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Estimating abundance of the federally endangered Mitchell's satyr butterfly using hierarchical distance sampling

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Abstract. 1. Estimates of animal abundance are essential to conservation biology and are sorely lacking for many endangered species in the United States of America. This lack of knowledge may disproportionately affect butterflies in the USA, which form the largest group of federally protected insects (20 of 62 species).

2. The Mitchell's satyr butterfly, *Neonympha mitchellii mitchellii*, is a federally endangered species found at 18 highly isolated sites in the Eastern USA. Currently, surveys are conducted by meandering through habitat and recording the number of butterflies observed. These surveys are efficient in terms of staffing and time, but the data from these surveys cannot be used to estimate abundance. Mark release recapture surveys generate estimates of demographic parameters and have been conducted, albeit infrequently, and require high staffing levels and weeks of fieldwork to generate estimates with reasonable error.

3. I employed hierarchical distance sampling along line transects to estimate *N. m. mitchellii* abundance at one site in lower Michigan, USA. This method requires one observer to traverse a series of transects at a walking pace and record the number of butterflies observed and their perpendicular distance to the transect line. My results suggest that this method is as cost efficient as meander surveys, but generates reasonable estimates of butterfly abundance.

Key words. Conservation, Lepidoptera, modelling, population.

Introduction

The estimation of animal abundance is essential to conservation biology and the preservation of biodiversity. These estimates are invaluable and help to form the foundation of evidence-based conservation biology, a field that all too often relies on anecdotal or unverified information (Sutherland *et al*., 2004). With knowledge of abundance, conservation managers can conduct population viability analysis, assess the effects of habitat management, and determine the need for captive rearing programs (Williams *et al*., 2002). Despite the obvious importance of abundance estimates, knowledge of population size is lacking for many insects of conservation concern in the United States of America and this lack of knowledge may hamper recovery efforts (Haddad *et al*., 2008). This lack of knowledge may disproportionately affect butterflies in the USA, which form the plurality of federally protected insect taxa (20 of 62 species; www.ecos.fws.gov/tess_public).

Researchers have a suite of methods at their disposal to estimate animal abundance and a number of these methods have been applied to butterflies (Pollard & Yates, 1993; Brown & Boyce, 1998; Barton & Bach, 2005; Powell *et al*., 2007; Haddad *et al*., 2008; Longcore *et al*., 2010;

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Isaac *et al*., 2011; Pellet *et al*., 2012). The choice of which method to use involves weighing a series of trade-offs involving: speed (which relates to financial cost), precision, and bias (Williams *et al*., 2002; Haddad *et al*., 2008). Timed-meander (TM) or 'wandering transect' surveys (in which small groups of surveyors meander through potential habitat and record the number of target organisms encountered) are efficient and may illuminate changes in occupancy patterns, but cannot estimate demographic parameters such as abundance (Longcore *et al*., 2010). Pollard-Yates (PY) transects are standardised, efficient (small groups of surveyors move quickly along pre-established transects), and allow for estimation of demographic parameters, but make assumptions concerning detectability and habitat homogeneity that may not always be justified (Pollard & Yates, 1993; Haddad *et al*., 2008; Nowicki *et al*., 2008; Isaac *et al*., 2011; Pellet *et al*., 2012). Mark-release-recapture (MRR) techniques allow for the estimation of demographic parameters, such as abundance, survival, and recruitment, but are labour intensive, often requiring large teams to be in the field for weeks, and can be costly in terms of financial resources (Gall, 1985; White & Burnham, 1999; Barton & Bach, 2005). High numbers of individuals must often be recaptured in order for error estimates to seem reasonable, a requirement that may be difficult to fulfil if the target organism is short lived or the study is not conducted over a long enough period (Barton, 2008b). In addition, MRR carries with it the increased risk of damaging butterflies, a risk that is correlated with the skill of the handlers (Murphy, 1987).

