Modelling insect demography from capture–recapture data: comparison between the constrained linear models and the Jolly–Seber analytical method

Nicolas Schtickzelle,[1] Michel Baguette, Éric Le Boulengé

Université catholique de Louvain, Biodiversity Research Centre, 4 Place Croix du Sud, B-1348 Louvain-la-Neuve, Belgium

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Abstract—Entomologists traditionally use the Jolly–Seber analytical method (JSAM) to estimate demographic parameters from capture–mark–recapture data, although more powerful approaches like the constrained linear models (CLM) have been developed and are commonly and successfully applied to vertebrates. Demographic parameters (*i.e.*, survival, capture, and recruitment rates, population size, and sex ratio) of a patchy population of the Bog Fritillary butterfly, *Proclossiana eunomia* (Esp.) (Lepidoptera: Nymphalidae), were estimated using CLM on the basis of daily captures of imagoes during 11 yearly generations (1992–2002). Comparing these results with JSAM results obtained on the same data lead us to stress that CLM are far more powerful tools which allow for optimal exploitation of capture–mark–recapture data. This method allows the identification of the variation patterns of demographic parameters and to link them to life-history traits; furthermore it gives more precise estimates of these crucial input parameters for the modelling of population trends and population viability analysis.

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Résumé—Les entomologistes utilisent traditionnellement la méthode analytique de Jolly–Seber (JSAM) pour estimer les paramètres démographiques à partir de données de capture–marquage–recapture alors que des approches plus puissantes comme les modèles linéaires sous contraintes (CLM) ont été développées et sont couramment appliquées avec succès aux vertébrés. Les paramètres démographiques (survie, piégeabilité, recrutement, taille de population et sex ratio) d'une population subdivisée du nacré de la bistorte, *Proclossiana eunomia* (Esp.) (Lepidoptera : Nymphalidae), ont été estimés par CLM sur base de captures journalières des imagos durant 11 générations annuelles (1992–2002). La comparaison de ces résultats avec ceux obtenus sur les même données par JSAM souligne que CLM représente un outil nettement plus puissant permettant une exploitation optimale des données de capture–marquage–recapture. En effet, cette méthode permet d'identifier les patrons de variation des paramètres démographiques et de les relier à des traits d'histoire de vie; de plus, elle donne des estimations plus précises de ces paramètres cruciaux pour la modélisation des trajectoires de population et l'analyse de viabilité de population.

Introduction

The capture–mark–recapture (also known as mark–release–recapture) method is frequently used for estimating population demography (death and birth rates, population

[1] Corresponding author (e-mail: schtickzelle@ecol.ucl.ac.be).

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size, and sex ratio) in natural environments (Schwarz and Seber 1999 and references therein); for insects and notably butterflies, it is often the only way of collecting such information because they cannot be followed individually as can birds or mammals. This information on demographic parameters, especially the precision with which they are estimated, is of prime importance for modelling population trends in the context of population viability analysis (Beissinger and McCullough 2002).

Entomologists, specially those working on butterflies, traditionally use the Jolly–Seber analytical method (hereinafter JSAM) (Jolly 1965; Seber 1965) to analyse capture–mark–recapture data. This method has indeed been widely disseminated in general methodological textbooks in the past and present (*e.g.*, Southwood 1978; it is referred to as "the method of choice for open populations" in Greenwood 1996: 32; Krebs 2000). Although more powerful approaches like the constrained linear models (hereinafter CLM[2]) have been developed and are commonly and successfully applied notably to birds (*e.g.*, Hestbeck *et al.* 1991; Spendelow *et al.* 1995) and mammals (*e.g.*, Nichols *et al.* 1994; Coffman *et al.* 2001), entomologists continue to use JSAM (*e.g.*, Gutierrez *et al.* 1999; Bergman 2001; Leisnham and Jamieson 2002) probably because it is easy to use (but see Begon 1983) and CLM are not yet well known by insect biologists.

Schtickzelle *et al.* (2002) used the CLM methodology to estimate adult demographic parameters of the Bog Fritillary butterfly, *Proclossiana eunomia* (Esp.) (Lepidoptera: Nymphalidae). This butterfly is an endangered species in Western Europe because its habitat is strongly fragmented at the landscape scale. In the framework of a population viability analysis, we analysed capture–mark–recapture data to infer reliable demographic parameter estimates.

