions for a given species. Appendix Table also shows the total number of grids within the temperature range for each drag-onfly among selected grids (Nt), and the number of grids in which the drag-onfly was actually observed (Np). Np/Nt ratio is the positive prevalence of species. Np/Nt value ranged between 0.0 and 0.9, indicating a wide spectrum in prevalence among species.

#### Model performances

Fig. 4a shows the frequency distribution of AUC. Pearce and Ferrier (2000) provide guidelines for interpreting the 0.5-1 ranges. They suggest that values greater than 0.9 indicate an excellent level of discrimination. Values between 0.7 and 0.9 indicate a reasonable level of discrimination, while values between 0.5 and 0.7 indicate poor to marginal discrimination ability. Based on this criteria, models for 73 species among 98 species showed acceptable (AUC greater than 0.7) levels of discrimination, while models for 25 species showed poor levels of discrimination.

Fig. 4b,c and d show frequency distributions of OPS, sensitivity and specificity, respectively. Average OPS was 0.697 ( $\pm$  0.066 s.d.). Average sensitivity and specificity were 0.744 ( $\pm$  0.101 s.d.) and 0.666 ( $\pm$  0.101 s.d.), respectively.

# Effects of landcover type on dragonflies

Results of model evaluations are summarized in Appendix table. We could obtain 98 statistically significant models among 128 dragonfly species.

As results of goodness-of-fit tests, we could identify which landcover types explain and how strongly each landcover type (positively or negatively) is associated with the occurrence of each species, as well as to assess the



**Fig. 4.** Discriminative performance of logistic models applied to 98 dragonfly species. Model-building data: grid-squares out of species temperature range were excluded from 361 well-surveyed grid-squares. (a) Frequency distribution of area under ROC curve (AUC), (b) Overall prediction success (OPS), (c) Sensitivity, and (d) Specificity.

temperature effects on it (Table 2 and 3). We will briefly describe general features of these parameters

Temperature had positive effects (P < 0.05) on 55 species out of 98 species, while on 24 species it had a negative effect, indicating that most of dragonflies prefer warmer climate conditions. For the remaining 19 species temperature had no significant effect. These species may have alternative responses to temperature conditions, including unimodal or uniform effects of temperature, or it is merely due to small sample size.

Broad leaved forests (BLF) had positive effects (preference) on 57 out of 98 species, and negative effects (avoidance) on 8 species. All Calopterygidae preferred BLF, and most of Aeshnidae, Gomphidae and Corduliidae also preferred BLF. On the other hand, the preference to BLF is variable within Coenagrionidae and Libellulidae.

Coniferous forests (CF) had positive effects on 43 species and negative effects on 26 species. All Calopterygidae preferred CF, and most of Gomphidae also preferred CF. Most of species that showed preference to CF also preferred BLF (39 out of 43 species). These results probably indicate that forest dragonflies generally prefer BLF to CF, but only a few of them show clear distinction between BLF and CF.

Grassy land (GL) had positive and negative effects on 6 and 18 species respectively, and it had no significant effects on 74 species, suggesting that this kind of habitat was not a critical habitat for most dragonfly species.

Tab	le 2. Effects of ten	perature and landcover types or	a the presence	:/absenc	e of 98	drage	onfly s	pecies	estima	ted b	y logist	ic models.
No	family	species				La	ndcove	r type	0			Landcover
		1	Temperature	$\mathbf{BLF}$	CF	$\mathbf{GL}$	WL	$\mathbf{BS}$	$\mathbf{PF}$	$\mathbf{AF}$	UR	heterogenity, H'
	Calopterygidae	Calopteryx japonica		XXX	XXX	XXX		000	XXX	XXX	XXX	XXX
5		Calopteryx atrata	XXX	XXX	XXX				XXX		XXX	XXX
റ		Calopteryx cornelia	Х	XXX	XXX				000		XXX	XXX
4		Mnais pruinosa	XXX	XXX	XXX		00			000		XX
2		Mnais costalis	0	XXX	XXX				XX	XXX	XXX	XXX
x	Lestidae	Lestes sponsa	000		00	0			XX	00	X	XXX
10		Lestes japonicus		•	000	000	00	000	XXX	000		XXX
11		Lestes temporalis		XXX			000	0	XXX	0	XXX	XXX
12		Indolestes peregrinus		XXX	XXX				XX		XXX	XXX
13		Sympecma paedisca	00					00			X	XXX
14	Platycnemididae	Platycnemis foliacea sasakii	XXX	XXX	X	XXX	XXX	000				
16	ð	Copera annulata		XXX						000	XXX	XXX
18	Coenagrionidae	Agriocnemis femina oryzae	XXX	XXX	XXX	0						XXX
19		$Mortonagrion\ selenion$	XXX					00		000		X
21		$Ceriagrion\ melanurum$			00							X
22		Ceriagrion nipponicum	XXX	00	XXX	0	X	X	XXX		X	XXX
24		$A ciagrion \ migratum$	XXX	XXX	XXX			0		000		X
25		Ischnura senegalensis	XXX	000	000						000	
27		Ischnura asiatica		000	000	0		0				
29		Cercion calamorum calamorum	X	X			XXX		XXX		XXX	X
30		Cercion sieboldii	000		0			000	X		X	
31		$Cercion\ sexlineatum$	XXX		00	. ,	XXX		XX	X		
32		Cercion hieroglyphicum	XXX		00		XXX			0	000	
33		$Cercion\ plagiosum$	000	000	000	XXX	0			000	000	
34		Coenagrion terue	000		00		000					X
35		Coenagrion lanceolatum	000	XXX	0	0			XX	00		XXX
40	Epiophlebiidae	$Epiophlebia\ superstes$		XXX	XXX						X	
41	Petaluridae	$Tanypteryx\ pryeri$		XXX	XXX	0	0		XXX		XXX	XXX
42	Aeshnidae	Oligoaeschna pryeri	XX	XXX	XXX				XXX			XXX
43		Boyeria maclachlani	XXX	XXX	XXX		000	0		8	XX	XXX

