Population size assessment using mark-release-recapture of 12 species of Orthoptera, Diptera and Hymenoptera: a comparison of methods

EDUARDAS BUDRYS [1], **ANNA BUDRIENĖ** [2], **SAULIUS PAKALNIŠKIS** [3]

Institute of Ecology, Vilnius University, Akademijos 2, LT-2600, Vilnius, Lithuania; e-mail:
[1] ebudrys@ekoi.lt , [2] anna@ekoi.lt , [3] saupak@ekoi.lt

BUDRYS E., BUDRIENĖ A., PAKALNIŠKIS S. 2004. POPULATION SIZE ASSESSMENT USING MARK-RELEASE-RECAPTURE OF 12 SPECIES OF ORTHOPTERA, DIPTERA AND HYMENOPTERA: A COMPARISON OF METHODS. – *Latv. entomol.*, 41: 32-43.

Abstract: For the first time in Lithuania the mark-release-recapture (MRR) method was applied for assessment of the insect population size. We evaluated abundance of model populations of species from the orders Orthoptera (*Metrioptera bicolor*, *Platycleis albopunctata*, *Oedipoda caerulescens*, *Psophus stridulus*, *Sphingonotus caerulans*), Hymenoptera (*Symmorphus allobrogus*, *S. debilitatus*, *Ancistrocerus antilope*, *Chrysis purpurata*) and Diptera (*Cheilosia illustrata*, *Volucella pellucens*, *Hydrotaea ignava*). The results were analysed using estimators based on closed population model (Lincoln-Petersen, Chapman, Schnabel, and Schumacher-Eschmeyer), and Jolly-Seber estimator, based on open population model. The conclusions of the study: (1) Lincoln-Petersen estimator is the least adequate, and should not be recommended to use; (2) in case of high recapture rate the estimators based on closed population model provided similar results, expectedly reflecting the real size of insect population; (3) in cases of low recapture rate Schnabel estimator was less susceptible to the fluctuation or partial lack of recaptures in the series of censuses, but combination of Chapman and Schumacher-Eschmeyer estimators provided the narrowest confidence interval; (4) Jolly-Seber estimator, originally designed to assess population dynamics, was little efficient in the assessment of the population size of insects, usually giving much more fluctuating results than the estimators based on the closed population model and often underestimating the probable population size; (5) estimators based on closed population model provided seemingly reliable results after 4-8 censuses, dependently on the recapture rate.

Key words: mark-release-recapture, Lincoln-Petersen, Chapman, Schnabel, Schumacher-Eschmeyer, Jolly-Seber methods.

Introduction

Population size assessment is one of frequently arising tasks in practical ecology. There are multiple methods to solve it (review: Lancia et all., 1994). Some of these methods (e.g. complete census or aerial photography counts) are applicable only for comparatively large and long-lived vertebrate animals. However, some advanced technology methods, as radio-telemetry, have been recently applied to invertebrates as well (Williams, 1999).

The commonly used techniques of the invertebrate population size assessment are counts (particularly transect counts) and mark-release-recapture (MRR) method (Settele et all., 2000). The first is applicable for easy to detect animals only (e.g. butterflies). The second is more universal and it has long history in ecology (Le Cren, 1965). Recent application of computers lead to development of sophisticated modelling of population dynamics and survival using marked animals (Lebreton et all., 1992; Anonymous, 2000).

The MRR method is applied to invertebrates particularly for population dynamics, longevity and survival research (e.g. Jonsen et all., 2001; Kawagoe et all., 2001), population density and mobility studies (García et all., 2000; Showers et all., 2001; Hein et all., 2003), sex ratio changes (Anholt et all., 2001), pest population monitoring (Harrington et all., 2001), as well as assessment of rare and endangered species populations (Jamieson et all., 2000, Ranius, 2000).

In MRR studies it is recommended to use

individual marks (Lancia et all., 1994). The batch marks (identical within one sample of animals) must be avoided, except for simple Lincoln-Petersen estimates. Individual marking by numbers is widely used for butterflies (Settele, 2000), however, for small insects with fine wings, as Hymenoptera and Diptera, such marking is technically difficult.

