



Original Articles

Breeding thresholds in opportunistic Odonata records

Michael A. Patten^{a,b,*}, Emily A. Hjalmarson^b, Brenda D. Smith-Patten^a, Jason T. Bried^c^a Oklahoma Biological Survey, University of Oklahoma, Norman, OK 73019, United States^b Department of Biology, University of Oklahoma, Norman, OK 73019, United States^c Department of Biological Sciences, Murray State University, Murray, KY 42071, United States

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ABSTRACT

Numerous interacting abiotic and biotic factors shape an organism's spatial distribution, and these factors vary spatially and temporally, such that habitat used for breeding may differ from habitat used at other times of the life cycle. We address this complex issue in the context of citizen science and opportunistic species occurrence records, a valuable data source for biogeography and conservation. We focus on the insect order Odonata, the dragonflies and damselflies, which as adults are popular in citizen science programs. Our goal was to devise a means to estimate with high confidence whether a site supports a breeding population if only opportunistic data are available. Our approach fitted logistic curves from occupancy models of observations of teneral (newly emerged adults that cannot yet disperse from a natal site) against counts of all adults, adult females only, and incidence of breeding behaviors (ovipositing, mate guarding, tandem pairs). Models included median body size and abundance class as covariates of detectability. We subjected logistic curves to a Bayesian two-segment piecewise regression to obtain best estimates of the threshold (with associated credible intervals as an estimate of uncertainty) to assess if a given predictor (e.g., adult count) or combination of predictors was associated with breeding occurrence. We found that no single threshold fit all odonates: thresholds of varying precision were identified for the suborders (dragonflies, damselflies) and for families and select genera in each suborder. Counts of females greatly reduced the required threshold, whereas breeding behavior data reduced the threshold in some cases. Our study shows it is possible to identify breeding occurrences in opportunistic adult Odonata records. It also highlights how citizen scientists should record not only a sound species list with rudimentary counts of adults but also note the sex and breeding behavior. The identification of breeding occurrences in extensive opportunistic data is pertinent to understanding species' distributions and habitat requirements along with their ecological sensitivity and value as bioindicators.

1. Introduction

A central question in ecology is what causes patterns of species' occurrences at particular locations. Typically, there are many interacting combinations of abiotic (e.g., the environment) and biotic (e.g., species interactions) factors that shape an organism's spatial distribution, and these factors vary greatly depending on aspects of a species' ecology, such as the organism's needs at that time (Moore and Gillingham, 2006). Having a relatively specialized breeding habitat is a well-known example of a need that drives a species to use potentially different environments than it would use at other times of its life cycle.

Species with complex life cycles, such as amphibious organisms, provide good study systems to explore how ontogenetic shifts between aquatic and terrestrial niches affect use of space. The insect order Odonata, the dragonflies and damselflies, offers such a study system to

use for answering these types of questions (Stoks and Cordoba-Aguilar, 2012). Moreover, it is well established that invertebrates are useful biological indicators of freshwater ecosystems (Cairns and Pratt, 1993; Rader et al., 2001; Hodkinson and Jackson, 2005; Bonada et al., 2006), and odonates are especially good choices as bioindicators (Oertli, 2008; Bried and Samways, 2015). Presence/absences, species abundance, and species diversity of odonates can hint at the health of the aquatic ecosystem in terms of water quality, habitat structure, and site connectivity (Tockner et al., 1999; Müller et al., 2003; Catling, 2005). Adult odonates also may be good taxonomic surrogates in large-scale biodiversity studies or water quality monitoring (Simaika and Samways, 2011; Rosset et al., 2013).

The life cycle of Odonata consists of discrete nymphal and adult stages that differ drastically in how much they depend on aquatic and wetland ecosystems (Corbet, 1999). Nymphs hatch from eggs laid in

* Corresponding author.