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Table

No	family	species				Land	lcover	type				Landcover
	·	L .	emperature	BLF	CF	GL V	VL E	S.	F A	F F	<b>R</b>	heterogenity, H'
44		Planaeschna milnei	XXX	XXX	XXX	0	00			X	XX	XXX
45		Aeschnophlebia longistigma	XX		000		X	X	XX C	~		XX
46		Aeschnophlebia anisoptera	XXX		00	X			õ	0 00	00	
47		Gynacantha japonica	XXX	XXX	XXX			r 1	2	×	XX	XXX
48		Polycanthagyna melanictera	XXX	XXX		-	0			X	XX	XXX
49		Aeshna juncea juncea	000					0	0	~		
50		Aeshna ni $groflava$	000	XXX		0		r 1	5	X	XX	X
54		Anaciaeschna martini	XXX			-	0					XXX
55		Anax parthenope julius	XXX		00			X	XX XX	XX	XX	X
56		Anax nigrofasciatus nigrofasciatus		XXX		-	0			X	XX	XXX
57	Gomphidae	$An isogomphus\ maacki$		XXX	XXX				2	X	XX	XXX
61		Gomphus postocularis		XXX	X	X	XX	X	XX	X	XX	XXX
62		$Asiagomphus\ melaenops$	XXX	XXX	XXX	-	0	X	X	X	XX	XXX
63		Asiagomphus pryeri	X	XXX	XXX	-	0	X	X			XXX
64		Davidius nanus	XXX	XXX	X XX X	XX				X	XX	
65		Davidius fujiama		XXX	XXX			0	Q			XX
66		Davidius moiwanus moiwanus	000			Õ	00	0	ŏ	00		
67		Lanthus fujiacus	00		XXX	0	0		ŏ	00		X
68		Trigomphus citimus tabei	XXX	XXX	XX	00		r 1	2			XX
69		$Trigomphus\ melampus$	000		0 000	00		•	0			XXX
20		$Trigomphus\ interruptus$	XXX	XXX				X	XX	~		XXX
71		Trigomphus ogumai	XXX	XXX					ŏ	<b>X</b> 00	XX	XXX
72		$Stylogomphus\ suzukii$	XXX	XXX	XXX			0	Q	×	XX	XXX
74		Sinogomphus flavolimbatus	XXX	XXX	XXX			ŏ	KX OC	X	X	XXX
75		$Nihonogomphus\ viridis$	XXX	XXX	XXX			X	XX XX	XX	XX	XXX
26		Onychogomphus viridicostus	XXX	XXX	XXX			X	X X	XX	XX	XXX
77		Sieboldius albardae	XXX	XXX	XXX		0	0		X	XX	XXX
78		$Ictinogomphus \ pertinax$	XXX		0	00			ŏ	00		XXX
62		Sinictinogomphus clavatus	XXX					X	X	×	XX	XXX
81	Cordulegastridae	$Anotogaster\ sieboldii$	XXX	XXX	XXX			X X	X	X	XX	XXX

Table	2. Continued.											
No fa	amily	species		a Id	Ę	La	nd cove	r type	0 0	L V		Landcover
			emperature	DLF	5	75	MF	20	1	AF	N N	neterogemuy, n.
82 C	Jorduliidae	Epophthalmia elegans elegans	XXX	0					XXX			
83		Macromia daimoji	XXX	XXX	X XXX	XX	XX	XXX	XXX	XXX	XX	
84		Macromia amphigena amphigena	XXX	XXX	XXX						X	XXX
85		$Epitheca\ marginata$	XXX	XXX					XXX	000		XX
86		Epitheca bimaculata sibirica	000				XXX		XXX			0
87		Cordulia aenea amurensis	000	XXX			XXX		XXX			
88		Somatochlora arctica					XXX					
92		$Somatochlora\ uchidai$	00	XXX	XXX						XX	XXX
93		$Somatochlora\ viridiaenea$	000		00		-	000		000	000	XXX
94		$Somatochlora\ clavata$	XXX	X			XX	00		000		XXX
95 L	ibellulidae	$Lyriothemis\ pachygastra$	X	XXX	XX	0					X	XXX
97		Libellula quadrimaculata asahinai	000		XXX					00		XXX
98		$Libellula\ angelina$	XXX			~	XXX		XXX		XXX	
101		Orthetrum albistylum speciosum	XXX	X	XX		XXX	ХХ	XXX	XXX	XXX	XXX
102		Orthetrum japonicum japonicum	X	XXX	XXX				XXX	0	XXX	XXX
103		Orthetrum triangulare melania	XXX	XXX	XXX						XXX	
104		Nannophya pygmaea					0		XX	0		
105		$Deielia \ phaon$		000	000				XXX			
106		Crocothemis servilia mariannae	XXX		000						X	XX
107		Sympetrum pedemontanum elatum	00	XXX	XXX		X				XXX	XXX
108		$Sympetrum \ darwinianum$		XX	XX		X	00	XX		XXX	XX
109		$Sympetrum \ frequens$	000		0	00	X		X		XXX	XX
110		Sympetrum striolatum imitoides	XXX	000	000	0	XXX		000		0	
111		$Sympetrum \ eroticum \ eroticum$	000	ХХХ				00	XXX		XXX	XXX
112		$Sympetrum \ kunckeli$		000	000		X		XXX	000		
113		$Sympetrum\ parvulum$	XXX	XXX	XXX						XX	XXX
116		$Sympetrum \ risi$	XXX		000	00				000		XX
117		$Sympetrum \ infuscatum$	000		000 C	000	XXX		XXX		XXX	
118		$Sympetrum\ baccha\ matutinum$					00			00	XX	XX
119		$Sympetrum \ gracile$	XXX	XXX					XXX			XXX