The Mitchell's satyr butterfly, *Neonympha mitchellii mitchellii* (Lepidoptera, Nymphalidae), is a federally endangered species with a wingspan of approximately 2.5 cm with protected populations in Michigan and Indiana (Hamm, 2012). Historically, this butterfly occurred in six states in the Eastern USA and was listed as an endangered species due to habitat loss in 1991 (USFWS, 1998; Hamm, 2012). These populations are confined to highly isolated yet relatively open wetlands known as prairie fens (Landis *et al*., 2011; Hamm, 2012). As of 2012 there are 18 known sites (most ~1 ha in size) with extant populations of Mitchell's satyr and the size of these populations is largely unknown (Hamm, 2012). Population size for most sites is thought to be very small, although infrequent MRR studies of three sites indicate that some populations can be rather large (up to 3000 individuals) (Szymanski *et al*., 2004; Barton & Bach, 2005; Barton, 2008a; Hamm, 2012). Mitchell's satyr population status is currently assessed using TM surveys in which small teams wander through habitat and count the number of *N. m. mitchellii* observed (Barton, 2008a). These surveys reported the number of butterflies observed during visits and may be used to monitor occupancy (Longcore *et al*., 2010). Although this method is efficient (workers can traverse most sites in approximately 3 h), the data generated from it cannot be extrapolated into estimates of abundance. Estimates of Mitchell's satyr population size are critically needed to guide management efforts.

A technique for the estimation of Mitchell's satyr abundance is needed that is both efficient and generates reasonable estimates of population abundance. The sampling technique known as line transect distance sampling may be ideal (Buckland *et al*., 2001). The following description is from Buckland *et al*., 2001: distance sampling has three key assumptions: (i) target objects are more or less uniformly distributed throughout the environment, (ii) all target objects on the line are observed, and (iii) that the ability to detect these objects (known as the detection function) decreases with distance (some objects will not be observed). To implement this method an observer walks down a series of line transects of known length, and records the distance (perpendicular to the transect) at which a target object is observed. These data are placed into bins of increasing distance away from the transect line and a detection function is fitted to the data (Fig. 1). The area under the detection function is integrated and the number of missed organisms can be estimated, and thus total abundance predicted. If these assumptions are met the method generates unbiased estimates of density. The models used in distance sampling are statistically robust in that they are not unduly affected by minor deviations from the model assumptions. Distance sampling has been frequently used in wildlife surveys and has recently been applied to butterfly surveys (Brown & Boyce, 1998; Powell *et al*., 2007; Isaac *et al*., 2011).

The Mitchell's satyr has a number of life-history traits that are ideal for distance sampling, these include: short adult lifespan (adult lifespan is approximately 3 days), populations are located in spatially closed habitats, and its flight is conspicuous (Barton, 2008a; Landis *et al*., 2011; Hamm, 2012). Distance sampling has the potential to be very efficient because transects can be walked in a

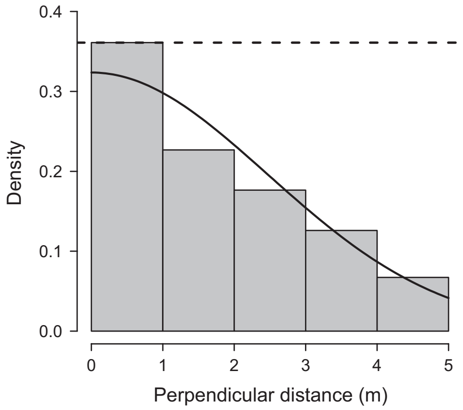

Fig. 1. A half-normal detection function (solid line) fitted to *Neonympha mitchellii mitchellii* data from 4 July 2011. Distance sampling models assume uniform distribution of target organisms (dashed line) with imperfect detection. The area under the detection function is integrated and the number of missed organisms can be estimated, and thus total abundance predicted (Buckland *et al*., 2001).

reasonable amount of time and this method does not require the handling of organisms (which may facilitate the permitting process).