The MRR results are analysed using two types of models (see overview in Lancia et all., 1994). The first type assumes that population is closed (births, deaths, immigration and emigration are disregarded). Models of the second type take into account the population changes (Jolly, 1982; Seber, 1982). The most exact estimates of population dynamics are provided by combination of both model types (Pollock, 1982). However, this method is relatively effort-consuming and practical only in detailed studies of multi-annual population dynamics of e.g. protected species.

A researcher, studying insects with a single generation per year, may be interested in the rough assessment of general population size within one season, but not in changes of it. In this case application of sophisticated open population models, for instance those provided by computer program MARK (Anonymous, 2000) is not practical.

The goal of the study was to explore the possibilities of rough but quick population size assessment within one season, using technically simple (batch instead of individual marking) and reasonably time- and effort-consuming methods. We expected to define the most practical estimator and the reasonable number of subsequent censuses to use them in the future studies.

All studied species of Orthoptera and Hymenoptera have single generation per year in Lithuania; population size of the studied Diptera was assessed during a shorter than their generation period. Having in mind that the natural decline of the abundance of imagos was compensated by laid eggs and new larvae, we considered the population size as virtually stable during the study period. Therefore we believed that usage of methods based on closed population model was acceptable.

Methods

Studied species. We assessed the size of model populations of five species of Orthoptera (Tettigoniidae: *Metrioptera bicolor* (Philippi), *Platycleis albopunctata* (Goeze); Acrididae: *Oedipoda caerulescens* (L.), *Psophus stridulus* (L.), *Sphingonotus caerulans* (L.)), four species of Hymenoptera (Vespidae: *Symmorphus allobrogus* (Saussure), *S. debilitatus* (Saussure), *Ancistrocerus antilope* (Panzer); Chrysididae: *Chrysis purpurata* F.), and three species of Diptera (Syrphidae: *Cheilosia illustrata* (Harris), *Volucella pellucens* (L.); Muscidae: *Hydrotaea ignava* (Harris)).

Study plots. For Orthoptera the sampling plot was located 3 km S of village Puvočiai (Varėna distr., 54°05'N, 24°20'E), 3 ha of dry, open perennial and annual siliceous grassland on inland dunes with dominating *Corynephorus canescens*, *Calamagrostis*, lichens and mosses, locally with *Calluna vulgaris*, surrounded by patches of young *Pinus silvestris* stands.

The MRR study of Hymenoptera was conducted in the village Varnupys (Anykščiai distr., 55°24'N, 25°17'E), at an old wooden building, infected by cerambycids *Hylotrupes bajulus*, *Callidium violaceum* and anobiids, with natural colonies of solitary xylicolous wasps and bees nesting in the beetle burrows. The building was surrounded by wet sedge meadows with scattered *Salix cinerea* shrubs, and with deciduous forest of *Quercus robur*, *Betula pendula*, *Populus tremula*, *Alnus glutinosa*, *A. incana*, *Padus racemosa*, *Salix caprea*, *S. pentandra* and *Pinus silvestris*. The building was isolated from the other buildings possibly suitable for xylicolous wasp nesting by few hundreds of meters, thus the studied wasp populations expectedly had the lowest, in comparison with studied Orthoptera and Diptera, migration rates.

The sampling plot for Diptera was in Visoriai (Vilnius suburb, 54°45'N, 25°15'E), a dry meadow with flowering Apiaceae (mainly *Heracleum sosnowskii*, some *Peucedanum oreoselinum*, *Angelica sylvestris*, *Pimpinella saxifraga*), surrounded by patches of young stands of *Betula pendula*, *Alnus incana*, *Populus tremula*, *Salix caprea* and *Pinus silvestris*.

Sampling. The sampling period for Orthoptera was mid July to end of August. Hymenoptera were sampled from end of May to the mid July, Diptera – in July or (*H. ignava*) August. The censuses were carried on in warm and sunny days only, with intervals of ca. one week for Orthoptera and Hymenoptera, and 1-3 days for Diptera. We captured insects by entomological net. For marking we applied nail enamels of 10 colours. Different colour was used on each census date. Sampling of Orthoptera was started at 11:00 and was finished it at 16:00; the specimens were immediately marked with a spot on their pronotum using small brush and released. The wasps and flies were captured between 12:00 and 13:00 and placed to glass tubes. Afterwards they were marked with a small spot of enamel, using binocular microscope MBS-10 (at 8×) and entomological pin, and released. The wasps were marked on the posterior surface of their propodeum; the flies were marked on their mesonotum. We nearly never found damaged marks on recaptured specimens, thus we expected that the probability of losing such marks was relatively low.

