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Using distance sampling to quantify Odonata density in tropical rainforests

Steffen Oppel

Wildlife Conservation Society, PO Box 277, Goroka, EHP, Papua New Guinea.
<steffen.oppel@gmail.com>
Present address: Department of Biology and Wildlife, 211 Irving 1, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

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Abstract

Quantitative data are essential for many aspects of ecological research. Several methods exist to quantify odonate abundance, but complications may arise when abundances in different habitats need to be compared. In this study, I explored a technique that can overcome the variable detectability of odonates in habitats with different visibility. Distance sampling is briefly introduced and the main assumptions are listed. I conducted line transect surveys using distance sampling protocol over several weeks in a rainforest locality in Papua New Guinea to assess the usefulness of distance sampling. The results suggested that estimates of encounter rate and density of odonates are substantially higher when distance sampling is employed. Density in habitats with poor visibility, like the forest interior, is severely underestimated by traditional sampling methods, and this can lead to a misclassification of habitats. Distance sampling is a very useful technique for quantitative odonate sampling, but the sampling effort required for precise estimates is very high. For the rainforest locality in this study at least 15 months of intensive sampling would be required. Further limitations of distance sampling are discussed.

Introduction

Quantifying the abundance of organisms is one of the major prerequisites for ecological studies. For studies both at the species and at the community level information about the size of populations is essential. When comparing the communities of different areas, for example when assessing changes in a community following human disturbance, diversity indices are powerful indicators (Hill et al. 1995; Heydon & Bulloh 1997; Willott et al. 2000; Cleary et al. 2005). Most diversity indices used to measure the composition and structure of ecological communities require some assessment of the abundance of the community members (Magurran 2004).

Line transect surveys are a useful method for quantitative sampling of flying insects (Pollard et al. 1975; Pollard 1977; Walpole & Sheldon 1999), and several studies of odonates have employed transect counts to assess the abundance of adult odonates (Samways 1989; Samways & Steytler 1996; de Marmels 1998; Stewart & Samways 1998; Dijkstra & Lempert 2003). Most of these studies focus on odonate assemblages that occur at a distinct water source. In tropical rainforests, however, a large proportion of species might occur away from permanent water sources (Oppel 2005b). In order to calculate a diversity index for a rainforest odonate community, several different habitats need to be sampled. The detection probability of odonates depends on the density of the habitat. The variable detectability between different habitats is a problem that can induce severe bias and undermine ecological inferences (Williams et al. 2002). Studies that attempt to quantify the diversity of an odonate assemblage in a given area featuring different habitats therefore require a method that takes into account the different detectability of odonate individuals across habitats.

Distance sampling methods extend the classic line transect survey methods without assuming that all objects are detected, or that transect width is constant (Burnham & Anderson 1984; Burnham et al. 1985). The basis of distance sampling methods is to measure the perpendicular distance of objects to the transect line, and to estimate their density by modelling a detection function (Buckland et al. 1993; Barry & Welsh 2001). This detection function calculates the probability of detecting an object at a given perpendicular distance from the transect line. The detection function can be calculated for every habitat or species, and accounts for all the environmental or experimental variables that could influence the number of objects detected. Variations in visibility between species, sites, or over years are therefore controlled by this method and no longer invalidate comparisons.

Several critical assumptions have to be met to ensure that distance sampling methods provide unbiased estimates of density (Buckland et al. 1993). First, the method assumes that all objects directly on the transect line are detected with certainty. Second, objects have to be recorded at their initial location before they move in response to the approaching observer. Third, the distances to the objects have to be measured with accuracy. Fourth, transect lines should be placed randomly with respect to the distribution of objects and should not run perpendicular to a gradient. Ideally, the distribution of objects within sampling units should approach uniformity (Welsh 2002), and populations should remain closed throughout the study period (Williams et al. 2002).

Distance sampling has been used with great success in a large number of ecological studies including butterflies (Buckland et al. 1993; Brown & Boyce 1998), but I am unaware of any odonatological studies using distance sampling. The main goal of this study was therefore to (1) evaluate whether the assumptions of distance sampling theory can be met when sampling odonates in rainforest habitats; (2) calculate the effort required to obtain accurate density estimates for odonates in a tropical rainforest habitat; and (3) discuss the benefits and limitations of distance sampling for odonate surveys.

Methods

Study area

The study was carried out in a natural lower montane rainforest at the Crater Mountain Biological Research Station (CMBRS) in Papua New Guinea (6°43'S, 145°05'E). A detailed description of the study site is presented elsewhere (Oppel 2005a). Briefly, the study site was situated in pristine rainforest with aseasonal climate and 6,500 mm of rainfall per year (Wright et al. 1997), and covered an area of ca 2.5 km^2 ranging from 850 m to 1,350 m a.s.l. Several different odonate assemblages have been identified at the study site, inhabiting distinct habitats such as permanent or temporary streams, rivers, or the forest interior (Oppel 2005b). For the purpose of this study I defined four broad habitat categories, namely (1) the forest interior, (2) small streams less than 1.5 m wide, (3) small creeks and rivers up to 8 m wide, and (4) big open rivers wider than 8 m.