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No family	species				La	ndcove	ir type				Landcover
		Temperature	$\mathbf{BLF}$	$\mathbf{CF}$	$_{ m GL}$	WL	BS	PF	$\mathbf{AF}$	UR	heterogenity, H'
120	Sympetrum maculatum	000	XXX	000		000	000	XXX	000	XXX	XXX
121	Sympetrum speciosum speciosum	XXX	XX	XXX			X	000		X	XXX
122	$Sympetrum \ croceolum$	000	XXX	0			000	X			XXX
123	$Sympetrum \ uniforme$	XXX				XXX	000	XXX			XXX
124	Leucorrhinia dubia orientalis	0	X	X							
126	$Pseudothemis\ zonata$	XXX	XX			XX	000	X		XXX	XX
127	$Rhyothemis\ fuliginosa$	XXX		0	0	XX		X	000		XXX
128	Tramea virginia	XXX		0	000		000		000		XXX
Note: Pearson's chi-	square test for likelihood-ratio P v	alues: Positiv	e effect	s: P $<$	0.05 =	= X, P	< 0.0	I = X	X, P <	0.001	= XXX Negative

Abbreviations, same as Table 1. H': Landcover heterogeneity calculated as Shannon-Weaner index.

effects; P < 0.05 = 0, P < 0.01 = 00, P < 0.001 = 000.

1 ... 4 Table 3. Number of species (N=98) on which temperature and landcover types showed positive and negative effects on their • occurrence (P < 0.05)

Landcover	Temperature	$\mathbf{BLF}$	$\mathbf{CF}$	GL	WL	BS	$\mathbf{PF}$	$\mathbf{AF}$	UR	H'
Positive effects	55	57	43	9	23	5	49	6	52	73
Non significant	19	33	29	74	57	72	41	58	40	24
Negative effects	24	×	26	18	18	21	x	31	9	1
Abbreviations, se	ume as Table 1. H	[': Landco	ver heterog	geneity cal	culated as	Shannon-W	Veaner's ind	dex.		

Wetland vegetation (WL) had positive and negative effects on 23 and 18 species respectively, and it had no significant effects on 57 species. Most of Coenagrionidae, Corduliidae and Libellulidae preferred WL, while some Calopterygidae, Lestidae, Aeshnidae and Gomphidae avoided WL.

Bamboo vegetation (BS) had positive and negative effects on 5 and 21 species respectively, and no significant effects on 72 species. No odonate family showed consistent preference or avoidance to BS, however, BS was generally avoided by most dragonfly species.

Paddy field (PF) had positive and negative effects on 49 and 8 species respectively. Most of Lestidae, Coenagrionidae, Aeshnidae, Corduliidae and Libellulidae showed preference to PF, reflecting that paddy fields are important habitat for various dragonfly species. However, some Gomphidae avoided PF.

Agricultural field (AF) excluding paddy field had positive and negative effects on 9 and 31 species respectively. No particular dragonfly family showed consistent preference or avoidance to AF.

Urban area (UR) had positive and negative effects on 52 and 6 species respectively. This was an unexpected result to us, however this result might reflect that UR area usually consisted of small but various types of landcover: i.e., private gardens with small ponds, cemetery parks, parks with ponds, small forests, school grounds. Sampling bias toward UR might increased the number of significant results, but it is still apparent that many dragonflies are inhabitants of urban areas.

Landcover heterogeneity (H') had positive effects on 73 species. Although one species showed a marginally significant negative effect (*Epitheca bimaculata sibirica*), the results suggest that dragonflies generally require multiple landcover types within about  $10 \times 10$  km size of habitat.

# Generation of habitat maps

Based on logistic models constructed using presence/absence data from 361 selected square-grids, together with landcover data for the whole area (3961 grids), we could extrapolate occurrence probabilities even for grid-squares without any dragonfly records. We show predicted habitat maps for three species in Fig. 5: *Calopteryx cornelia, Ischnura senegalensis* and *Orthetrum albistylum speciosum*, which are representatives of three different levels of prevalence (Np/Nt = 0.405, 0.572, 0.963, respectively). Dark squares in each predicted habitat map represent occurrence probability higher than the threshold cut-off. A grid map of occurrence records is shown immediately to the right of the predicted map. Even on the commonest species (*O. a. speciosum*), it is suggested that there are many grids in which the species is expected to occur but not recorded yet.



**Fig. 5.** Habitat maps predicted for three dragonflies: (a) *Calopteryx cornelia*, (b) *Ischnura senegalensis* and (c) *Orthetrum albistylum speciosum*. Dark squares in each predicted habitat map represent grids with occurrence probability higher than the threshold cut-off estimated (see Fig. 2). Grid maps of occurrence records are shown immediately to the right of the predicted maps.

### DISCUSSION

Predicting species distributions is an important step for environmental conservation and biodiversity management. For this purpose, many modeling techniques to predict species presence/absence have been developed (e.g., Fielding and Bell 1997, Mantel et al. 1999, Austin 2002). Model prediction is



Fig. 6. Frequency distributions of positive prevalence estimated for 98 dragonfly species. (a) pseudo positive prevalence without any data screening (all the available presence-absence information). (b) positive prevalence calculated using 361 well-surveyed grid-squares. (c) positive prevalence calculated using well-surveyed gridsquares excluding grids out of distributional temperature range for each species. largely influenced by the prevalence of modelbuilding data, and several researchers tested the effects of the prevalence on assessing indices for model performance (e.g., King and Zeng 2000; Liu et al 2005). However, there are some more practical problems before building models.