Since the initial development of distance sampling a number of significant advances have been made related to the statistical theory underlying the models, in particular the development of hierarchical models (Royle, 2004b). Hierarchical models recognise that biological surveys may suffer from significant measurement error due to two major processes that affect the estimation of population size. These processes are as follows: (i) ecological processes that affect abundance and (ii) observation processes that affect detection (Royle & Dorazio, 2008). Hierarchical models account for these processes by separately modelling explanatory variables that affect abundance and detection (Royle, 2004a,b; Fiske & Chandler, 2011). Within this framework, covariates that may affect abundance and detection processes (such as environmental or habitat variables) may be incorporated into the model and applied to distance sampling (Royle *et al.*, 2004). These models have recently been implemented in the R package 'unmarked' (Fiske & Chandler, 2011). Within this package, the function 'distsamp' generates parameter estimates using the hierarchical multinomial-Poisson model of Royle (2004b), which has the general form:

$$N_i \sim \text{Poisson}(\lambda_i)\ \text{for}\ i = 1, 2, \ldots, M$$

$$\mathbf{Y}_i | N_i \sim \text{Multinomia}(N_i, \boldsymbol{\pi})$$

where λ_i is the abundance at site *i*, N_i is the latent (unobserved) abundance at site *i*, and $\boldsymbol{\pi}$ is the vector of cell probabilities where $\boldsymbol{\pi} = (\pi_1, \pi_2, \ldots, \pi_J)^T$ that correspond to the vector counts of $\mathbf{Y}_i$ (Royle, 2004b). The probability of detection is modelled as:

$$\log(\sigma_i) = \mathbf{v}_i^T \alpha$$

where σ is the positive shape parameter of the detection function, $\mathbf{v}_i$ is a vector of observation-level covariates, and α is a vector of their corresponding effect parameters.

I investigated the application of hierarchical distance sampling (HDS) using line transects on *N. m. mitchellii* at one large (8 ha) site in lower Michigan. Although the primary objective of this study was to demonstrate the utility of HDS on *N. m. mitchellii*, I also investigated the relative cost of different survey methods (TM, MRR, and HDS) based on previously reported staffing requirements (Barton, 2008a). In order for distance sampling to be considered a viable alternative to TM surveys it must be cost efficient and generate reasonable demographic estimates. Although formal comparisons of the survey methods applied to *N. m. mitchellii* cannot be made (the data were derived from different sources), it may be informative to visualise the numbers generated by each method. To this end I compiled data reflecting all three survey methods from the past 25 years. The results provide the basis for future surveys of Mitchell's satyr abundance.

Materials and methods

Line transect surveys were conducted at the Jackson County Central (JCC) site, located in central Southern Michigan, which is owned and managed by The Nature Conservancy. A total of five surveys were conducted from 4 to 12 July 2011 between 1000 and 1300 h when the temperature ranged between 24 and 29 °C and the winds were light. The JCC site contained approximately 8 ha of prairie fen wetland, although transects covered approximately three and one half hectares of this land. The Nature Conservancy has divided the JCC site into management units that reflect the schedule with which the units were burned. Three of these units (Units A, B, and C) were covered by this survey and were treated as covariates during analysis (Fig. 2).

On 3 July 2011, I accessed the site and established transects using coloured flagging, a 100-m measuring tape, and a compass. The first transect was established at the northern boundary of the study area along an east–west axis (Fig. 2). The next transect was placed 20 m to the south and all remaining transects were established as such until the southern boundary of the study area was reached (Fig. 1). Along the length of each transect a series of coloured flags was placed such that an observer could remain on the transect line by aligning any two flags. Were this study to be conducted on an annual basis, permanent transect markers should be considered. Although the length of each transect was measured with a 100-m tape, a handheld GPS receiver (GPS Map 360x; Garmin Inc., Olathe, KS, USA) was accurate to be within 2 m of the total distance traversed each day.