E-mail address: mpatten@ou.edu (M.A. Patten).

aquatic plant tissue or directly into water and are exclusively aquatic through 9–17 molts until metamorphosis and emergence to enter the adult stage, which begins after several months or years, depending on the species and geographical location (Corbet, 1980, 1999). Adults are terrestrial (and aerial), meaning their relationship with specific aquatic features is less fixed because often they disperse away from water to forage. Some even migrate or eventually reproduce at water bodies other than their natal site (Corbet, 1999; Stoks and Cordoba-Aguilar, 2012). Because most of their lives transpire as nymphs, it has been suggested that the nymphal stage is more affected by ecological change than is the adult stage (Bried et al., 2015); however, obvious mobility restriction of nymphs may render them less useful as indicators of landscape conditions beyond the breeding site (Tangen et al., 2003; Raebel et al., 2012; Meyer et al., 2015). Conversely, the adult stage is not considered to be a useful indicator of local conditions in cases where vagility is high (Raebel et al., 2010), and inferences on species–environment relationships depend strongly on whether species are locally natal (Patten et al., 2015; Bried et al., 2016).

Ecologists are therefore faced with a conundrum. Nymphs may tell us where odonates attempt to breed, but adults are far easier to detect. We need to bridge adult detection with breeding occurrence. Citizen science is a powerful means to gather extensive data (Bonney et al., 2009) and has supported a wealth of research on biogeography and conservation, including for odonates (e.g., White et al., 2015; Rapacciuolo et al., 2017; Bried and Siepielski, 2018). Citizen science data are lacking for larvae and exuviae, which are far more challenging to find and identify (Tennessee, 2019), yet there is a wealth of citizen science data for adults, which are more conspicuous and far easier to identify, especially at the species level. Citizen science datasets are inherently messy, but sample sizes are large and there are potentially many records of breeding occurrences. The challenge is to determine which records can be classified as such.

Bried et al. (2015) differentiated breeding occurrences by predicting exuviae presence from information typical of standardized observational surveys. Their criteria were based on repeated observations of adults and exuviae, whereas citizen science efforts generally lack repeat visits and exuviae observations. Here we aimed to identify breeding success criteria applicable to large datasets lacking standardized repeat visits or exuviae detections. We used the presence of newly emerged adults (teneral) as our indicator of breeding success, modeled in relation to abundance-based metrics and body size categories. To provide robust and general criteria, we included species in both Odonata suborders, Anisoptera (dragonflies) and Zygoptera (damselflies) and analyzed data at family and genus levels. Our goal was to determine how many instances of metrics of adult occurrence (e.g., abundance, tandem pairs) at a site are needed to conclude with high confidence that a site is occupied by breeding odonates and not just transient species or recent colonists that have yet to complete their life cycle. Our work extends that of Bried et al. (2015) through its applicability to citizen science data, its greater variety of taxa, and by incorporating combinations of adult information for better accuracy.

2. Methods

2.1. Data set

We used a dataset of > 20,000 geocoded adult odonate records obtained from 2013 to 2017 across Oklahoma, USA. Data primarily included those obtained during Patten and Smith-Patten's statewide opportunistic surveys; these data are part of the Oklahoma Odonata Project (OOP) database housed with the Oklahoma Natural Heritage Inventory at the Oklahoma Biological Survey. We limited data to five recent years because surveys during that time were particularly focused on obtaining details such as sex, age, and breeding behavior (e.g., ovipositing, tandem pairs, mate guarding). A large number of other records came from citizen scientists who submitted data directly to OOP

or to two online portals that accept public submission of records accompanied by photographs: Odonata Central (<https://www.odonatacentral.org/>) and iNaturalist (<https://www.inaturalist.org/>). Each submission to Odonata Central is vetted by a designated regional expert (in this case Patten and Smith-Patten). The vetting process for iNaturalist is laxer: if at least two members of the iNaturalist community agrees on an identification the record is classified as “research grade,” although such a classification does not necessarily equate to a correct identification. As such, Hjalmarson (with some input from Patten) examined each “research grade” record and included only those records positively identified to species, along with any ancillary data (as noted above). When necessary, we removed duplicate data or data entered as different record types but not the result of sampling a species at a site on the same date (e.g., an entry for a specimen and an entry for a photograph that represented the same encounter). We excluded records that lacked specific coordinates (e.g., those with only county centroids) or specific dates. All told, ~15% of records were excluded.