Using this case study, we aim at convincing field biologists analysing capture–recapture data to rely on model selection procedures (CLM) to explore demographic parameters and their sources of variations instead of applying methods such as the JSAM. For that purpose, we give a short overview of CLM methodology and of its main differences with JSAM, and using our data on the Bog Fritillary butterfly, illustrate the differences between the two methods. Our aim is not to provide a complete picture of capture–mark–recapture data analysis using CLM, but rather to make the reader aware of the existence of the CLM methodology and of its possibilities.

Materials and methods

The species

The Bog Fritillary is a glacial relict species inhabiting unfertilized wet hay meadows and peat bogs in which grows the Bistort, *Polygonum bistorta* L. (Polygonaceae), which is the sole food plant of both larvae and adults. In Belgium, this seminatural habitat is restricted to the banks of some rivers and to peat bogs in the Ardenne region (Nève *et al.* 1996), where it becomes more and more fragmented as meadows are drained, pastured, and (or) planted with Norway spruce, *Picea abies* (L.) Karst (Pinaceae), thus increasing the threat on *P. eunomia*. For this reason, the Bog Fritillary is a vulnerable species in Western Europe and is protected in Belgium (Goffart *et al.* 1992). Therefore, suitable conservation measures should be defined, which implies the building of a population viability analysis model for which precise estimates of key demographic parameters are needed.

[2] There is no generic acronym for the constrained linear models. The choice and name of the specific model is typically based on the type of capture–recapture data available.

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Capture–mark–recapture data collection

The study area (named the Prés de la Lienne; southern Belgium, about 50°18′N, 5°49′E; altitude: approximately 350 m) consists of a network of suitable habitat patches spread along the Lienne River (9 patches totalling 2.3 ha in 2002). It supports a single patchy population, which forms the core area of a metapopulation system (Baguette and Nève 1994; Nève *et al.* 1996; Petit *et al.* 2001). The Prés de la Lienne population of *P. eunomia* imagoes was monitored by capture–mark–recapture from 1992 to 2002. During the entire flight period (end of May to end of June), all the patches were visited daily (weather permitting) and every encountered imago was individually marked with a thin-point permanent pen and immediately released. For each (re)capture, the following data were recorded: tag number, sex, age (estimated by the wear of the wing), date and hour, patch, and behaviour.

Proclossiana eunomia is a univoltine species without generation overlap (no individual survives from one year to the next), thus datasets collected in different years (*i.e.*, different generations) may be considered repetitions through time of the same processes. Consequently, these 11 datasets were analysed separately with the same strategy.

JSAM

JSAM is the outcome of statistical developments by Cormack (Cormack 1964), Jolly (Jolly 1965), and Seber (Seber 1965). It allows the estimation of survival, capture, and recruitment rates and population size from capture–mark–recapture data. JSAM estimates a separate parameter value (for survival, capture, and recruitment rates) for each time step (*i.e.*, a time effect), but it does not allow the direct estimation of a group effect; if some groups of individuals differ in terms of demographic parameters, it is necessary to apply JSAM separately on each group. Variants of this method have been developed (reviewed in Pollock *et al.* 1990) to constrain for instance the survival rate to 1 (no mortality, *i.e.*, birth-only model) or to be a constant value through time (Jolly–Dickson models; see for example Arnason *et al.* 1998); these variants are not the subject of the present comparison, as they are not widely used and are in fact *ad hoc* modifications of JSAM, which can be viewed in some way as precursors of model selection procedures only fully developed in CLM. JSAM is said to have analytical solutions because algebraic formulas are available to obtain estimates of these parameters, which was of great interest prior to the widespread availability of personal computers and numerical optimization algorithms; this is probably a major reason for its large success in the past 30 years.

In the present analysis, we used the full (birth and death) JSAM with bias correction for small sample sizes as implemented in the POPAN-5 software (Arnason *et al.* 1998). The estimate of the total population size (number of different individuals present at some time during the flight period), not directly available with JSAM, was computed according to a modified version of JSAM (Schwarz *et al.* 1993).