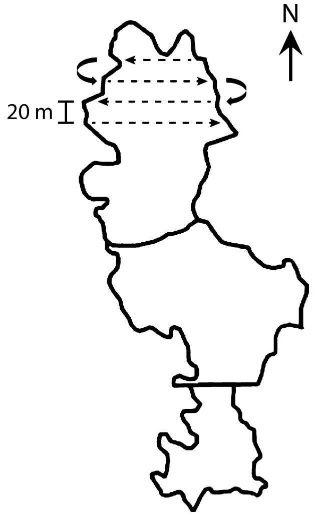

Fig. 2. Representation of study design through management units A, B, and C (from north to south) at the Jackson County Central site in lower Michigan. The pattern initiated at the northern boundary of the site continued to the southern boundary. Subsequent daily transects were offset by 2 m to the south to reduce overlap.

On 4 July 2011, I began the survey and walked each transect at a pace of approximately 1 m every 2 s. Once each transect walk was completed I walked outside of the study area to pick up the next transect and traversed it in the opposite direction of the previous transect (Fig. 2). Additional sampling was conducted on 6, 7, 8, and 12 July 2011. With each subsequent survey the transect line was shifted south by 2 m to reduce the overlap of surveys. Not all management units were surveyed during each survey day.

Mitchell's satyr butterflies, which were often flushed from resting positions, were noted and the perpendicular distance from the transect line to the point of first observation was noted. Observations for each day were pooled into intervals (0–0.9 m, 1.0–1.9 m, 2.0–2.9 m, 3.0–3.9 m, and 4.0–5.0 m), which makes the data take on the required multinomial distribution (Royle, 2004b) and analysed in R 2.14 (R Core Development Team, 2011) using the 'distsamp' function from the 'unmarked' package (Fiske & Chandler, 2011). For each survey day I fit the half-normal and negative exponential detection functions because these were biologically plausible and should produce reasonable fits of the data (Buckland *et al.*, 2001). For each detection function I evaluated four models to estimate butterfly density: a null (with no covariates affecting detectability or abundance), a model where management unit affected detectability only, a model where management unit affected abundance only, and a model where management unit affected both detectability and abundance.

Models were evaluated using Akaike's Information Criterion (AIC) (Akaike, 1974) and the AIC model weighted averages were calculated for parameter estimates (and 95% CI). This information theoretic approach has a number of advantages over simply using the AIC best model or the single model with the most AIC weight because models other than the AIC best may contain information that can improve parameter estimation (Burnham & Anderson, 2002). To confirm that the AIC best models were capturing essential information, however, I conducted a chi-squared goodness-of-fit test using 1000 simulations of a parametric bootstrap against a significance value of $\alpha = 0.05$. All data and R code used for this project have been digitally archived and are freely available from the online data archive datadryad.org (doi: 10.5061/dryad.v977b).

Estimates of density can easily be extrapolated into estimates of abundance. To generate daily estimates of abundance for visual comparison I multiplied the density estimates made by the AIC best model by the total area of habitat at the site. Because error may not scale linearly when multiplied I fitted the extrapolated parameter estimates to the AIC best model using 1000 parametric bootstrap pseudo-replicates, which also generated 95% CIs. Butterfly counts for the JCC site from TM surveys were provided by the Michigan Natural Features Inventory and MRR estimates were extracted from the literature and published reports (Barton & Bach, 2005; Barton, 2008a).

I estimated the minimum cost (excluding field equipment and fuel) of conducting each of the three sampling methods for up to 21 days. I estimated staffing considerations based on this and previous research (Barton, 2008a) and estimated a MRR study to require eight people working 8 h per day, a TM study requiring two people to work 3 h per day, and a HDS study requiring one person to work a 5 hour day to establish the transects and 3 h per day to conduct the surveys. I assumed a pay rate of 15 USD per h.

Results

A total of 275 *N. m. mitchellii* were observed during this survey covering approximately 6700 m of walked transects over five sampling days at the Jackson County Central site (Table 1). Each survey lasted no more than 3 h and the number of *N. m. mitchellii* observed daily varied from 103 to 15 (Fig. 3). The AIC model weighted averages and 95% CIs for butterfly density by survey date and management unit are presented in Fig 4. All AIC best models passed the chi-squared goodness-of-fit test ($P > 0.05$), indicating that the AIC best models captured essential information regarding parameter estimates (Buckland *et al.*, 2001).