A key assumption of occupancy modeling (see below) is the independence of sampling sites. Closely spaced sites, which are numerous in our data set, violate this assumption: detection of a species at one site influence the probability of detection at a nearby site. We lessened effects of spatial autocorrelation by defining a site as a 1 km × 1 km grid cell, so chosen because it is a reasonable estimate of maximum dispersal distance of adult odonates (Conrad et al., 1999; Angelibert and Gianni, 2003). We created the 1 km × 1 km grid in ArcMap and using Python overlaid the grid onto a layer of the original coordinates of each odonate record. Records were “collapsed” such that the centroid of a grid cell represented all points that fell within that cell, with maxima of the set of records (e.g., maximum adult count or number of pairs) retained. This process reduced to 1105 the number of independent sites (Table 1).

Multiple seasons typically are sampled when the objective focuses on dynamics (colonization and extirpation) of the occupancy state over time. Such questions were not central to our study, and given the messiness of the dataset, we developed single-season occupancy models. This choice required addressing the assumption of a closed system, meaning that species found at a site once are assumed to be

Table 1
Taxonomic information and sample size for each division.

Division	English Name	Taxon	Species	Body Size ¹	Sites
suborder	damselflies	Zygoptera	57	1	1105
suborder	dragonflies	Anisoptera	107	3	1105
family	broad-winged damselflies	Calopterygidae	3	2	1103
family	spreadwings	Lestidae	9	2	1105
family	pond damselflies	Coenagrionidae	45	1	1105
family	petaltails	Petaluridae	1	3	845
family	darners	Aeshnidae	12	3	1105
family	clubtails	Gomphidae	21	3	1101
family	spiketails	Cordulegastridae	2	3	860
family	cruisers	Macromiidae	5	3	1100
family	emeralds	Corduliidae	12	3	1086
family	skimmers	Libellulidae	54	3	1105
genus	bluets	<i>Enallagma</i>	15	1	1103
genus	forktails	<i>Ischnura</i>	10	1	1103
genus	dancers	<i>Argia</i>	14	1	1101
genus	common clubtails	<i>Phanogomphus</i>	4	2	1010
genus	spinylegs	<i>Dromogomphus</i>	2	3	1015
genus	baskettails	<i>Epiheca</i>	6	3	1045
genus	king skimmers	<i>Libellula</i>	12	3	1099
genus	pondhawks	<i>Erythemis</i>	4	2	1103
genus	dashers	<i>Pachydiplax</i>	1	1	1099
genus	meadowhawks	<i>Sympetrum</i>	7	1	1103

¹ Mode of body size category, where 1 is < 41 mm, 2 is 41–51 mm, and 3 is > 51 mm.

Table 2
Predictors for models of teneral occupancy; body size class and abundance class were used as covariates of detection probability.

Group	Description (per site)
Adults (overall)	Maximum number of adults Total number of adults Mean number of adults recorded at that site Mode of abundance category ¹
Adults (by sex)	Maximum number of males Maximum number of females Mean number of males Mean number of females
Breeding	Total number of pairs (tandem with or without copulatory wheel) Maximum number of pairs (tandem with or without copulatory wheel) Total number of females ovipositing (laying) eggs (with or without male presence) Maximum number of females ovipositing (laying) eggs (with or without male presence) Total number of males “mate guarding” females (with or without females ovipositing) Maximum number of males “mate guarding” females (with or without females ovipositing)
Size	Maximum body size category ²

¹ There were four abundance categories (1–5, 6–20, 21–100, > 100 individuals), following [Bried et al \(2015\)](#).

² See text for explanation of body size assignments.

there for the duration of the sampling period. Variation in adult flight season may violate this assumption, so we truncated data by the earliest and latest flight dates for each species in Oklahoma (Smith-Patten and Patten, unpubl. data).