Any wildlife distributional predictive models require an accurate presence/absence dataset. However, it is not always easy to obtain a high quality model-building data. One of the serious problems in obtaining an accurate presence/absence data comes from characteristics of "absence" records. Absence records are almost always less reliable than present records, because we can be confident about the presence of species if we observed one or more individuals within a local area but we are generally less confident about absence even if we did not see any individual during many times of surveys within the same area. Reliability of absence records is expected to increase only by increasing survey efforts, although perfect confidence of absence will not be obtained practically. We believe that the method used here is an efficient way to select well-surveyed squaregrids. Fig. 6a shows the frequency distribution of pseudo-positive prevalence for all the available presence-absence information (without any data screening). While Fig. 6b shows the frequency distributions of positive prevalence for well-surveyed square-grids without considering upper and lower temperature limits of each species. It is apparent that model building without any data screening is misleading. Therefore the inclusion of poorly surveyed grids into model-building data always lead to underestimation of positive prevalence.

Several accuracy indices derived from a confusion matrix are usually used to assess the model prediction (for example, OPS (operational sex-ratio), Sensitivity, Specificity). However, some values are sensitive to prevalence (p). For example, OPS is affected by the prevalence since  $OPS = p \cdot$  sensitivity – (1-p)  $\cdot$  specificity (Ruttiman 1994), where sensitivity is the ratio of correctly predicted positive cases to the total number of positive cases and specificity is the ratio of correctly predicted negative cases of the total number of negative cases. Liu et al. (2005) examined the effects of prevalence of model-building data on indices of model predictive ability (including OPS, sensitivity, and specificity) in relation to threshold determining approaches (including sensitivity-specificity sum maximization approach that is used in this study). They confirmed that OPS is highly sensitive to very low or very high prevalence, while sensitivity and specificity are less sensitive to prevalence when sensitivity-specificity sum maximization approach was used.

Our second data screening procedure was to discard meaningless records from model-building data by establishing upper and lower temperature limits, which aimed to balance the numbers of presence and absence records as much as it is possible. We will now examine the effects of this data screening on AUC and on three indices of model performance (OPS, sensitivity and specificity). Fig. 7 shows frequency distributions of AUC, OPS, sensitivity and specificity of



Fig. 7. Discriminative performance of logistic models applied to 98 dragonfly species. Model-building data: 361 well-surveyed grid-squares. (a) Frequency distribution of area under ROC curve (AUC), (b) Overall prediction success (OPS), (c) Sensitivity, and (d) Specificity.

well-surveyed grids when upper and lower temperature limits were not taken into account. Average AUC was  $0.773 (\pm 0.076 \text{ s.d.})$ , which was slightly larger than that of well-surveyed grids with establishments of temperature limits (Fig. 4; 0.754  $\pm$  0.068 s.d.), but there was no significant difference between them (ttest, P=0.09). Average OPS was 0.701 ( $\pm$  0.082 s.d.) that was almost the same as Fig. 4b, and there was no difference between them (*t*-test, P=0.730). Average sensitivity of Fig. 7c was 0.786 ( $\pm$  0.121 s.d.) and was significantly larger than that of Fig. 4c (t-test, P=0.009). Average specificity of Fig. 7d was 0.661  $(\pm 0.118 \text{ s.d.})$  and was not different to that of Fig.4d (t-test, P=0.769). In conclusion, the exclusion of grid-squares out of species temperature range did not generally increase the model predictive ability measured as OPS, sensitivity or specificity. However, the effect of the establishment of temperature range was variable from species to species. This may be because this treatment reduced the size of model-building data. The difference in sensitivity between models with and without temperature limitations was negatively correlated with the difference in specificity between models (Fig. 8). Therefore, it is a matter of choice which model-building data we should use in the conservation practice. For example, if a model is used to find grids likely be present, a modelbuilding data that gives high sensitivity may be preferred. On the other hand, if a model is used to find grids likely be absent, a model-building data that gives high specificity may be preferred.

We have shown that relatively simple logistic models have the ability to describe habitat preferences and produce habitat maps for dragonfly species after careful data screening. The logistic regression models we used for the analysis were successful in describing landcover-habitat relationships for 98 species, with acceptable levels of model performance for 73 species. However,



Fig. 8. Relationship between the increases (or decreases) in sensitivity and specificity caused by the exclusion of grid-squares out of species temperature range from model-building data.

we still have 25 species with poor levels of model performance and some more species not analyzed properly. One way to improve the model performance is to increase the number of reliable gird-squares. However, it is not always an efficient procedure, because most species have a small geographic range. It might be useful to change the grid size, for example from 10km (as used here) to 1 km or smaller, and make sampling in a more confined area. Cowley et al. (1999) found, by mapping at the fine scale, British butterflies to be declining faster than conventional coarse-scale maps suggested.

We have not used river data for our analyses, because digital cartography of the small (first order) streams is not available at this moment. This means that we assumed there are no 10 km grids without streams. Although this is generally correct, it is not always the case. Incorporation of river data may improve our predictions particularly for stream dwelling dragonflies (mainly Calopterygidae and Gomphidae).

By analyzing habitat relational models independently on all species, we can give insight to habitat preference of species in a quantitative manner, as well as rank species according to their sensitivities to environmental change. When models for all (or most) species are constructed, the difference in species composition between a list predicted from the models and a list from actual records would be useful as an indicator of environmental conditions of the grid.