Extrapolated abundance estimates for the JCC site are presented with data generated by TM and MRR studies (Table 2). The maximum number of Mitchell's satyr observed during a TM study was 240, and the maximum population estimate generated by a MRR study was over 3000 individuals. The estimated cost for labour of each sampling method for 21 days of sampling was as follows: MRR – 20160 USD, TM – 1890 USD, and distance sampling – 1020 USD (Fig. 5).

Discussion

This survey generated estimates of *N. m. mitchellii* density that can be used to aid in recovery and management efforts and the estimates from this survey appear reasonable when compared with MRR estimates (Table 2). Each daily survey was conducted in approximately the same

Table 1. Descriptive statistics from this study grouped by date: total length of transects, the number of *Neonympha mitchellii mitchellii* observed, management units surveyed by date, and the time in hours required to complete that day's survey.

Survey date	Total length (m)	No. observed	Units surveyed	Time (h)
4 July	1548	103	A, B, C	3
6 July	1474	58	A, B	2.5
7 July	1395	45	A, B	2.5
8 July	1576	54	A, B, C	3
12 July	763	15	B, C	2

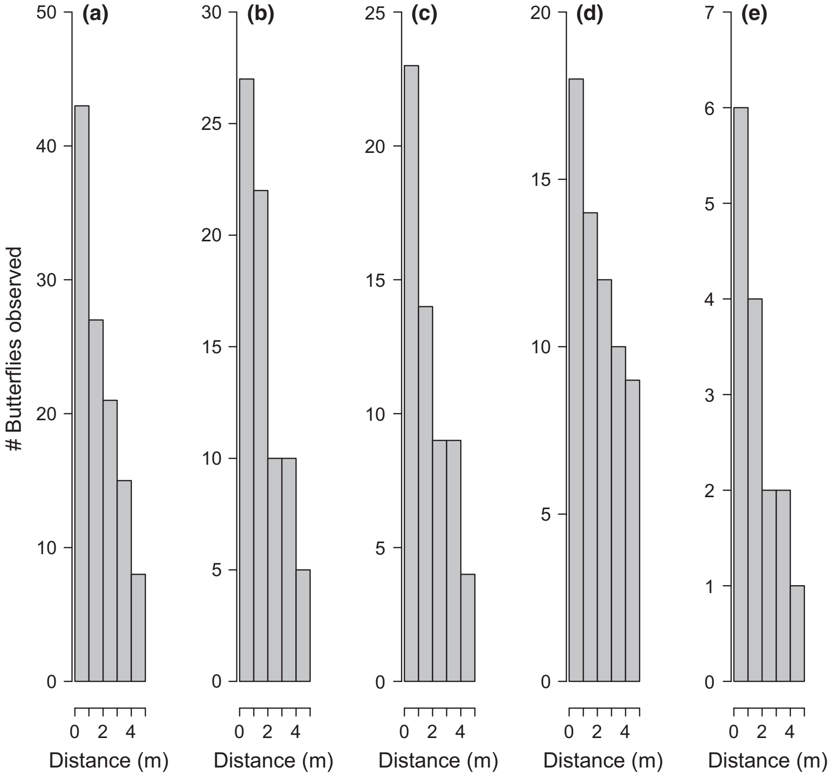

Fig. 3. Histograms of the number of *Neonympha mitchellii mitchellii* individuals as a function of perpendicular distance (m) from transect by survey date in 2011: (a) 4 July; (b) 6 July; (c) 7 July; (d) 8 July; and (e) 12 July.