2.2. Analyses

We created a site × year matrix for each taxonomic group ([Table 1](#)). Each site (grid cell) contained presence/absence data for each group from 2013 to 2017. Most survey data were not the result of strict sampling regimes; we entered “N/A” if a site was not visited that year or for a visit that fell outside a species’ flight season (see above). Our response variable was teneral presence, and we used a suite of predictors of occupancy ([Table 2](#)), with non-categorical data generally log-transformed to lessen skew from the high frequency of low values (i.e., many 1s) or the few instances of high values (> 1000). For each species we incorporated median body length, from minimum and maximum values for both sexes ([Needham et al. 2014](#)), as a covariate for detection probability. We divided species into three size classes, small (< 41 mm; e.g., *Perithemis tenera*), medium (41–51 mm, e.g., *Erythemis simplicicollis*), and large (> 51 mm, e.g., *Brachymesia gravida*). We likewise included abundance class ([Table 1](#)) as a covariate for detectability.

All analyses were run in or via R. Our first step was to build occupancy models (see [Appendix A](#)), which we accomplished with package *unmarked* ([Fiske and Chandler 2011](#)), for any taxonomic group with $n > 5$ teneral presences ([Table 3](#)). We estimated occupancy first with no predictors, then with predictors added, singly and combined. We used AIC-based model selection to determine the “best” model, parameters of which we used to build the logistic curve of occupancy probability. Occupancy models demand more than a single survey of a site, else detection probability cannot be estimated. Repeated surveys are considered valid provided they are of a population considered closed and stationary (e.g., it is not strongly seasonal) during the period in question. Generally surveys of a given site are conducted weekly or monthly within a season, but because our sites were grid cells that we often enough sampled annually, we treated year as the repeat, under the logic that a population not rapidly expanding or contracting its

range was effectively closed and stationary at a given site from year to year. As a consequence, we could include a site that was surveyed in, say, 2013, 2014, and 2016 but not a site surveyed three times in 2013 alone.

It was these logistic curves that we used to determine thresholds, by which we mean the minimum number of, say, adults that would need to be detected to conclude with high confidence that a taxon breeds at the site. Our approach was a piecewise regression model ([Toms and Lesperance, 2003](#)), which we implemented in a Bayesian framework so we could obtain an estimate of uncertainty rather than solely a point estimate. We wrote code for a two-segment piecewise regression in JAGS (see [Appendix A](#)) that we ran (via R with package *rjags*; [Plummer 2016](#)) with flat priors (i.e., no prior assumptions about threshold values), 3 Markov chains, a burn in of 30,000, and posterior distributions built from 50,000 iterations. To facilitate the Monte Carlo Markov chain process, which is used to estimate parameters (in this case the threshold and uncertainty around it), we seeded the sampler with initial values for the threshold from a frequentist piecewise regression run in package *segmented* ([Muggeo 2008](#)). We interpreted results only if chains mixed properly (via standard diagnostic plots; [Appendix A](#)); for these we calculated a threshold as the mean of the posterior distribution and uncertainty as the 95% highest posterior density interval, so named because anywhere inside the interval has a higher density than anywhere outside the interval.

3. Results

In general, thresholds for Zygoptera were lower—meaning fewer individuals or instances need to be tallied to conclude with high confidence that breeding takes place at the site—than those for Anisoptera ([Fig. 1A](#)). For Zygoptera, counts of females plus breeding behaviors produced the best (lowest AIC) models, whereas for Anisoptera, counts of adults plus counts of total females produced the best models. Estimated thresholds differed markedly among families ([Fig. 1B](#)), although neither *Petaluridae* nor *Macromiidae* had sufficient sample size for teneral presence ([Table 3](#)). Best criteria to estimate thresholds also varied ([Fig. 1B](#)). For example, results for *Coenagrionidae* varied because the three best models yielded different (albeit broadly similar) thresholds depending on predictors included. By contrast, *Cordulegastriidae* and *Corduliidae* had only one model that yielded a good estimate. The lowest threshold for *Gomphidae* included a combination of total adults plus females, thresholds for *Lestidae* were similar for both females alone and total adults, and *Libellulidae* had a large uncertainty but with female count yielded the best model.