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Appendix tabl range within r	le. Temperature range main four islands of Ja d mumber of those wit	estin vpan, th di	nun istrib	l fron lber (	l spe of gri	d-squ	listril lares	within Mart	nal recontemp in temp forman	erasti erasti	umb∈ are ra	ar of $\frac{1}{2}$ in $\frac{1}{2}$	grid- nmon	squa: 1g sel	res w lected 198	drag	tempe grid-s	rature quares
inhabiting ma	in four islands of Japai	n. n. d	dam.M	TOLUDI	נמו דע יייק מוויי	scorde	bin tom	r PCLI		Numb	nergor m form			101 o	1 10 1 10	urag.	e Attito	poutos
1 - lower temperate squares within temp 10 - Threshold cut-o specificity	emme, z - mgret elemperature m erature range, Nt; 6 - Number of off to predict distribution; 11 - tı	f grid-s rue neg	quares gative;	er or g with re 12 - fals	ecords, se posit	ares wit Np; 7 - Jive; 13	Positiv - false 1	e preval negative	e range; 4 lence , Np e; 14 - tru	- 1 Num /Nt; 8 - e positiv	7er or gr P of goo 7e; 15 - 1	odness-i oCCR C	of-fit to	at la est; 9 - classifi	AUC AUC cation	ecoru, o (Area u rate; 16	- Ivuuuo nder RO - sensiti	r or gru- C curve); vity; 17 -
		3	Mai islands 961 gri	n four of Japa id-squar	un res)	gri sel	lected 3 id squar	61 tes			Pe	rformai	ice of	lositic	models			
No family	species	-	2	ŝ	4	5	9	7	, w	6	10	11	12	13	14	15	16	17
1 Calopterygidae	Calopteryx japonica	8.8	15.5	2145	133	302	37	0.123	<0.0001	0.759	0.464	169	96	6	28	0.652	0.7568	0.6377
2	Calopteryx atrata	9.5	16.4	1658	009	325	221	0.680	< 0.0001	0.719	0.498	68	36	63	158	0.695	0.7149	0.6538
3	Calopteryx cornelia	7.8	16.1	2160	506	333	135	0.405	< 0.0001	0.835	0.529	153	45	23	112	0.796	0.8296	0.7727
4	Mnais pruinosa	8.7	16.3	1935	552	332	154	0.464	<0.0001	0.788	0.493	123	55	31	123	0.741	0.7987	0.6910
5 Meranoda-	Mnaıs costalıs Rhimidolestes aculeatus	4.9	16.8	2079	50	303 318	140 4	0.462 0.013	<0.000 1 000 1	0.759	0.532	711	10	30	104	0.713	0.7429	0.6871
7 grionidae	Rhipidolestes hiraoi	9.0	16.1	2308	44	328	18	0.055	0.974									
8 Lestidae	Lestes sponsa	3.2	16.3	3224	429	361	193	0.535	< 0.0001	0.690	0.576	135	101	33	92	0.629	0.7360	0.5720
9	Lestes dryas	1.6	7.1	995	12	20	5	0.250	1.000									
10	Lestes japonicus	8.8	15.9	2333	65	323	33	0.102	< 0.0001	0.732	0.423	210	80	16	17	0.703	0.5152	0.7241
11	Lestes temporalis	7.7	16.0	2209	487	332	210	0.633	<0.0001	0.736	0.472	22	45	52	158	0.708	0.7524	0.6311
12	Indolestes peregrinus	7.7	17.8	2247	543	337	205	0.608	<0.0001	0.686	0.472	140	62	23 24	146 76	0.641	0.7122	0.5303
14 Platvcnemididae	Sympecma paeaisca Platucnemis foliacea sasakii	4.4 9.8	15.4	1825	240 87	282 282	28	0.099	<0.0001	0.804	0.407	159	95 97	91 4	24 0	0.649	0.8571	0.6260
15	Platycnemis echigoana	7.6	12.3	1368	14	69	4	0.058	1.000									
16	Copera annulata	6.6	16.2	2542	457	347	198	0.571	< 0.0001	0.685	0.582	124	25	90	108	0.669	0.5455	0.8322
17 10 a · · · ·	Copera tokyoensis	12.8	3 15.0	775	11	190	10	0.053	0.997		. c	. 5	. 6			1 1 1 		1 2 1 
15 Coenagrionidae	Agrochemis Jemina oryzae	14.1 0 9	0.7 L	0000	74	94	5	0.090	1000.02	0.010	0.000	001	70	0 5	۲ ת ۲	0.706	1.0000	0.7440
19 90	Mortonagron selenion	0.0	691 .	1045	00T	000	7 61	012.0	<0.000 1	0.009	0.040	761	00	10	41	0.700	0.0094	0.1442
107	Conjection malaneer	101	10 C	0101	161	0T0	101	0 5 40	-0.0001	0 800	. 100		. 60	. ī	. 191	0 200	. 7001	. 1590
22	Ceriagrion nipponicum	12.2	16.5	1295	104	274	44	0.161	<0.0001	0.817	0.516	96	20	5 88	101	0.704	0.5243	0.6316
23	Ceriagrion auranticum	14.6	17.8	572	16	105	2	0.019	1.000									
	ryukyuanum																	
24	Aciagrion mignatum	10.5	16.2	1600	187	307	83	0.270	<0.0001	0.783	0.487	146	28	21	62	0.678	0.7470	0.6518
25 96	Ischnura senegalensis	11.4	17.8	1201	533	297	170	0.572	<0.0001	0.816	0.570	104	73	53	117	0.744	0.6882	0.8189
70	rectitiva eteganie eteganie	4.1	9.4	0071	<del>1</del>	10	-	700.0	1.9991									