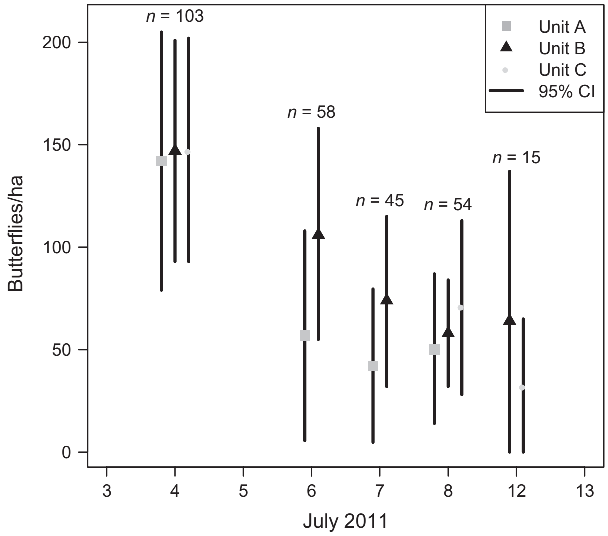

Fig. 4. AIC model weighted averages and 95% CIs of butterfly density by day and management unit with sample sizes above the corresponding estimates.

time as the meander surveys, yet generated estimates of butterfly density and uncertainty. Other transect-based methods, such as PY surveys, do not presently incorporate covariates into the modelling framework. In the case of the Mitchell's satyr, the addition of covariates is a key because conservation managers seek to determine the effects of management practices on butterfly abundance, which can be easily determined by explicitly modelling these features. Knowledge of the number of *N. m. mitchellii* at a particular site, and how population size fluctuates over time, will be invaluable to conservation managers because these data could distinguish long-term declines from stochastic fluctuation, as has been demonstrated in Great Britain and Europe (Roy *et al.*, 2007; van Swaay *et al.*, 2008). For each federally endangered species in the USA, recovery criteria are set forth in a formal 'recovery plan' that state the minimum number of 'viable' populations that must be extant in order for the protected status to be changed or lifted (USFWS, 1998). Without knowing the number of individuals present in a population, it is impossible to determine its viability. Abundance estimated from surveys such as this is a crucial first step towards determining population viability.

Abundance estimates generated by distance sampling seem reasonable when compared with estimates made using MRR studies (Table 2), whereas the absolute counts generated by TM surveys appear to consistently underestimate *N. m. mitchellii* population size. Although we cannot statistically compare the data generated by these methods it seems clear that TM surveys are missing a significant

Table 2. *Neonympha mitchellii mitchellii* counts and estimates for the Jackson County Central site in Michigan. Data from Timed-meander (TM) surveys represent absolute counts, whereas those from mark-release-recapture (MRR) and hierarchical distance sampling (HDS) studies are estimates of total population size. All data are from the Michigan Natural Features Inventory unless otherwise noted.

		Method		
Year	Date	TM	MRR	HDS
1986	14 July	5		
1989	3 July	4		
	5 July	26		
	6 July	12		
	11 July	28		
	14 July	2		
1992*		36		
1995	10 July	55		
1996	9 July	33		
	16 July	5		
1998	1 July	2		
	2 July	2		
1999	30 June	25		
2000	11 July	9		
	12 July	8		
2002	9 July	58		
2003[†]	7 July		111	
	8 July		387	
	9 July		831	
	10 July		582	
	12 July		457	
	13 July		679	
	14 July		566	
	15 July		448	
	17 July		714	
	18 July		554	
	19 July		250	
	22 July		431	
	23 July		166	
	24 July		127	
	25 July		66	
2005	8 July	8		
2006	7 July	29		
2007[‡]	23 June	50	3020 (1913–4127)	
	24 June		2625 (1596–3655	
	25 June		1698 (1054–2343)	
	26 June	64	2155 (1438–2873)	
	27 June		1758 (947–2569)	
	28 June	150	2329 (1595–3064)	
	29 June		1568 (1119–2018)	
	30 June		1923 (1046–2799)	
	1 July	84	1119 (657–1580)	
	2 July	10	2099 (349–3848)	
	3 July		614 (234–993)	
	4 July		767	
	5 July	93	597	
	7 July	26		
2008	1 July	32		
	8 July	1		
	10 July	39		
2009	30 June	8		
	8 July	240		
2011[§]	4 July			1305 (944–1798)
	6 July			469 (181–723)
	7 July			439 (143–699)
	8 July			531 (296–798)
	12 July			523 (176–1655)

*Date unknown.