Variation also was the rule among genera ([Fig. 1C](#)) with sufficient sample size ([Table 3](#)). For example, the “best” models for *Enallagma* and *Ischnura* featured a combination of females + breeding behaviors, with a size covariate on detectability, whereas for *Argia*, both the threshold and uncertainty decreased with addition of specific information moving from total adults to females only to females + breeding behavior. Among Anisoptera species, adult count alone yielded the “best” models except for *Libellula*, for which female count did ([Fig. 1C](#)).

Neither abundance ([Fig. 2](#)) nor body size was associated with threshold level; i.e., even if commoner or larger species are detected more often, it did not translate to lower threshold estimates. In general, though, counts specifically of females rather than of just unsexed adults greatly lowered thresholds ([Fig. 3](#)), with practical implications for using abundance-based criteria to infer breeding success.

4. Discussion

A key finding of our study is phylogenetic signal (as represented by taxonomy) in threshold estimates: the threshold varied a good deal among suborders, families, and genera ([Fig. 1A–1C](#)), such that there was no single threshold (say, number of adults) across Odonata that could be used to conclude that a particular site supported a breeding population. The lack of a single threshold for all Odonata could be

Table 3
Summary statistics and predictors for each taxonomic division.

Taxon	Proportion of sites		Teneral		Adults	♂	♀	Breeding behaviors ⁴
	overall ¹	w/sex ²	ψ^3	<i>n</i>				
Zygoptera	0.72	0.66	0.58	174	103,107	47,917	19,683	9112
Anisoptera	0.88	0.78	0.567	234	76,981	39,375	11,979	2440
Calopterygidae	0.25	0.22	0.687	5	7093	2437	994	39
Lestidae	0.20	0.18	0.909	31	1859	1260	556	166
Coenagrionidae	0.68	0.62	0.612	153	94,150	44,219	18,132	8907
Petaluridae	0.01	0.01	0.155	0	37	32	4	0
Aeshnidae	0.35	0.28	0.455	9	4469	1853	568	232
Gomphidae	0.45	0.40	0.445	96	3609	2408	761	136
Cordulegastridae	0.03	0.02	0.714	5	52	35	8	1
Macromiidae	0.13	0.10	0.433	3	435	235	81	26
Corduliidae	0.29	0.23	0.945	29	2682	869	352	63
Libellulidae	0.74	0.66	0.475	140	65,696	33,942	10,205	1982
<i>Enallagma</i>	0.46	0.42	0.482	92	49,380	21,370	7438	6033
<i>Ischnura</i>	0.40	0.37	0.395	40	19,579	8100	5534	507
<i>Argia</i>	0.51	0.47	0.202	57	24,066	13,862	4931	2245
<i>Phanogomphus</i>	0.19	0.17	0.155	52	781	541	280	26
<i>Dromogomphus</i>	0.18	0.15		22	693	445	147	30
<i>Epitheca</i>	0.27	0.21	0.005	22	2140	706	190	47
<i>Libellula</i>	0.46	0.42	0.223	44	13,072	7206	2107	260
<i>Erythemis</i>	0.36	0.31		22	10,631	3553	2329	146
<i>Sympetrum</i>	0.23	0.20	0.277	45	4085	1767	776	429
<i>Pachydiplax</i>	0.33	0.28	0.988	28	14,444	7341	1229	91

¹ The proportion of sites for which that taxon, at any life stage, was observed at least once out of all possible visits during which a species could be seen.

² Excluding sites that did not have sex-level information (e.g., individuals assigned as “unsexed”). Of necessity, then, models that do not include sex have *n* somewhat larger than models that do include sex.

³ Occupancy probability without predictors included; models failed to converge for *Dromogomphus* and *Erythemis*.