Analysis. Analysing the MRR data, we used estimators based on the closed population model for two subsequent censuses (method of Lincoln-Petersen and its modification by Chapman) and for multiple censuses (methods of Schnabel and Schumacher-Eschmeyer), and method of Jolly-Seber, based on open population model. The formulas for calculations were as follows:

<u>Lincoln-Petersen</u> estimator (Lancia et all., 1994):

$N' = n_1 n_2 / m_2$,

$$S.E._{(N')} = \sqrt{n_1^{\,2} n_2 (n_2 - m_2) / m_2^{\,3}}$$

where N' – estimated size of population; n_1 – individuals captured and marked in the previous sample (“last marked” values in Fig. 1) or all earlier samples (“all marked” values in Fig. 1); n_2 – individuals captured in the current sample; m_2 – individuals in the current sample that are marked (recaptures).

<u>Chapman</u> estimator (Chapman, 1951):

$$N' = \frac{(n_1+1)(n_2+1)}{m_2+1} - 1,$$

where N' – estimated size of population; n_1 – individuals captured and marked in all previous samples; n_2 – individuals captured in the current sample; m_2 – individuals in the current sample that are marked (recaptures).

For the standard error of Chapman estimator, instead of formula

$$S.E._{(N')} = \sqrt{\frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)}}$$

(Seber, 1982)

we used

$$S.E._{(N')} = \sqrt{\frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2+1)}{(m_2+1)^2(m_2+3)}}$$

to avoid zero variance in the cases when all captured insects were marked ($n_2 = m_2$).

The confidence limits of the Lincoln-Petersen and Chapman estimators were calculated as $N \pm \boldsymbol{t}_{(0.05,\, n_2-1)}$ S.E.

<u>Schnabel</u> estimator (Schnabel, 1938):

$$N' = \frac{\sum_{i=2}^{c}\left(n_i \sum_{j=1}^{i-1} n_j\right)}{\sum_{i=2}^{c} m_i + 1}$$

$$S.E._{(N')} = \sqrt{\frac{\left(\sum_{i=2}^{c}\left(n_i \sum_{j=1}^{i-1} n_j\right)\right)^2}{\sum_{i=2}^{c} m_i}}$$

, or standard error of the reciprocal of N':

$$S.E._{(1/N')} = \sqrt{\frac{\sum_{i=2}^{c} m_i}{\left(\sum_{i=2}^{c}\left(n_i \sum_{j=1}^{i-1} n_j\right)\right)^2}};$$

<u>Schumacher-Eschmeyer</u> estimator (Ricker, 1975):

$$N' = \frac{\sum_{i=2}^{c}\left(n_i \left(\sum_{j=1}^{i-1} n_j\right)^2\right)}{\sum_{i=2}^{c}\left(m_i \sum_{j=1}^{i-1} n_j\right)},$$

S.E.$_{(N')}$ =

$$\sqrt{\frac{N^3}{(c-1)\sum_{i=2}^{c}\left(m_i\sum_{j=1}^{i-1}n_j\right)}\left(\sum_{i=2}^{c}\frac{m_i^2}{n_i}-\frac{\left(\sum_{i=2}^{c}\left(m_i\sum_{j=1}^{i-1}n_j\right)\right)^2}{\sum_{i=2}^{c}\left(n_i\left(\sum_{j=1}^{i-1}n_j\right)^2\right)}\right)}$$

, or

S.E.$_{(1/N')}$ =

$$\sqrt{\frac{1}{(c-1)\sum_{i=2}^{c}\left(n_i\left(\sum_{j=1}^{i-1}n_j\right)^2\right)}\left(\sum_{i=2}^{c}\frac{m_i^2}{n_i}-\frac{\left(\sum_{i=2}^{c}\left(m_i\sum_{j=1}^{i-1}n_j\right)\right)^2}{\sum_{i=2}^{c}\left(n_i\left(\sum_{j=1}^{i-1}n_j\right)^2\right)}\right)}$$

(Schneider, 2000), where N' – estimated size of population; n_i – individuals captured and marked in the i-th census; $\sum_{j=1}^{i-1}n_j$ – individuals captured and marked in earlier censuses; m_i – individuals in the i-th census that are marked (recaptures); c – total number of censuses.