[†] Barton & Bach, 2005; point estimates extracted from Fig. 2 with Engauge Digitizer software (http://digitizer.sourceforge.net), no error estimates provided.

[‡] Barton, 2008a.

[§] Data from this study.

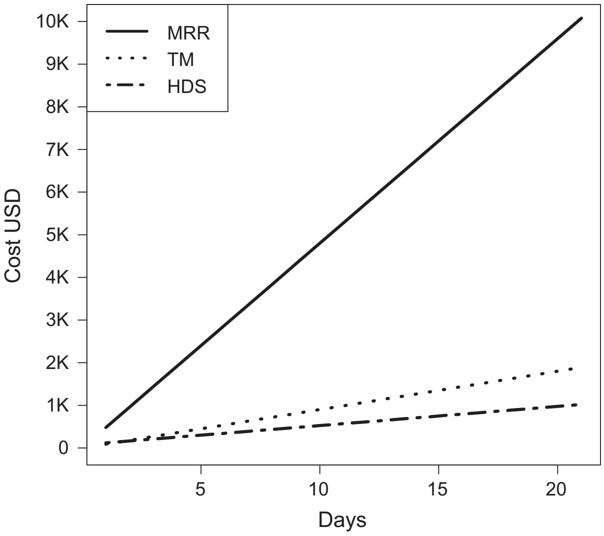

Fig 5. The estimated cost (USD) in labour for three methods of butterfly sampling for 21 days: mark release recapture (MRR), timed meander (TM), and distance sampling. MRR required eight workers, TM required two workers, and distance sampling required one worker.

number of Mitchell's satyr. The cost efficiency of HDS and TM surveys is impressive compared with MRR surveys (Fig. 5). Indeed, both TM and distance surveys are nearly 20 times less expensive than a MRR study, although HDS has the added benefit of generating abundance estimates.

Although distance sampling seems ideally suited for abundance estimates it does have certain limitations that must be addressed. A mark-recapture study, although expensive and time consuming, is able to generate demographic parameter estimates that HDS cannot. For example, estimates of home range size, dispersal among management units have been generated for *N. m. mitchellii* and were based on MRR studies (Szymanski *et al.*, 2004; Barton & Bach, 2005). Perhaps future survey regimes could incorporate occasional MRR studies to supplement the more cost-effective distance sampling (Haddad *et al.*, 2008).

Other butterflies of conservation concern that exist in relatively open habitat may also benefit from HDS, although this method may not be ideal for taxa that are difficult to observe. The method is quick, transects can be established with minimal effort, and small teams or individual researchers can conduct the surveys. If distance sampling is conducted annually long-term trends can emerge and be separated from population stochasticity, and thus better guide management decisions.

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References

Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716–723.

Barton, B.J. (2008a) 2007 Mitchell's Satyr (Neonympha mitchellii mitchellii) Research Report to the US Fish and Wilflife Service. 28 pp.

Barton, B.J. (2008b) 2008 Mitchell's satyr (Neonympha mitchellii mitchellii) Research Report to the US Fish and Wilflife Service. 17 pp.

Barton, B.J. & Bach, C. (2005) Habitat use by the Federally Endangered Mitchell's satyr butterfly (Neonympha mitchellii mitchellii) in a Michigan Prairie Fen. *The American Midland Naturalist*, **153**, 41–51.

Brown, J. & Boyce, M. (1998) Line transect sampling of Karner blue butterflies (Lycaeides melissa samuelis). *Environmental and Ecological Statistics*, **5**, 81–91.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*. Springer-Verlag, New York, New York.

Fiske, I.J. & Chandler, R.B. (2011) Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, **43**, 1–23.

Gall, L.F. (1985) Measuring the size of Lepidopteran populations. *Journal of Research on the Lepidoptera*, **24**, 97–116.