⁴ Sum of records that indicate presence of tandem pairs, ovipositing, or mate guarding.

viewed as drawback to our study. It would have been convenient if data for any odonate, regardless of taxonomic group, could be assessed identically, but such a finding would have been a shock given how widely ecologies and life histories vary across the Odonata. Instead, our work underscores the importance to consider taxonomy at a finer scale when using citizen science data. This finding extends work of Bried et al. (2015), which apart from *Anax junius* (Aeshnidae) included only species in Libellulidae. If we wish to determine residency with survey data, field researchers and citizen scientists would do best to adopt different thresholds for different taxonomic groups. For those groups with high uncertainty of estimated threshold, a conservative approach to determine residency would be to set the threshold as the upper bound of the credible interval rather than the mean of the posterior distribution. Moreover, a broader taxonomic level—e.g., order rather than genus—could be used as long as it was recognized that uncertainty would be higher.

Predictors that produced the “best” models likewise varied across taxonomic division, even if adult count was a common thread. A specific count of females frequently both produced a better model and reduced the threshold, meaning fewer individuals needed to be counted to conclude with high confidence that a site supported breeding of that taxon. Treating the thresholds as instances is a good way to interpret results for predictor combinations, which Bried et al. (2015) could not evaluate. For example, roughly, a threshold of 20 instances of total adults + breeding could be read to mean that any combination of these instances could satisfy the criterion, from 1 adult + 19 breeding instances to its inverse or anything in between. Inclusion of breeding behaviors (usually tandem pairs + ovipositing) also tended to yield better models. Either result is intuitive: female presence is necessary for successful breeding, and observation of breeding behavior implies reproductive effort even if, ultimately, breeding success is zero (i.e., no tenerals).

Our threshold estimates were reasonable given the biology of the taxa. For instance, the threshold for *Enallagma* of ~17 instances of females + breeding behaviors is exceeded frequently because various

species in the genus gather at high densities where behaviors can be observed and sex ratio judged. Even among families such as Corduliidae whose species can seem scarce, a threshold of ~16 is possible given the tendency for some species in some genera, such as *Epitheca* (baskettails) and *Somatochlora* (emeralds), to form feeding swarms in the spring and summer, swarms that ostensibly form within the cruising radius of breeding sites (i.e., within the same 1 km × 1 km cell). Importantly, because adult abundance was not associated with threshold level (Fig. 2), we have no reason to think a species rarity affects our ability to determine breeding sites. Likewise, body size was not correlated with threshold level, even though we might have expected a correlation given both the negative relationship between organism body size and abundance, especially for large predatory species, and the power law of fewer species toward the large end of the body size continuum (Kozłowski and Gawelczyk, 2002; Woodward et al., 2005). We detected no obvious pattern of body size vs. threshold level among taxa, either for total adults or the thresholds based on females, breeding, or a combination of both (lowest).

Most threshold models were improved (decreased) by adding females and female-related characteristics such as breeding behaviors (Fig. 3). Hence, surveys during which males and females are differentiated would be more informative than general species records if the goal is to determine breeding sites. Female odonates are generally more challenging to identify than males, but our results suggest that acquiring the skill is worth the time and effort. Surveys that aim to detect females ought to target different parts of the wetland landscape. In Odonata, males tend to be found closer to the water feature, where they often patrol for females or defend territories, whereas females tend to congregate in adjacent vegetation away from the water bodies (Bried and Ervin, 2006), where they can avoid harassment by eager males. Habitats where females (and often immature males) tend to occur more frequently differ in structure (e.g., more shaded), are used differently (e.g., foraging rather than breeding), and often are not as well surveyed as water features (De Marco, 1998). In our data set, males were observed 2.7 × more often than females, a skew that says nothing about