CLM

Since 1985 (Clobert and Lebreton 1985), a new approach to obtain demographic estimates from capture–mark–recapture data has been developed; CLM represent the application of linear models to the specific case of capture–mark–recapture data (Burnham *et al.* 1987; Pollock *et al.* 1990; Lebreton *et al.* 1992; Schwarz and Arnason 1996; Schwarz and Seber 1999; Pollock 2000; Schwarz 2001; Cooch and White 2002). This was made easier with advances in computer technology and the associated possibility of using methods with nonanalytical solutions through numerical optimization. Since the beginning, capture–mark–recapture methods have been largely enhanced and

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extended to cover a wide variety of capture–mark–recapture data types, including dead recoveries, telemetry data, etc. (Cooch and White 2002 and references therein). For live-recapture data, CLM fit into two categories according to the way first captures of individuals are treated: (1) Cormack–Jolly–Seber models treat first captures as uninformative constants, and therefore depend on (and allow the estimate of) survival and capture rates, whereas (2) Jolly–Seber models treat first captures as random variables that provide information on population size; they also include (and allow the estimate of) recruitment rate, which is used to estimate population size. The general methodology consists of, exactly as in standard linear regression, the creation of a set of candidate regression models for predicting the demographic parameters (response variables) as a function of factors that the user believes influence them and for which data are available. Among these candidate models, the analysis will select the one that is best supported by the data. This regression method is more flexible and more powerful than previous analysis methods; through model selection, it is possible to (*i*) test hypotheses concerning factors influencing demography and (*ii*) gain precision in estimates *via* model simplification by removing factors not supported by the data. "The goal in model selection is to identify a biologically meaningful model that explains the significant variability in the data but excludes unnecessary parameters (Occam's razor) (…)" (Lebreton *et al.* 1992: 80); this is the principle of parsimony, which recognizes the importance of a trade-off between the bias resulting from the use of an overly simple model *versus* the lack of precision resulting from the use of an overly general model. Consequently, the test of factors having a significant effect on demographic parameters is directly associated with parameter estimation; the best model gives the significant factors and the parameter estimates.

The best model is selected from a set of candidates by way of Akaike's information criterion corrected for small sample sizes (AIC_c): the lower the AIC_c value the better the model is supported by the data. Models differing in AIC_c value from the best model by less than two units are substantially supported by the data. For a general review of model selection, in a broader context than CLM, see Burnham and Anderson (1998) and references therein. Details on the application of the CLM methodology to the present data on the Bog Fritillary, including the candidate models tested and all selection results, can be found in Schtickzelle *et al.* (2002).

Results and discussion

Eleven years of capture–mark–recapture data total 6666 captures (2178 females, 4488 males) of 3050 imagoes (1275 females, 1775 males). Yearly numbers of marked imagoes range from 42 to 343 females and from 36 to 295 males, during 6–25 sample times. To our knowledge, this constitutes one of the largest and most long-term capture–mark–recapture datasets ever collected on butterflies.

Male *P. eunomia* have a lower survival rate but are easier to catch than females, owing to behavioural differences (Baguette *et al.* 1998; Schtickzelle *et al.* 2002); thus, estimates with JSAM were obtained for each sex, and several models with sex and time effects were tested with CLM.

Comparison of results between CLM and JSAM is about (*i*) intra-annual dynamics, which is the daily estimates of individual (survival and catchability) and population (recruitment rate and population size) parameters, and (*ii*) inter-annual dynamics, which is the global estimates of population size and sex ratio over the whole flight period. For intra-annual dynamics (daily estimates), we have chosen to present only results for two generations (1994 and 1996), but the same conclusions can be drawn from the other years. These two generations have been chosen because they have the highest (1994)

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and smallest (1996) number of sample times, respectively, which can influence the simplifications achieved in the best CLM.

Intra-annual dynamics (daily estimates)