Line transect sampling

I conducted transect surveys between March and June 2004. All surveys were carried out between 11:00 and 14:00 h solar time during calm and sunny weather, in order to ensure that odonates were active and the probability of discovery on the transect line was 1. I defined transects to have a roof of 2.5 m, since it was virtually impossible to discover odonates above 2.5 m in dense rainforests. Odonates observed above this height were excluded from analysis.

Transects were placed in a stratified random pattern across the study area. The number of transects was stratified among the four habitat types in approximate proportion of each habitat type's coverage of the total area (Williams et al. 2002). Classic odonate transect surveys usually follow the banks of rivers and ponds (Steytler & Samways 1995; Samways & Steytler 1996; Samways 2003). This technique, however, violates one of the assumptions of distance sampling theory, since such transects run perpendicular to a density gradient (the density of odonates along a river bank is different from the density in the river or in the forest next to the river). In order to overcome this problem I placed transects differently for every water source.

For large rivers I chose transects at least 50 m in length that started near a bend in the river and thus traversed the river bed and its banks at least twice while running in a straight line. For smaller rivers and creeks, where the above mentioned method was not feasible, I ran transects perpendicular to the water course, which limited the transect length to a maximum of 10 m. The smallest streams were sampled in a similar fashion as the big rivers, namely by following a straight line and traversing the meandering water course multiple times along the length of one transect. Since the gradient of these small streams was within the range covered by one distance class (see below) a negative effect on the sample distribution was unlikely.

Transects were conducted by one observer. I attached a small rope at a firm object at the start point of each transect and 2 m further along the transect, and pulled the rope behind me to ensure that transects were straight. Every transect was walked very slowly at a pace of 2 m min^{-1} to enable scanning the transect line and

Table 1. Results of odonate line-transect sampling at CMBRS, Papua New Guinea, in 2004. — Length required was calculated based on a formula given in Buckland et al. (1993) for precise estimation of object density. Effort required was calculated from the required length and a sampling speed of 2 m min^{-1}.

Habitat	Length surveyed [m]	Individuals encountered	Encounter rate [Ind. km^{-1}]	Length required [km]	Effort required [h]
Forest (n = 39)	770	14	18.63	66.0	550
Stream (n = 16)	252	30	120.63	10.1	84
Creek (n = 16)	320	52	187.50	7.4	62
River (n = 8)	325	16	47.92	20.6	172
Totals	1,667	112	76.46	104.1	868

the immediate vicinity for the presence of odonates. I used a butterfly net mounted on a 0.5 m handle to flush resting odonates on and close to the transect line. For every odonate I memorized the spot of first discovery or position before it was disturbed by the observer (e.g. stone, leaf, branch). I then measured the perpendicular distance to the transect line in six distance categories: 0-25 cm, 26-75 cm, 76-150 cm, 150-250 cm, 251-400 cm, and > 400 cm. I used markings on my outstretched arm and the net handle to indicate distance categories, and conducted several training runs to ensure accurate estimation of distance categories beyond net-length (categories 4-6).

For the purpose of this study identification of odonates was not essential. Names of all species present in the study area and respective abundances have been presented elsewhere (Oppel 2005a, 2005b). Some anisopterans could not be captured during transect surveys and had to be identified on the wing. Most zygopterans were captured and preserved as specimens. If an odonate was too far off the transect line to be readily captured, I marked the spot where I left the transect with a small wooden stick and attached the transect rope to the stick. I then left the transect line to capture the specimen and returned to the exact spot where I had left the transect line to resume the transect survey from there.

Analysis

I calculated the standard encounter rate for each transect as the number of observed individuals divided by the transect length. Then I calculated the average encounter rate per habitat as the mean encounter rate of all transects run through this habitat type. For an estimation of sampling effort I calculated the transect length that would be required for accurate estimation of odonate density at a precision level of 5% (Buckland et al. 1993). This required transect length, $L_{required}$, was calculated for every habitat type as

$$L_{required} = b/cv^2 * \text{(number encounters/total transect length)},$$

with the coefficient of variation cv = 0.05 as a measure of precision, and b being a dispersion parameter that was set equal to 3 in this study (Eberhardt 1978; Burnham et al. 1980; Buckland et al. 1993).

Using my survey speed of 2 m min^{-1} I then derived the time effort required for a survey permitting an accurate estimation of odonate density.

I then analysed the existing transect data with the program DISTANCE for estimates of odonate densities in each habitat type (Laake et al. 1993). The program calculates the effective strip width, ESW, defined as the width of the transect where all individuals are discovered and on which density calculation is based, as well as the encounter rate, and the density of encountered objects. Due to the low sample size of most species, I pooled the sightings of all species and calculated a detection function for all species combined. Pooling of several species does not violate assumptions of distance sampling theory, and has been successfully employed in other studies (Heydon & Bulloh 1997).

Results

I sampled odonates along 79 transects with a total length of 1,667 m, and encountered 112 individuals of 25 species (Table 1).