Confidence limits for Schnabel and Schumacher-Eschmeyer estimates were calculated using reciprocal of N' $[1/(1/N' \pm \boldsymbol{t}_{(0.05,\ c-1)}\text{S.E.}_{(1/N')})]$, as recommended by Ricker (1975), or by the usual formula ($N' \pm \boldsymbol{t}_{(0.05,\ c-1)}$ S.E.$_{(N')}$), if the latter provided closer value (higher minimum or lower positive maximum) than the former one.

Jolly-Seber estimator (Seber, 1982):

$$\tilde{N}_i = \frac{n_i+1}{m_i+1}\left(m_i + \frac{z_i}{r_i+1}(n_i+1)\right),$$

where $\tilde{N}$ – estimated population size; n_i – individuals captured / marked in the i-th census; m_i – individuals in the i-th census that are marked; r_i – the number of animals released at i-th census that will be captured again; z_i – the number of animals that have been captured before i-th census, not captured at i-th sample, and will be captured again later.

The size of the population should be with the probability of 95% within confidence interval established using any of the listed methods. Therefore we tallied narrower "summarising" interval, partly overlapping any of the calculated confidence intervals (Tables 1-3, column N', values in bold), presuming that size of the population being assessed should be within it with reasonably high probability. Afterwards the latter interval was used for comparisons with each estimator result separately. The criteria for defining the best estimator were as follows: after reasonably low number of censuses the result (1) should be close to the "summarising" interval, (2) should have low fluctuations between censuses, and (3) should have small interval of the confidence limits.

The calculations were done using computer program Microsoft Excel 2000.

Results and Discussion

The results of the population size estimations, starting from the third census, are presented in Tables 1-3 (95% confidence intervals for each estimation) and Figures 1-12 (estimator values in subsequent censuses).

Table 1. Orthoptera: 95% confidence intervals of population estimates and values of the Jolly-Seber estimator at each census (n/a – not available).

Legends: N' – the smallest overlapping confidence interval for each estimation and (in bold) for all estimations ("summarizing" interval – see text). For Jolly-Seber estimator the range of estimates is given in brackets; * number of captured specimens (n_i); ** total number of recaptures (m_i).

	Census No (*i*)								
Species	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	***N'***
Metrioptera bicolor	10*/3**	8/4	5/3	3/2	2/1	3/3	1/1	0/0	**33-44**