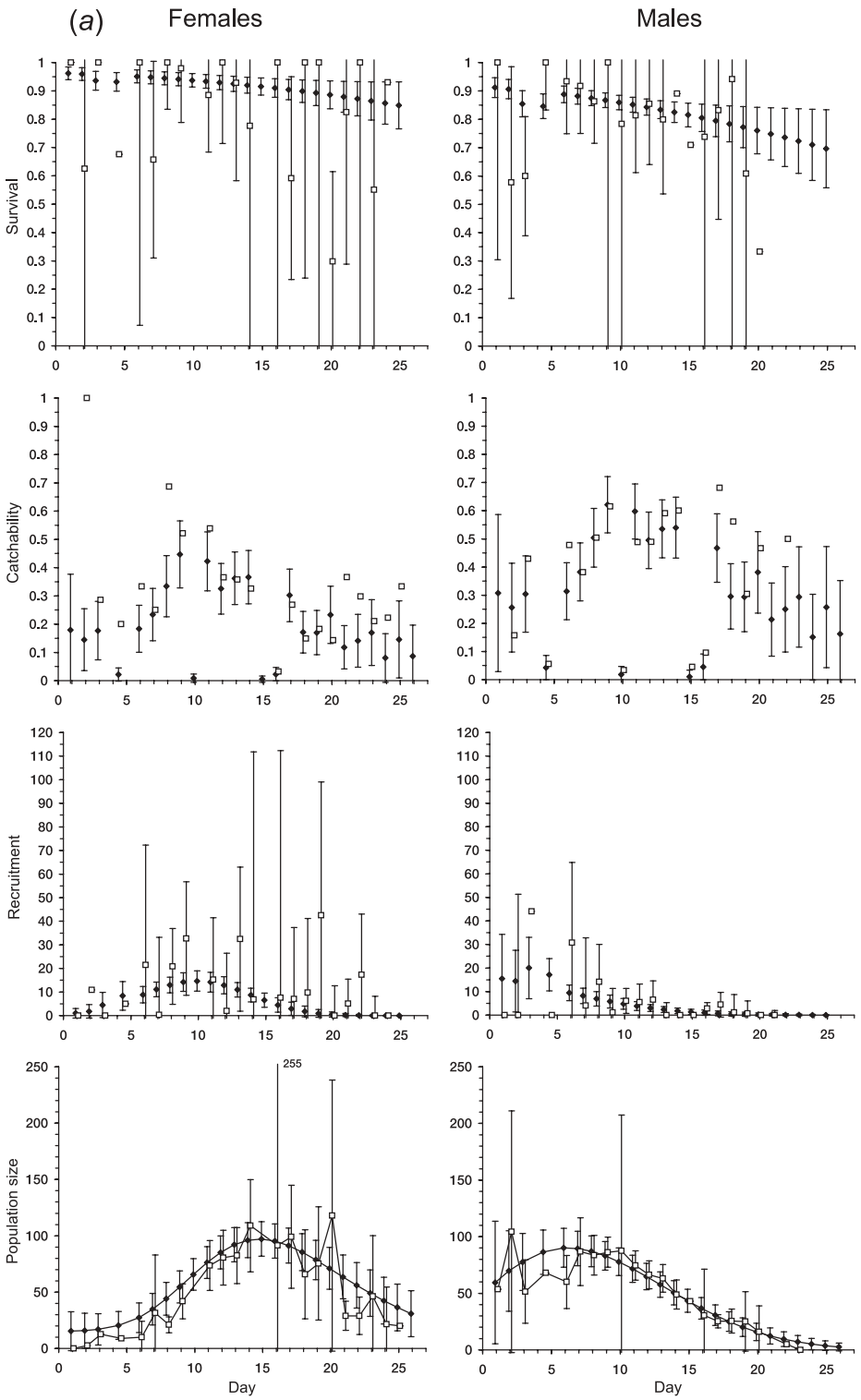
JSAM imposes a rigid and usually overparameterised model whereby the time variation of the three demographic components (survival, capture, and recruitment rates), associated with separate group analysis, corresponds to a time × group interaction model. In contrast, the CLM methodology allows (*i*) for the identification of patterns of demographic parameter variations and to link them to life-history traits and (*ii*) for a simplification of the model that leads to more precise estimates.

For illustration of the first difference between methods (identification of patterns), we summarize the conclusions of model selection with CLM (details can be found in Schtickzelle *et al.* 2002). For almost all generations, CLM show that (*i*) survival is lower for males and decreases linearly during the flight period; (*ii*) catchability is lower in females and changes from day to day; (*iii*) recruitment rate follows a parabola for each sex. These effects are consistent with the following life-history traits of *P. eunomia* (Baguette *et al.* 1998; Schtickzelle *et al.* 2002; Schtickzelle 2003): (*i*) lower survival and higher catchability for males are consequences of differences in mate-locating behaviour (*i.e.*, males are constantly patrolling in search of females, whereas females spend most of their life in the vegetation in search of oviposition sites); (*ii*) the linear decrease of survival during the flight season is probably related to the senescence or vanishing food supply; (*iii*) weather conditions and changes in catch effort are responsible for daily variations in catchability; and (*iv*) parabolic recruitment is expected in species with discrete generations, whereas protandry (*e.g.*, Wiklund and Fagerström 1977) explains why males and females present shifted recruitment curves. Apart from the difference between sexes, which was tested prior to applying JSAM (tests 2 and 3; Burnham *et al.* 1987), none of these effects could have been detected with JSAM, as this method does not provide tests of factors. Consequently, a lot of valuable information contained in the data would not have been exploited, despite important investments usually put in capture–mark–recapture field data collection.