Continued.
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Appendix

		i (39	Main lands c 61 grid	four if Japar I-square	(ss	gri	ected 3 d squar	65 es			Pe	rforma	nce of	lositic	models			
No family	species	1	2	3	4	5	9	7	8	9	10	11	12	13	14	15	16	17
27	Ischnura asiatica	7.1	15.9	2232	588	343	250	0.729	< 0.0001	0.715	0.481	61	32	62	171	0.676	0.6840	0.6559
28	Enallagma boreale circulatum	0.9	12.0	2361	87	82	23	0.280	0.5021									
29	Cercion calamorum calamorum	2.6	16.4	2649	727	361	295	0.817	< 0.0001	0.730	0.492	46	20	66	196	0.670	0.6644	0.6970
30	Cercion sieboldii	7.5	16.0	2451	276	335	137	0.409	< 0.0001	0.639	0.504	118	80	53	84	0.603	0.6131	0.5960
31	Cercion sexlineatum	11.4	16.9	1596	122	297	62	0.209	< 0.0001	0.780	0.528	174	61	20	42	0.727	0.6774	0.7404
32	Cercion hieroglyphicum	6.8	16.0	2591	316	346	164	0.474	< 0.0001	0.730	0.542	135	47	65	66	0.676	0.6037	0.7418
33	Cercion plagiosum	10.0	15.0	1660	21	258	12	0.047	0.0122	0.934	0.652	219	27	1	11	0.891	0.9167	0.8902
34	Coenagrion terue	3.5	13.2	2646	89	151	28	0.185	< 0.0001	0.835	0.380	88	35	5	26	0.755	0.9286	0.7154
35	Coenagrion lanceolatum	2.4	13.7	2829	174	197	50	0.254	< 0.0001	0.910	0.438	122	25	7	43	0.838	0.8600	0.8299
36	$Coenagrion\ ecornutum$	1.7	7.5	1061	53	24	15	0.625	1.000									
37	Coenagrion hylas	1.6	6.1	778	15	14	2	0.143	1.000									
38	$Erythromma\ humerale$	3.5	5.2	390	4	6	2	0.222	1.000									
39	Nehalennia speciosa	2.9	12.1	2392	30	81	13	0.160	1.000									
40 Epiophlebiidae	Epiophlebia superstes	4.3	15.4	3102	313	320	69	0.216	< 0.0001	0.804	0.478	172	79	14	55	0.709	0.7971	0.6853
41 Petaluridae	$Tanypteryx \ pryeni$	7.4	15.6	2402	260	322	89	0.276	< 0.0001	0.701	0.581	182	51	45	44	0.702	0.4944	0.7811
42 Aeshnidae	$Oligoa eschna\ pryeri$	6.9	16.3	2611	290	346	142	0.410	< 0.0001	0.679	0.504	125	62	47	95	0.636	0.6690	0.6127
43	Boyeria maclachlani	9.6	15.8	1882	242	350	114	0.326	< 0.0001	0.730	0.504	144	92	22	92	0.674	0.8070	0.6102
44	$Planaeschna \ milnei$	8.5	16.0	2205	390	329	152	0.462	< 0.0001	0.780	0.535	135	42	44	108	0.739	0.7105	0.7627
45	A eschnophlebia longistigma	8.7	16.2	2259	170	331	100	0.302	< 0.0001	0.771	0.542	171	60	34	99	0.716	0.6600	0.7403
46	Aeschnophlebia anisoptera	12.8	16.3	1047	92	251	57	0.227	< 0.0001	0.698	0.479	121	82	15	42	0.649	0.7368	0.5961
47	Gynacantha japonica	9.8	16.7	1869	329	322	153	0.475	$<\!0.0001$	0.697	0.448	86	83	28	125	0.655	0.8170	0.5089
48	Poly can thag melanic tera	10.3	16.3	1779	271	315	137	0.435	< 0.0001	0.679	0.452	88	06	31	106	0.616	0.7737	0.4944
49	Aeshna juncea juncea	2.3	14.1	2893	304	229	26	0.332	< 0.0001	0.840	0.341	100	53	×	68	0.734	0.8947	0.6536
50	Aeshna nigroflava	2.9	14.6	2920	403	268	127	0.474	<0.0001	0.791	0.373	62	62	16	111	0.709	0.8740	0.5603
51	Aeshna subarctica subarctica	1.9	7.1	986	12	20	5 L	0.250	0.731									
52	Aeshna mixta soneharai	5.5	13.9	2426	61	207	$^{24}$	0.116	0.717									
53	Anaciaeschna jaspidea	15.0	15.6	247	5	263	1	0.004	1.000									
54	$Anaciaeschna\ martini$	10.5	16.5	1778	223	315	119	0.378	< 0.0001	0.649	0.427	83	113	21	98	0.575	0.8235	0.4235
55	Anax parthenope julius	7.1	16.6	2168	773	342	286	0.836	< 0.0001	0.860	0.471	41	15	42	244	0.833	0.8531	0.7321
56	Anax nigrofasciatus nigrofasciatus	8.8	16.2	2025	505	331	223	0.674	< 0.0001	0.679	0.594	54	54	58	165	0.662	0.7399	0.5000
57 Gomphidae	Anisogomphus maacki	5.4	15.6	2924	217	307	73	0.238	< 0.0001	0.691	0.526	151	83	27	46	0.642	0.6301	0.6453
58	Stylurus oculatus	8.3	16.2	2538	20	334	7	0.021	0.2829									
59	Stylurus nagoyanus	8.4	15.8	2422	35	324	13	0.040	0.333									
60	Stylurus annulatus	13.0	16.2	1029	10	230	4	0.017	1.000									
61	Gomphus postocularis	3.5	15.6	3025	195	342	91	0.266	< 0.0001	0.674	0.545	167	84	32	59	0.661	0.6484	0.6653
62	Asiagomphus melaenops	9.7	16.4	1780	458	323	182	0.563	<0.0001	0.790	0.493	66	42	44	138	0.734	0.7582	0.7021