Lincoln-Petersen	0-91	7-73	0-81	0-108	0-539	28	(n/a)	(n/a)	28-73
Chapman	12-63	15-59	9-64	0-81	0-251	4-52	(n/a)	(n/a)	15-52
Schnabel	11-367	17-377	21-91	23-66	26-55	27-48	27-45	28-44	28-44
Schum.-Eschm.	17-74	26-55	30-50	32-47	33-48	31-45	31-44	(n/a)	33-44
Jolly-Seber	99	45	59	24	8	7	1	(n/a)	(1-99)
Platycleis albopunctata	29/1	11/1	12/0	26/3	24/5	14/3	8/2	11/4	**574-619**
Lincoln-Petersen	0-2883	0-2097	(n/a)	0-1524	90-928	0-1228	0-1332	44-738	90-738
Chapman	11-1007	0-761	0-2116	127-1005	161-728	105-838	31-789	110-574	161-574
Schnabel	193-5845	252-4878	396-6293	440-5703	415-1824	421-1493	441-1181	442-896	442-896
Schum.-Eschm.	531-2114	535-1219	619-3399	578-1464	478-940	495-838	501-783	451-701	619-701
Jolly-Seber	315	198	845	385	333	124	47	(n/a)	(47-845)
Oedipoda caerulescens	35/3	18/0	17/2	26/3	34/1	33/3	28/6	40/6	**614-879**
Lincoln-Petersen	0-941	(n/a)	0-1801	0-1891	0-12871	0-3710	227-1537	336-2478	336-941
Chapman	86-614	0-2980	64-1002	155-1247	11-4432	293-2425	316-1257	480-2001	480-614
Schnabel	90-3038	182-3977	277-1184	382-989	573-1430	718-1554	726-1400	806-1504	806-989
Schum.-Eschm.	98-1085	197-3509	296-2110	411-1711	616-3143	788-2955	764-1953	879-1880	879-1085
Jolly-Seber	27	361	138	567	1549	989	746	(n/a)	(27-1549)
Psophus stridulus	21/2	7/0	19/1	6/0	3/0	10/3	12/3	4/0	**349-379**
Lincoln-Petersen	0-631	(n/a)	0-2950	(n/a)	(n/a)	0-544	0-714	(n/a)	0-544
Chapman	30-349	0-862	0-1041	0-1211	0-1053	50-383	63-494	0-1342	63-349
Schnabel	61-1895	105-2089	201-3129	315-981	350-1022	280-868	265-824	289-877	350-824
Schum.-Eschm.	154-379	163-1262	291-1599	376-2301	443-2621	289-968	288-701	315-820	379-443
Jolly-Seber	176	32	110	33	32	39	10	(n/a)	(10-176)
Sphingonotus caerulans	47/2	37/9	47/4	26/11	46/9	32/7	52/9	63/15	**621-697**
Lincoln-Petersen	0-1856	132-509	46-2445	186-518	334-1343	293-1545	511-2100	621-1639	509-621
Chapman	85-1001	156-443	296-1757	199-474	382-1167	365-1300	581-1823	647-1511	443-647
Schnabel	156-4897	195-2367	348-1546	333-878	430-843	489-867	608-947	697-1014	697-843
Schum.-Eschm.	310-1605	243-528	342-1319	309-769	398-926	468-999	577-1242	682-1306	528-682
Jolly-Seber	416	443	591	204	610	415	1265	(n/a)	(415-1265)

Table 2. Hymenoptera: 95% confidence intervals of population estimates and values of the Jolly-Seber estimator at each census (n/a – not available).

Legends: *N'* – the smallest overlapping confidence interval for each estimation and (in bold) for all estimations ("summarizing" interval – see text). For Jolly-Seber estimator the range of estimates is given in brackets; * number of captured specimens (n_i); ** number of recaptures (m_i).

	Census No (*i*)							
Species	**3**	**4**	**5**	**6**	**7**	**8**	**9**	***N'***
Symmorphus allobrogus	37*/12**	37/21	23/19	12/11	5/4	2/2	1/1	**155-186**
Lincoln-Petersen	118-338	124-225	112-167	105-155	57-243	121	(n/a)	121-155
Chapman	132-305	129-214	113-164	101-157	58-230	0-516	(n/a)	124-159
Schnabel	109-2486	129-372	132-261	134-226	141-206	148-190	154-179	154-179
Schum.-Eschm.	191-255	158-234	137-214	134-199	137-193	138-188	139-186	186-191
Jolly-Seber	109	204	72	111	26	5	(n/a)	(5-204)
Symmorphus debilitatus	4/2	1/1	5/3	2/1				**15-22**
Lincoln-Petersen	0-47	(n/a)	0-37	0-260				0-37
Chapman	0-31	(n/a)	5-29	0-121				5-29
Schnabel	5-164	6-127	9-105	10-47				10-47
Schum.-Eschm.	14-26	11-25	13-22	15-24				15-22
Jolly-Seber	20	9	14	(n/a)				(9-20)
Ancistrocerus antilope	3/2	2/0	2/2	2/2	1/1	1/1		**6-9**
Lincoln-Petersen	0-12	(n/a)	6	6	(n/a)	(n/a)		6-12
Chapman	1-8	0-112	0-23	0-23	(n/a)	(n/a)		1-8
Schnabel	1-33	2-42	3-45	3-15	3-14	4-11		4-11
Schum.-Eschm.	3-6	3-26	4-13	4-10	5-9	5-9		5-9
Jolly-Seber	29	23	14	8	3	(n/a)		(3-29)
Chrysis purpurata	5/4	3/2						**7-12**
Lincoln-Petersen	4-16	0-37						4-16
Chapman	5-14	0-28						5-14
Schnabel	3-123	5-74						5-74
Schum.-Eschm.	7-12	7-14						7-12
Jolly-Seber	8	(n/a)						(8)