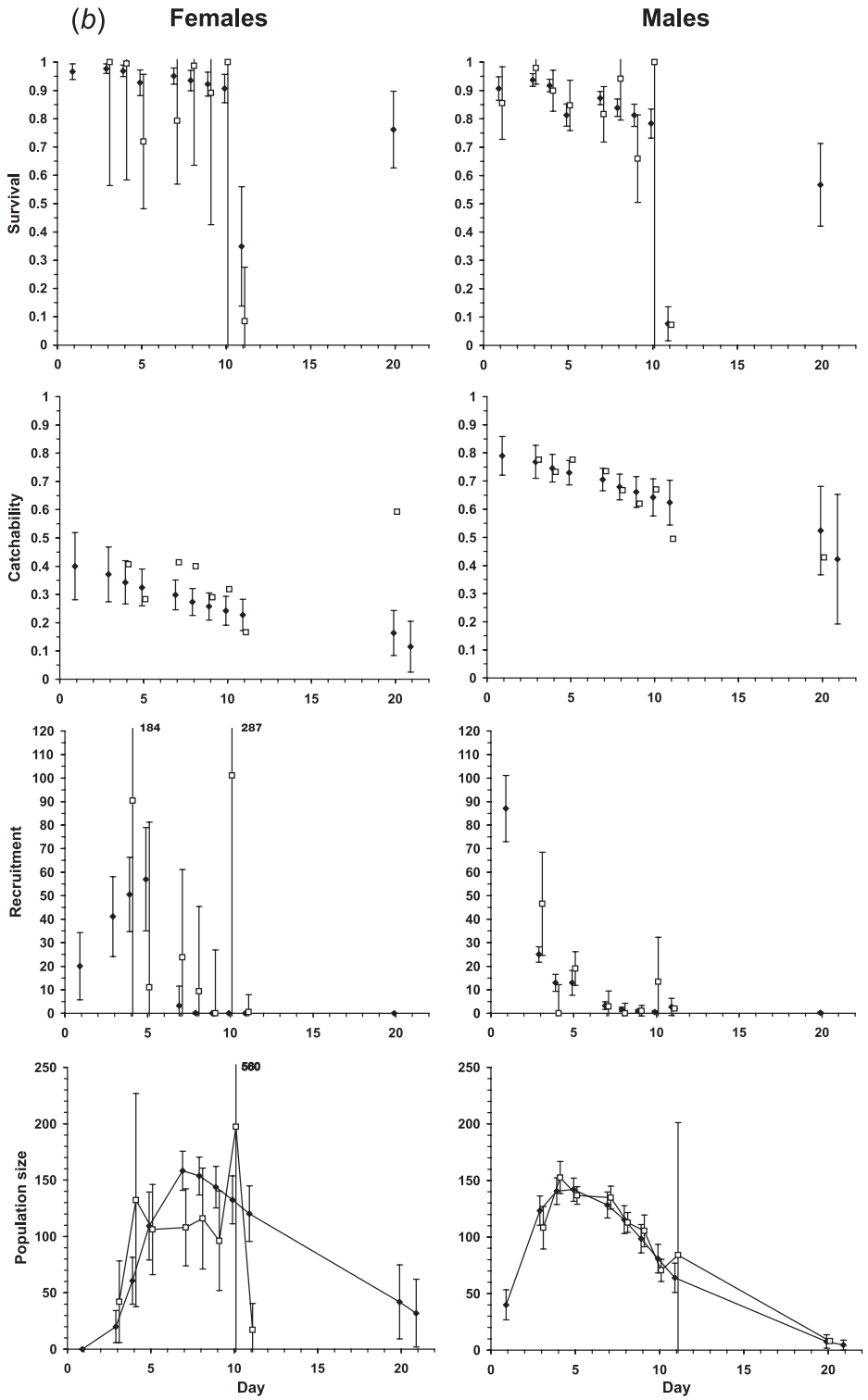
The second difference between these methods lies in the precision of the estimates. Due to its large number of parameters, JSAM in general gives highly variable daily estimates with large confidence intervals, several presenting a confidence interval covering all the range of possible values (0–1). This illustrates the way both methods handle the trade-off between bias and precision underlying the principle of parsimony: whereas JSAM automatically sacrifices precision for a low bias, CLM allow one to find, through model selection based on statistical theory, which simplifications can be made in the model to increase the precision of the estimated parameters without significantly increasing the bias. We illustrate this gain in the precision of estimates on two datasets: the 1994 generation (Fig. 1*a*) and the 1996 generation (Fig. 1*b*). Because of the inverse proportional relationship between the number of parameters and their precision, a general comparison of the numbers of parameters estimated with each method (Table 1) is another obvious way to appreciate the gain in precision.