Actual encounter rates along the transect surveys differed widely between habitat types, and the effort required for accurate density estimation was therefore significantly different between the habitats (Table 1). A survey aiming at an accurate estimation of odonate density in the rainforest interior would require 550 hours of transect sampling, whereas 84 hours and 62 hours would be sufficient for creeks and streams, respectively (Table 1).

Estimates of encounter rate using the program DISTANCE differed strongly from the actual encounter rates calculated above. In all habitats an encounter rate of > 100 individuals km^{-1} was predicted, and rivers had a lower encounter rate than the forest interior (Table 2). The encounter rate estimated for the forest interior was seven times as high as the encounter rate calculated with the standard technique.

The effective strip width was almost twice as high in open rivers than in the forest interior, and creeks and streams had only slightly reduced ESW compared to rivers (Table 2). The standard error of these estimates was highest in rivers and streams due to the comparatively small sample size.

Density estimates yielded substantial differences of odonate density between habitat types. Creeks had the highest density of odonates, followed by the rainforest interior (Table 2). Large open rivers had the lowest odonate density in the study area.

Discussion

Distance sampling is a useful technique to calculate and compare the density of odonates in different habitats. The application of distance sampling in this study demonstrates that densities and encounter rates calculated from standard transect sampling can be highly misleading. The estimates of encounter rate derived from distance sampling were much higher than actually recorded encounter rates that did not account for habitat density and incomplete detection. In the forest interior, the estimated encounter rate was seven times as high as calculated by the standard method. This indicates that classic transect sampling underestimates encounter

Table 2. Distance sampling estimates of encounter rate, effective strip width (ESW), and density of odonates at CMBRS, Papua New Guinea, in 2004 — estimates are given ± standard error.

Habitat	Encounter rate [Ind. km^{-1}]	ESW [cm]	Density [Ind. ha^{-1}]
Forest (n = 39)	127.29 ± 15.24	87.29 ± 9.32	729.16 ± 116.98
Stream (n = 16)	172.55 ± 13.28	157.17 ± 32.16	548.94 ± 120.00
Creek (n = 16)	275.86 ± 71.22	156.73 ± 19.56	880.04 ± 252.35
River (n = 8)	107.14 ± 25.82	165.97 ± 31.97	322.78 ± 99.49

rates and densities especially in dense habitats with reduced visibility. This in turn can lead to a different classification of habitats, as is shown by a comparison between river and forest habitat in this study. Classic sampling would suggest that rivers have an encounter rate more than twice as high as in forest, but distance sampling yields an odonate density for forests that is more than twice as high as in rivers. Studies from Africa suggest that open sunny rivers have a much richer odonate fauna than shadier stream assemblages or forests (Stewart & Samways 1998; Clausnitzer 2003). By contrast, this study supports an earlier stated theory (Oppel 2005b) that big rivers in montane rainforests in PNG may be depauperate of odonates. Furthermore, the density estimates indicate that the rainforest interior may host much more odonates than certain water sources, and therefore needs to be considered in diversity and community calculations (Oppel 2006).

The critical assumptions required for distance sampling could all be met in this study. Even though there is no way of knowing whether assumption one (complete detection on the transect line) holds, visual inspection of frequency distributions indicated a shape close to the required 'shoulder' outlined by Buckland et al. (1993). Meeting the uniformity assumption mentioned by Welsh (2002) is, however, problematic, especially when no information exists about the distribution of odonates within or among certain habitats. It remains to be shown whether distance sampling is a robust technique that can overcome heterogenous distribution of objects within sampling units (Barry & Welsh 2001; Welsh 2002). Violation of a key assumption of distance sampling would lead to high bias, potentially overestimating odonate densities in the habitats under study and invalidating the comparison with the classic transect method. I do not have any evidence of violation of key assumptions in this study, and therefore consider the comparison valid.

However, since the sampling effort was insufficient for precise estimates of density and encounter rates, the absolute results of this study should be interpreted with caution. The sampling effort required for accurate estimation of odonate densities in tropical rainforests is very high, and might limit the usefulness of distance sampling. I calculated a required effort of 868 hours to obtain sufficient data for precise density estimation. The weather pattern of the tropical rainforest studied here limited effective sampling to about two hours per day on average. Therefore, a period of approximately 15 months of intensive sampling would be required for a complete density estimate. This might be beyond the resources available for most odonatological studies, and it might also interfere with the assumption of a closed population during the investigation (Williams et al. 2002).

Given the large sampling effort required for a density estimate of all species combined, a survey aiming at the determination of species-specific densities would be

unrealistic in tropical forests. In this study I pooled all species together. A better approach would be to pool species of similar size, conspicuousness, behaviour or other features that limit or enhance detection. If detection probability is equal among members of a group pooled for analysis the assumptions of distance sampling are not violated (Heydon & Bulloh 1997). It will, however, be problematic to calculate diversity indices for communities that require a relative abundance of every species. I suggest to use a relative encounter rate for every species and habitat type multiplied by the density of the species pool for that habitat type to obtain relative abundances of species.

Distance sampling will be a useful technique in other environments with a lower species diversity. Especially surveys in habitats with ill-defined and widely scattered water sources, such as peat bogs, swampy reeds or sedge swamps should benefit from the application of distance sampling.

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