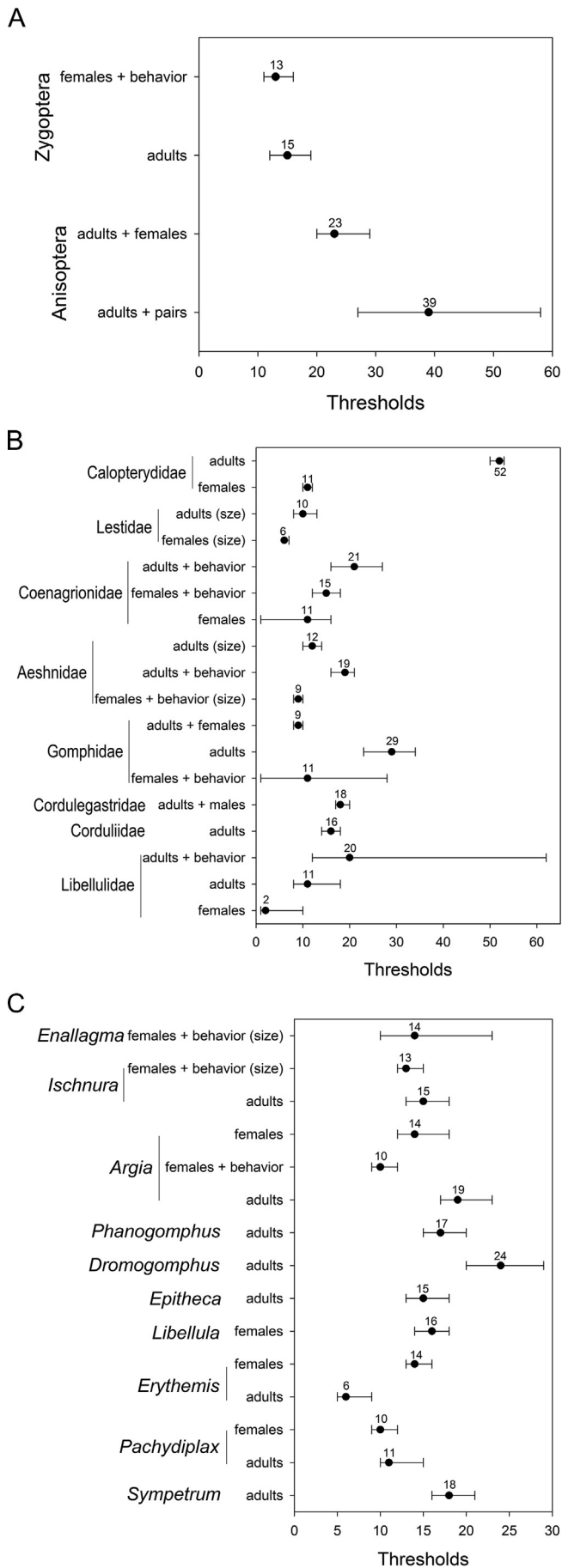


Fig. 1. Threshold values (means of the Bayesian posterior distribution), with associated highest density credible intervals, that need to be achieved to conclude with high confidence that an odonate A) suborder, B) family, of C) genus breeds at a site. Thresholds are interpreted as counts when there is a single factor (e.g. “adults”) or additive instances when factors are combined (e.g., “females + behavior” can be read as the sum of individual females detected plus individual breeding behaviors detected).

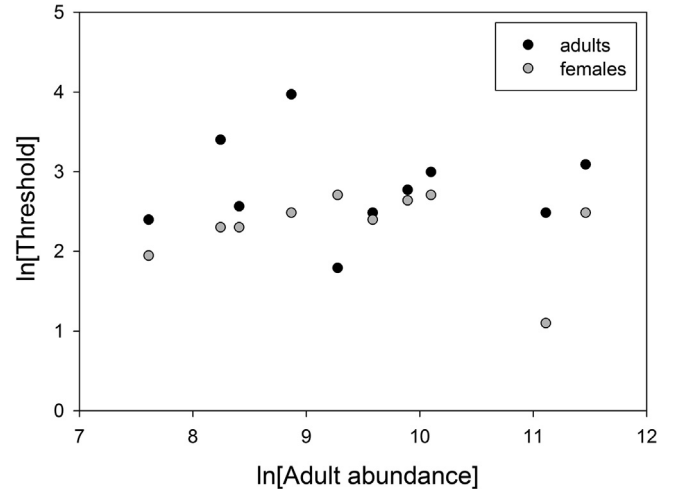


Fig. 2. Scatter plot of adult abundance vs. threshold for counts of all adults or of females only.