FIGURE 1. Comparison between daily estimates (with 95% confidence intervals when available) of demographic parameters obtained with the constrained linear models (solid symbols) and the Jolly-Seber analytical method (open symbols) for the 1994 (*a*) and 1996 (*b*) generations of *Proclossiana* eunomia. The smaller confidence intervals of the constrained linear models indicate a gain in precision. Recruitment and population size are given in numbers of individuals.

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TABLE 1. Comparison of number of parameters to be estimated for each generation with the Jolly–Seber analytical method (JSAM) and the most parsimonious constrained linear models (CLM).

		No. of parameters	
Generation	No. of sample times	JSAM	CLM
1992	15	67	25
1993	20	81	44
1994	25	119	35
1995	17	71	25
1996	11	49	12
1997	16	76	27
1998	6	17	17
1999	17	81	24
2000	14	67	24
2001	15	73	9
2002	11	49	20

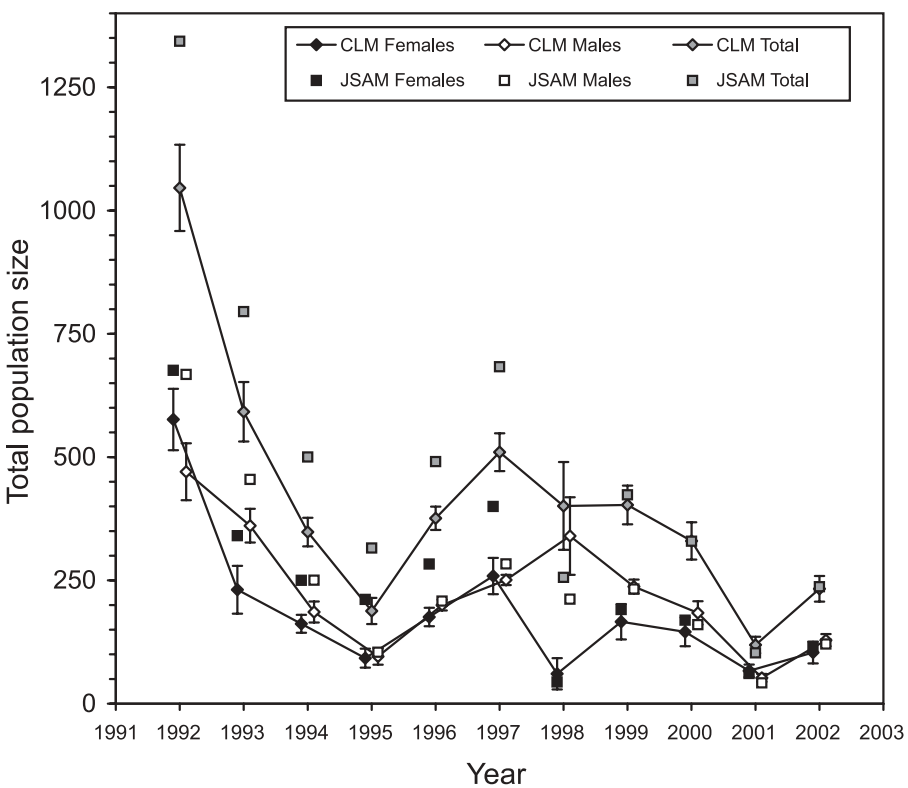


FIGURE 2. Total population size of *Proclossiana eunomia* (with 95% confidence intervals when available) calculated over the entire flight period (in number of individuals).