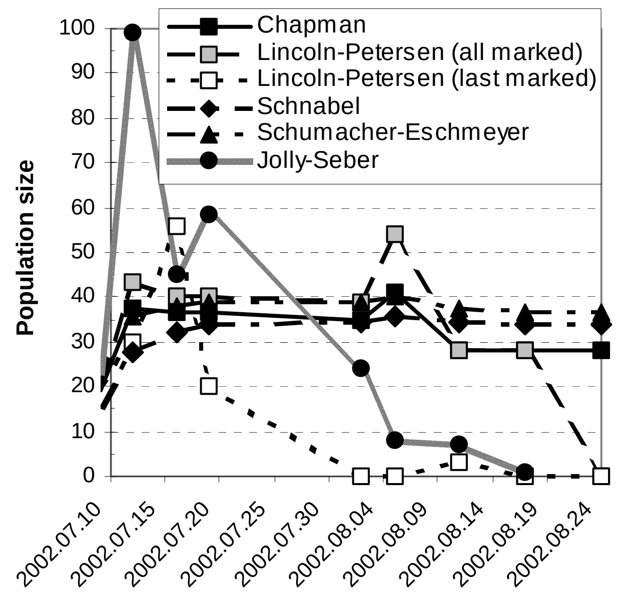
Table 3. Diptera: 95% confidence intervals of population estimates and values of the Jolly-Seber estimator at each census (n/a – not available).

Legends: *N'* – the smallest overlapping confidence interval for each estimation and (in bold) for all estimations ("summarizing" interval – see text). For Jolly-Seber estimator the range of estimates is given in brackets; * number of captured specimens (n_i); ** number of recaptures (m_i).

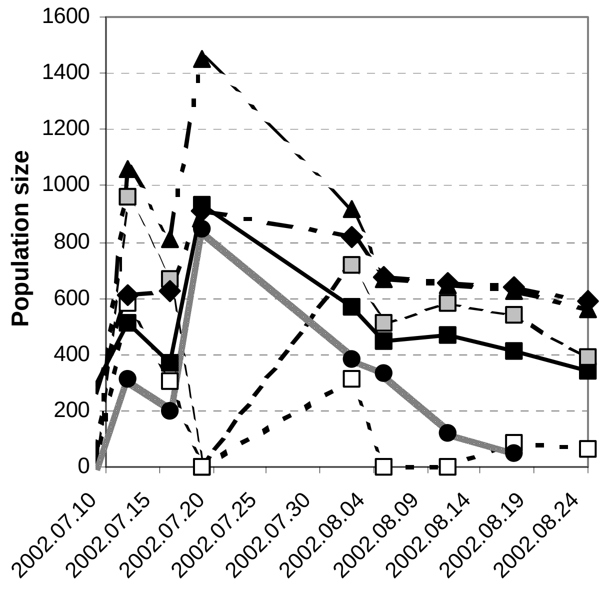
	Census No (*i*)							
Species	**3**	**4**	**5**	**6**	**7**	**8**	**9**	***N'***
Volucella pellucens	34*/0**	20/1	6/2	4/1	6/1	1/0	3/0	**350-739**
Lincoln-Petersen	(n/a)	0-3466	0-566	0-1202	0-1667	(n/a)	(n/a)	0-566
Chapman	0-1805	0-1219	8-350	0-486	0-639	(n/a)	0-1248	8-350
Schnabel	(n/a)	396-7564	285-4651	279-4203	305-3009	366-1286	443-997	443-997
Schum.-Eschm.	(n/a)	739-2969	242-1342	257-973	290-861	309-877	340-1006	739-861
Jolly-Seber	0	11	37	15	4	0	(n/a)	(0-37)