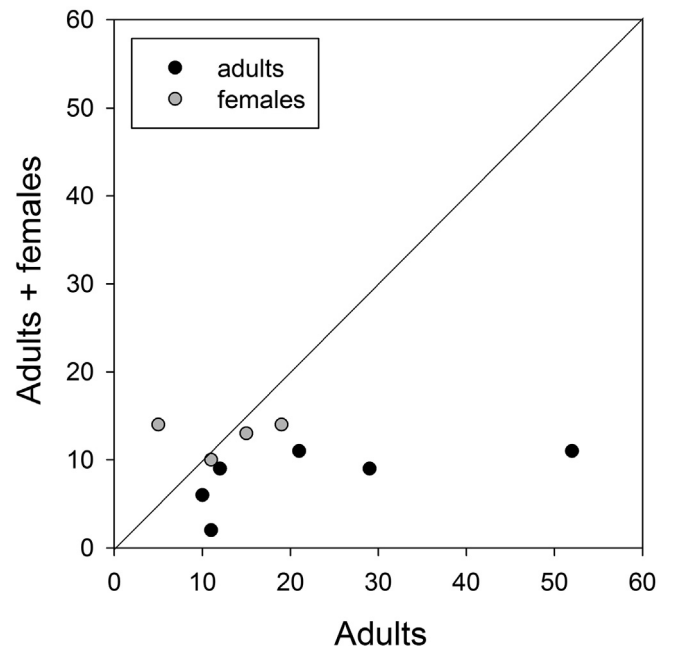


Fig. 3. Comparison of thresholds for counts of adults vs. counts of adults + females. The line is a 1:1 reference if thresholds for both data were equal. Note that most thresholds fall below the reference line, meaning that additional information on female abundance greatly reduces the count needed (i.e., the threshold) to conclude with high confidence that breeders occupy a site. In other words, counts of adults alone yield thresholds that range from ~10 to > 50 individuals, whereas counts that include specific data on females range from 10 to 15 individuals, a greatly lower overall threshold that needs to be achieved to conclude breeders occupy a site.

the operational sex ratio but everything about detectability and survey bias. We recommend that vegetation and fields near water features, whether lentic or lotic, are surveyed more regularly.

Sample size and observer effort likely affected estimates for some groups more than others. There were several differences between the proportion of records that contained sex-level information across taxa. For example, despite relative ease of distinguishing male and female species in Libellulidae, only 67% had sex data, likely because observers are prone to record, for common species—and many skimmers are abundant and ubiquitous—say, “500 *Libellula luctuosa*” with no effort to estimate counts of males and females. By contrast, less common species such as those in Lestidae, had sex data for 98% of records, likely a result of their relative infrequency compared to other Zygoptera and their “percher” behavior (Corbet, 1980), lending them to careful study.

Odonata have charismatic appeal, are relatively easy to capture or photograph, and have several user-friendly databases in which records can be submitted, so there is great potential to maximize the use of citizen-science efforts (such as Odonata Central or the Migratory Dragonfly Partnership, <http://migratorydragonflypartnership.org>) to establish breeding success from opportunistic adult records. The infrastructure is in place, so we feel the next step is to increase awareness among citizen scientists of data needs. Even if only a percentage could be persuaded to focus on a wider array of species, count individuals, note breeding behavior, and hunt specifically for females (and thus acquire the requisite skill to identify them), then such efforts will aid our ability to monitor freshwater ecosystems in many parts of the world.

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Declaration of Competing Interest

We have no competing interest to declare.

Appendix A. Supplementary data

Supplementary data (Analytical pathway, including JAGS code, for statistics performed to determine thresholds) to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.105460>.

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