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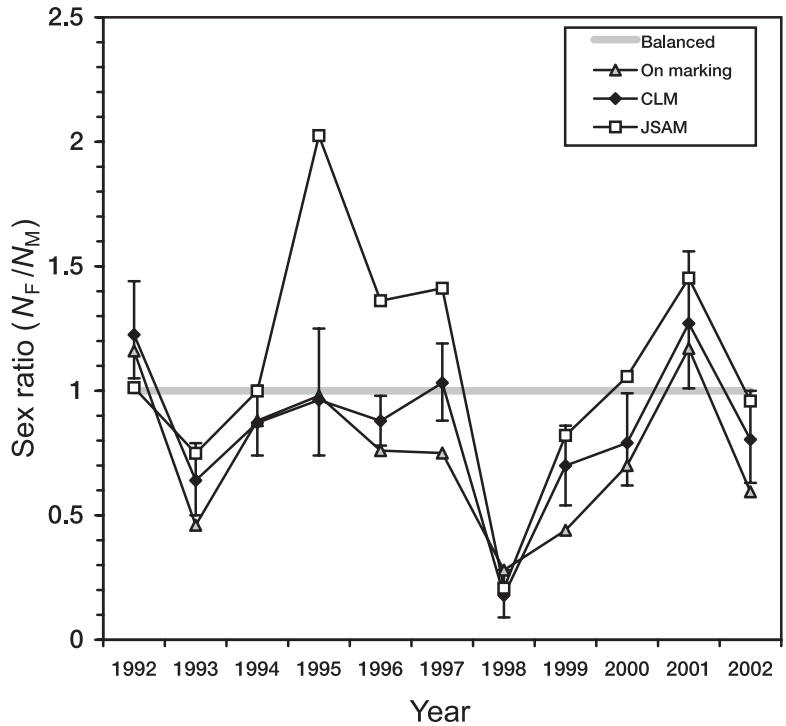


FIGURE 3. Sex ratio of *Proclossiana eunomia* (total female population size divided by total male population size). "Balanced" indicates an equal number of males and females.

Inter-annual dynamics (estimates over all the flight periods)

As in many insect populations, the total population size varies greatly between years for both sexes (Fig. 2), owing to weather conditions and density dependence associated with parasitoids (Schtickzelle *et al.* 2002). Two conclusions are reached from the comparison of estimation methods. (1) JSAM does not provide a direct estimate, only a modified JSAM does, such as the one we used here (Schwarz *et al.* 1993). (2) JSAM tends to give a higher estimate of the total population size than CLM, except for datasets with few (re)captures (1998 and 2001) where it seems to be the reverse but for which results should be interpreted with much caution. Overestimating the population size is a particularly dangerous error in a conservation context. But, even if this second conclusion seems to be confirmed by analyses on capture–mark–recapture datasets of the Cranberry Fritillary [*Boloria aquilonaris* Stichel (Lepidoptera: Nymphalidae)] (N Schtickzelle, unpublished data), the generality of this statement is unknown because it has not yet been reported in the literature.

Because of protandry, the operational sex ratio changes during the flight season, from 100% male at the beginning to 100% female at the end. Nevertheless, the global sex ratio (defined here as the ratio between female and male total population sizes) computed from CLM estimates reveals that the population globally contains fewer females than males (Fig. 3). The sex ratio calculated on the basis of JSAM total population size estimates is much more variable between years and the deviation from the balanced sex ratio observed with CLM does not appear. When the marking effort is high (which is the case in the present study), the sex ratio on marking should reflect the

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real sex ratio despite differences in catchability between the sexes. The CLM sex-ratio estimates are always closer to this sex ratio on marking than are the JSAM estimates.

Conclusion

Obtaining high-quality estimates of demographic parameters is often vital for modelling population trends, notably in the framework of population viability analysis. JSAM has been a major innovation in estimating demographic parameters from capture–mark–recapture data and has consequently been used extensively with good reason by entomologists. Nevertheless, new methods like CLM have been developed more recently, which allows a far more in-depth analysis. The comparison of results between CLM and JSAM clearly shows that CLM represent far more powerful tools, giving more reliable and more precise estimates of demographic parameters, and allowing the linking of patterns in their variations to life-history traits. We therefore advocate that it is time for entomologists to follow ornithologists, mammalogists, and ichthyologists in using the power of CLM in analysing their capture–mark–recapture datasets. The already old statement by Pollock *et al.* (1990: 8) is still relevant: "Studying natural populations and conducting manipulative field experiments often are extremely expensive of time and effort. We believe that the data analysis associated with such field efforts deserves far greater attention than it often receives."

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References

Arnason AN, Schwarz, CJ, Boyer, G. 1998. *POPAN-5. A data maintenance and analysis system for mark–recapture data*. Scientific Report, Department of Computer Science, University of Manitoba, Winnipeg

Baguette M, Nève G. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). *Ecological Entomology* **19**: 1–5

Baguette M, Vansteenwegen C, Convié I, Nève G. 1998. Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclossiana eunomia*. *Acta Oecologica* **19**: 17–24.