		isi.	Main ands of	four Lanan		sel	ected 3 d somar	61 es			Ā	erforma	nce of	lositic	: model	s		
		(396	1 grid	square	s)	D												
No family	species	1	2	3	4	5	9	7	8	6	10	11	12	13	14	15	16	17
63	$A  siagomphus \ pryeri$	12.0	16.3	1346	116	283	65	0.230	< 0.0001	0.707	0.499	126	92	18	47	0.611	0.7231	0.5780
64	Davidius nanus	7.6	15.7	2212	435	327	126	0.385	< 0.0001	0.848	0.430	141	60	13	113	0.777	0.8968	0.7015
65	Davidius fujiama	5.7	15.6	2851	206	333	57	0.171	< 0.0001	0.809	0.469	184	92	x	49	0.700	0.8596	0.6667
99	Davidius moiwanus moiwanus	2.6	13.3	2727	98	158	19	0.120	< 0.0001	0.848	0.536	114	25	5	14	0.810	0.7368	0.8201
67	Lanthus fujiacus	5.5	14.8	2524	284	276	68	0.246	< 0.0001	0.743	0.436	116	96	6	59	0.634	0.8676	0.5472
68	Trigomphus citimus tabei	11.5	15.8	1392	142	285	67	0.235	< 0.0001	0.794	0.438	142	$\overline{76}$	x	59	0.705	0.8806	0.6514
69	$Trigomphus \ melampus$	2.6	14.8	2951	264	284	06	0.317	< 0.0001	0.769	0.521	140	59	18	54	0.683	0.7500	0.7035
20	$Trigomphus \ interruptus$	12.1	15.9	1188	138	271	72	0.266	< 0.0001	0.743	0.514	127	72	17	55	0.672	0.7639	0.6382
71	$Trigomphus \ ogumai$	10.7	15.9	1685	122	306	65	0.212	< 0.0001	0.808	0.641	205	36	23	42	0.807	0.6462	0.8506
72	$Stylogomphus\ suzukii$	9.8	15.8	1767	276	311	101	0.325	< 0.0001	0.766	0.469	132	78	15	86	0.701	0.8515	0.6286
73	$Stylogomphus \ ryukyuanus$	14.7	17.8	543	6	92	2	0.022	1.000									
	ryukyuanus																	
74	Sinogomphus flavolimbatus	8.7	15.7	2196	145	320	48	0.150	$<\!0.0001$	0.835	0.462	184	88	9	42	0.706	0.8750	0.6765
75	Nihonogomphus viridis	9.1	15.7	2026	222	318	86	0.270	$<\!0.001$	0.788	0.559	166	66	24	62	0.717	0.7209	0.7155
26	Onychogomphus viridicostus	9.1	15.7	1997	268	318	108	0.340	< 0.0001	0.789	0.523	140	20	27	81	0.695	0.7500	0.6667
77	Sieboldius albardae	2.6	16.0	2610	554	357	199	0.557	< 0.0001	0.786	0.566	119	39	58	141	0.728	0.7085	0.7532
78	Ictinogomphus pertinax	12.6	17.1	1208	102	257	49	0.191	< 0.0001	0.791	0.414	131	17	2	42	0.673	0.8571	0.6298
- 20	$Sinictinogomphus\ clavatus$	8.5	16.1	2188	300	332	155	0.467	< 0.0001	0.711	0.437	91	86	24	131	0.669	0.8452	0.5141
80 Cordulegastridae	: Chlorogomphus brunneus brunneus	12.1	17.3	1489	32	276	10	0.036	1.000									
81	$Anotogaster \ sieboldii$	2.6	16.2	2483	938	361	299	0.828	< 0.0001	0.738	0.511	43	19	79	220	0.729	0.7358	0.6935
82 Corduliidae	Epophthalmia elegans elegans	5.8	16.2	2456	478	349	226	0.648	< 0.0001	0.693	0.468	64	59	49	177	0.691	0.7832	0.5203
83	Macromia daimoji	10.1	15.7	1844	58	300	23	0.077	< 0.0001	0.846	0.410	182	95	2	21	0.677	0.9130	0.6570
84	Macromia amphigena amphigena	2.6	16.2	2576	512	361	194	0.537	$<\!0.001$	0.787	0.531	117	50	50	144	0.723	0.7423	0.7006
85	Epitheca marginata	9.9	16.3	1871	227	321	113	0.352	< 0.0001	0.757	0.512	145	63	32	81	0.704	0.7168	0.6971
86	Epitheca bimaculata sibirica	2.6	12.2	2423	40	92	19	0.207	< 0.0001	0.855	0.552	64	6	5	14	0.848	0.7368	0.8767
87	Cordulia aenea amurensis	2.1	11.7	2216	65	71	21	0.296	< 0.0001	0.803	0.349	26	24	7	19	0.634	0.9048	0.5200
88	Somatochlora arctica	1.9	7.1	974	21	20	9	0.300	0.0469	0.815	0.351	12	7	2	4	0.800	0.6667	0.8571
89	$Somatochlora\ alpestris$	-1.1	0.7	10	°°	0	0	0.000										
90	Somatochlora japonica	1.6	7.4	1039	40	22	6	0.409	0.0716									
91	$Somatochlora\ graeseri$	0.7	9.4	1592	34	35	11	0.314	1.000									
92	$Somatochlora\ uchidai$	4.1	15.6	3013	460	344	168	0.488	< 0.0001	0.686	0.506	108	68	45	123	0.672	0.7321	0.6136
93	Somatochlora viridia en ea	3.6	15.9	3466	223	354	39	0.110	$<\!0.001$	0.774	0.534	226	89	11	28	0.718	0.7179	0.7175
94	$Somatochlora\ clavata$	4.9	16.4	3375	97	354	45	0.127	< 0.0001	0.687	0.529	206	103	16	29	0.664	0.6444	0.6667
95 Libellulidae	Lyriothemis pachygastra	8.5	16.6	2145	443	333	189	0.568	< 0.0001	0.631	0.524	86	58	73	116	0.607	0.6138	0.5972
96	Lyriothemis elegantissima	14.6	17.5	578	9	102	2	0.020	0.424									
97	Libellula quadrimaculata asahinai	2.6	17.0	3314	413	361	182	0.504	< 0.001	0.683	0.493	105	74	60	122	0.629	0.6703	0.5866

Appendix table. Continued.