Haddad, N.M., Hudgens, B., Damiani, C., Gross, K., Kuefler, D. & Pollock, K. (2008) Determining optimal population monitoring for rare butterflies. *Conservation Biology*, **22**, 929–940.

Hamm, C.A. (2012) *Natural history and conservation genetics of the federally endangered Mitchell's satyr butterfly, Neonympha mitchellii mitchellii*. Dissertation, Michigan State University, East Lansing, Michigan.

Isaac, N.J.B., Cruickshanks, K.L., Weddle, A.M., Marcus Rowcliffe, J., Brereton, T.M., Dennis, R.L.H., Shuker, D.M. & Thomas, C.D. (2011) Distance sampling and the challenge of monitoring butterfly populations. *Methods in Ecology and Evolution*, **2**, 585–594.

Landis, D.A., Fiedler, A.K., Hamm, C.A., Cuthrell, D.L., Schools, E.H., Pearsall, D.R., Herbert, M.E. & Doran, P.J. (2011) Insect conservation in Michigan prairie fen: addressing the challenge of global change. *Journal of Insect Conservation*, **16**, 131–142.

Longcore, T., Lam, C.S., Kobernus, P., Polk, E. & Wilson, J.P. (2010) Extracting useful data from imperfect monitoring schemes: endangered butterflies at San Bruno Mountain, San Mateo County, California (1982–2000) and implications for habitat management. *Journal of Insect Conservation*, **14**, 335–346.

Murphy, D. (1987) Are we studying our endangered butterflies to death? *Journal of the Research on the Lepidoptera*, **26**, 236–239.

Nowicki, P., Settele, J., Henry, P.-Y. & Woyciechowski, M. (2008) Butterfly monitoring methods: the ideal and the real world. *Israel Journal of Ecology & Evolution*, **54**, 69–88.

Pellet, J., Bried, J.T., Parietti, D., Gander, A., Heer, P.O., Cherix, D. & Arlettaz, R. (2012) Monitoring butterfly abundance: beyond Pollard walks. *PLoS ONE*, **7**, e41396.

Pollard, E. & Yates, T.J. (1993) *Monitoring Butterflies for Ecology and Conservation – The British Monitoring Scheme*. Springer, New York, New York.

Powell, A.F.L.A., Busby, W.H. & Kindscher, K. (2007) Status of the regal fritillary (Speyeria idalia) and effects of fire management on its abundance in northeastern Kansas, USA. *Journal of Insect Conservation*, **11**, 299–308.

R Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/> 15th January 2011.

Roy, D.B., Prothery, P. & Brereton, T. (2007) Reduced-effort schemes for monitoring butterfly populations. *Journal of Applied Ecology*, **44**, 993–1000.

Royle, J. (2004a) Generalized estimators of avian abundance from count survey data. *Animal Biodiversity and Conservation*, **27**, 375–386.

Royle, J. (2004b) N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, **60**, 108–115.

Royle, J.A., Dawson, D.K. & Bates, S. (2004) Modeling abundance effects in distance sampling. *Ecology*, **85**, 1591–1597.

Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations,* *Metapopulations and Communities*. Academic Press, San Diego, California.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology & Evolution*, **19**, 305–308.

van Swaay, C., Nowicki, P., Settele, J. & Strien, A.J. (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation*, **17**, 3455–3469.

Szymanski, J., Shuey, J. & Oberhauser, K. (2004) Population structure of the Endangered Mitchell's satyr, Neonympha mitchellii mitchellii (French): implications for conservation. *The American Midland Naturalist*, **152**, 304–322.

United States Fish and Wildlife Service (USFWS) (1998) *Mitchell's Satyr Butterfly Neonympha mitchellii mitchellii Recovery Plan*. US Fish & Wildlife Service – Region 3, Snelling, Minnesota, 71 pp.

White, G.C. & Burnham, K.P. (1999) Program MARK: Survival Estimation from Populations of Marked Animals. *Bird Study*, **46 Suppl**: 120–138.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, New York, New York.

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