Begon M. 1983. Abuses of mathematical techniques in ecology: applications of Jolly's capture–recapture method. *Oikos* **40**: 155–8

Beissinger SR, McCullough DR. 2002. Population viability analysis. Chicago: The University of Chicago Press

Bergman KO. 2001. Population dynamics and the importance of habitat management for conservation of the butterfly *Lopinga achine*. *Journal of Applied Ecology* **38**: 1303–13

Burnham KP, Anderson, DR. 1998. *Model selection and inference: a practical information – theoretic approach*. New York: Springer-Verlag

Burnham KP, Anderson, DR, White, GC. 1987. Design and analysis methods for fish survival experiments based on release–recapture. *American Fisheries Society Monograph* **5**

https://doi.org/10.4039/n02-045 Published online by Cambridge University Press

Clobert J, Lebreton JD. 1985. Dépendance de facteurs de milieu dans les estimations de taux de survie par capture–recapture. *Biometrics* **41**: 1031–7

Coffman CJ, Nichols JD, Pollock KH. 2001. Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches. *Oikos* **93**: 3–21

Cooch E, White GC. 2002. *Program MARK – analysis of data from marked individuals. A gentle introduction.* 2nd edition. Available from http://www.cnr.colostate.edu/~gwhite/mark/mark.htm (accessed 13 August 2001)

Cormack RM. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* **51**: 429–38

Goffart Ph, Baguette M, De Bast B. 1992. La situation des Lépidoptères rhopalocères en Wallonie ou que sont nos papillons devenus? *Bulletin et Annales de la Societe Royale Belge d'Entomologie* **128**: 355–92

Greenwood JJD. 1996. Basic techniques. pp 11–110 *in* WJ Sutherland (Ed), *Ecological census techniques*. Cambridge: Cambridge University Press

Gutierrez D, Thomas CD, Leon-Cortes JL. 1999. Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). *Oecologia* **121**: 506–17

Hestbeck JB, Nichols JD, Malecki RA. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada geese. *Ecology* **72**: 523–33

Jolly GM. 1965. Explicit estimates from capture–recapture data with both death and immigration-stochastic model. *Biometrika* **52**: 225–47

Krebs CJ. 2000. *Ecological methodology.* 2nd edition. New York: Longman

Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**: 67–118

Leisnham PT, Jamieson IG. 2002. Metapopulation dynamics of a flightless alpine insect *Hemideina maori* in a naturally fragmented habitat. *Ecological Entomology* **27**: 574–80

Nève G, Barascud B, Hughes R, Aubert J, Descimon H, Lebrun P, Baguette M. 1996. Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). *Journal of Applied Ecology* **33**: 14–22

Nichols JD, Hines JE, Pollock KH, Hinz RL, Link WA. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology* **75**: 2052–65

Petit S, Moilanen A, Hanski I, Baguette M. 2001. Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. *Oikos* **92**: 491–500

Pollock KH. 2000. Capture–recapture models. *Journal of the American Statistical Association* **95**: 293–6

Pollock KH, Nichols JD, Brownie, C, Hines, JE. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* **107**

Schtickzelle N. 2003. Metapopulation dynamics and viability of the bog fritillary butterfly *Proclossiana eunomia*. PhD thesis, Biodiversity Research Centre, Université catholique de Louvain, Louvain-la-Neuve

Schtickzelle N, Le Boulengé E, Baguette M. 2002. Metapopulation dynamics of the bog fritillary butterfly: demographic processes in a patchy population. *Oikos* **97**: 349–60

Schwarz CJ. 2001. The Jolly–Seber model: more than just abundance. *Journal of Agricultural, Biological, and Environmental Statistics* **6**: 195–205

Schwarz CJ, Arnason AN. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* **52**: 860–73

Schwarz CJ, Seber GAF. 1999. Estimating animal abundance: review III. *Statistical Science* **14**: 427–56

Schwarz CJ, Bailey RE, Irvine JR, Dalziel FC. 1993. Estimating salmon spawning escapement using capture–recapture methods. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 1181–97

Seber GAF. 1965. A note on the multiple recapture census. *Biometrika* **52**: 249–59

Southwood TRE. 1978. *Ecological methods.* 2nd edition. London: Chapman and Hall

Spendelow JA, Nichols JD, Nisbet ICT, Hays H, Cormons GD, Burger J, Safina C, Hines JE, Gochfeld M. 1995. Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. *Ecology* **76**: 2415–28

Wiklund C, Fagerström T. 1977. Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia* **31**: 153–8

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