Appendix table. Continued.

		101	Main .	four f Tanar	_	sel	lected 3	199 So:			Ϋ́	erform	mce of	lositic	models			
		(39)	61 grid	-square	ss)	19	mhe n											
No family	species	1	2	3	4	5	9	7	8	6	10	11	12	13	14	15	16	17
98	Libellula angelina	12.6	16.8	1373	120	279	48	0.172	< 0.0001	0.777	0.452	153	78	6	39	0.688	0.8125	0.6623
66	Orthetrum sabina sabina	11.0	17.8	1802	14	305	2	0.007	1.000									
100	Orthetrum poecilops miyajimaensis	; 14.3	14.3	1	1	361	0	0.000										
101	Orthetrum albistylum speciosum	5.2	17.8	3409	1135	353	340	0.963	< 0.0001	0.859	0.286	6	4	42	298	0.870	0.8765	0.6923
102	Orthetrum japonicum japonicum	5.9	16.3	2509	641	350	240	0.686	< 0.0001	0.740	0.549	82	28	85	155	0.677	0.6458	0.7455
103	Orthetrum triangulare melania	6.6	16.4	2340	724	346	270	0.780	< 0.0001	0.703	0.477	49	30	67	203	0.728	0.7519	0.6203
104	Nannophya pygmaea	6.4	16.3	2876	204	347	75	0.216	< 0.0001	0.667	0.445	121	151	14	61	0.524	0.8133	0.4449
105	$Deielia \ phaon$	8.9	16.4	2116	373	332	182	0.548	< 0.0001	0.812	0.498	111	39	43	139	0.753	0.7637	0.7400
106	Crocothemis servilia mariannae	8.9	16.5	1889	604	332	254	0.765	< 0.0001	0.722	0.434	45	33	51	203	0.747	0.7992	0.5769
107	Sympetrum pedemontanum elatum	2.6	15.6	3100	448	343	142	0.414	< 0.0001	0.700	0.456	110	91	32	110	0.641	0.7746	0.5473
108	$Sympetrum \ darwinianum$	7.9	16.3	2018	730	337	271	0.804	< 0.0001	0.659	0.445	34	32	20	201	0.697	0.7417	0.5152
109	Sympetrum frequens	2.6	15.9	2588	1059	359	316	0.880	< 0.0001	0.746	0.422	26	17	74	242	0.747	0.7658	0.6047
110	Sympetrum striolatum imitoides	4.8	16.6	3375	133	354	48	0.136	< 0.0001	0.748	0.439	197	109	11	37	0.661	0.7708	0.6438
111	Sympetrum eroticum eroticum	2.6	16.4	2565	829	361	282	0.781	< 0.0001	0.721	0.501	48	31	80	202	0.693	0.7163	0.6076
112	$Sympetrum \ kunckeli$	7.0	16.5	2598	315	344	148	0.430	< 0.0001	0.718	0.506	139	57	54	94	0.677	0.6351	0.7092
113	$Sympetrum\ parvulum$	6.7	16.0	2584	354	341	158	0.463	< 0.0001	0.667	0.479	116	67	63	95	0.619	0.6013	0.6339
114	Sympetrum flaveolum flaveolum	2.9	6.0	674	12	13	2	0.154	1.000									
115	$Sympetrum \ danae$	0.6	0.0	1440	49	31	10	0.323	1.000									
116	$Sympetrum \ risi$	5.6	16.4	2822	433	346	200	0.578	< 0.0001	0.704	0.552	110	36	82	118	0.659	0.5900	0.7534
117	$Sympetrum \ infuscatum$	2.6	16.0	2646	875	357	281	0.787	< 0.0001	0.791	0.446	52	24	67	214	0.745	0.7616	0.6842
118	Sympetrum baccha matutinum	5.3	16.5	3002	373	352	148	0.420	< 0.0001	0.642	0.519	126	78	59	89	0.611	0.6014	0.6176
119	$Sympetrum \ gracile$	12.2	15.9	1226	82	269	47	0.175	< 0.0001	0.731	0.493	137	85	12	35	0.639	0.7447	0.6171
120	$Sympetrum\ maculatum$	9.1	15.5	2158	23	302	12	0.040	< 0.0001	0.831	0.369	178	112	1	11	0.626	0.9167	0.6138
121	Sympetrum speciosum speciosum	7.2	16.4	2585	320	341	119	0.349	< 0.0001	0.724	0.519	147	75	37	82	0.672	0.6891	0.6622
122	$Sympetrum \ croceolum$	4.7	16.0	3195	218	352	108	0.307	< 0.0001	0.692	0.475	140	104	25	83	0.634	0.7685	0.5738
123	$Sympetrum \ uniforme$	9.5	16.0	2147	48	321	29	0.090	< 0.0001	0.764	0.531	206	86	10	19	0.701	0.6552	0.7055
124	Leucorrhinia dubia orientalis	0.3	7.5	1059	57	23	10	0.435	0.003	0.908	0.660	12	1	2	x	0.870	0.8000	0.9231
125	Leucorrhinia intermedia ijimai	3.5	5.9	588	6	13	4	0.308	1.000									
126	$Pseudothemis\ zonata$	9.4	16.3	1763	588	327	260	0.795	< 0.0001	0.807	0.604	56	11	66	161	0.664	0.6192	0.8358
127	$Rhyothemis\ fuliginosa$	10.0	16.5	1770	356	319	170	0.533	< 0.0001	0.778	0.543	106	43	52	118	0.702	0.6941	0.7114
128	Tramea virginia	10.4	17.4	1935	85	315	34	0.108	< 0.0001	0.835	0.569	227	54	6	25	0.800	0.7353	0.8078