Cheilosia illustrata	15/2	30/3	17/3		**454-732**
Lincoln-Petersen	0-1339	0-1845	0-1364		0-1339
Chapman	47-751	152-1210	115-918		152-751
Schnabel	148-4929	266-6042	343-1388		343-1388
Schum.-Eschm.	282-732	378-1077	454-907		454-732
Jolly-Seber	32	103	(n/a)		(32-103)
Hydrotaea ignava	42/3	126/1	75/2	80/1	**4440-6971**
Lincoln-Petersen	0-6838	0-103096	0-36529	0-112448	0-6838
Chapman	525-4440	317-34781	1283-19411	249-38062	525-4440
Schnabel	1107-38255	2974-67486	4718-17062	6971-16092	6971-16092
Schum.-Eschm.	2437-3723	2707-27468	4274-27851	6167-38762	3723-6167
Jolly-Seber	495	65	2080	(n/a)	(65-2080)

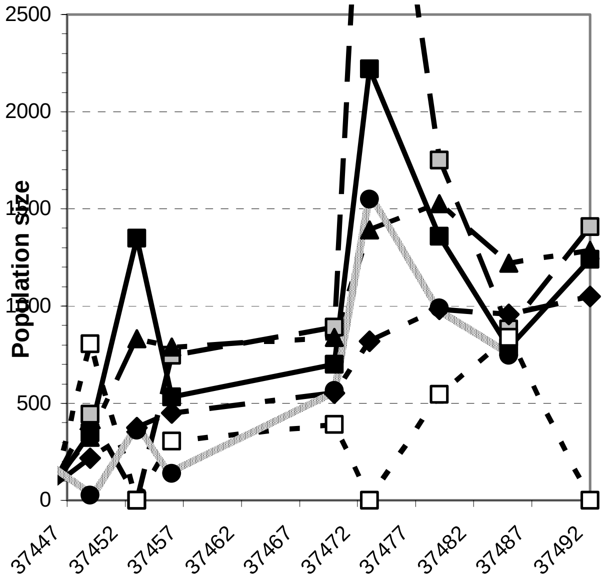
1. *Metrioptera bicolour*



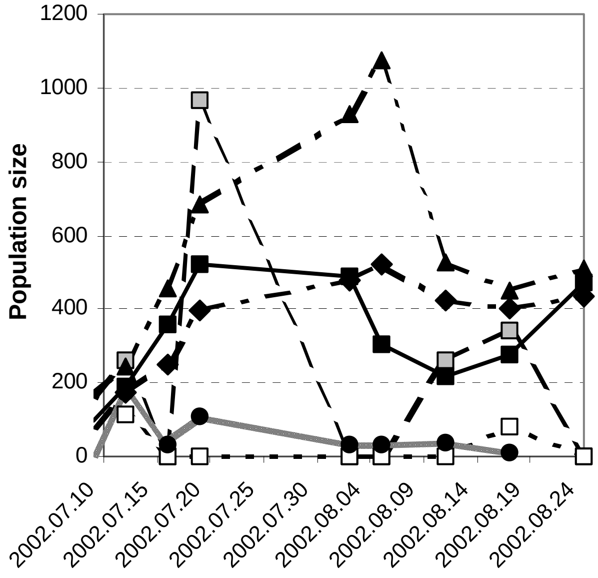
2. *Platycleis albopunctata*



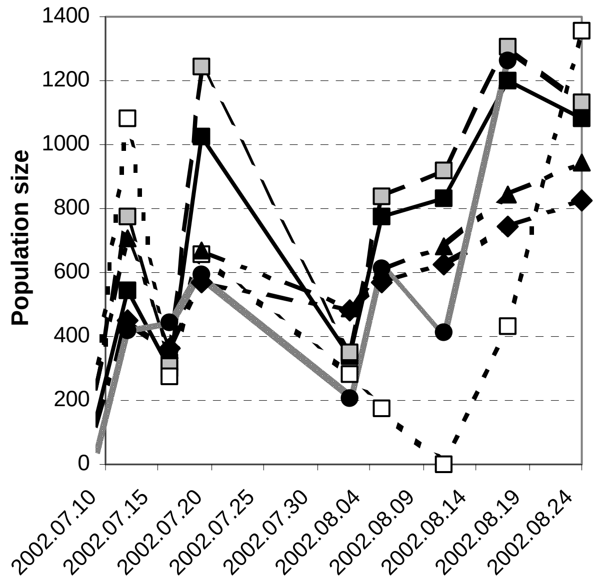
3. *Oedipoda caerulescens*



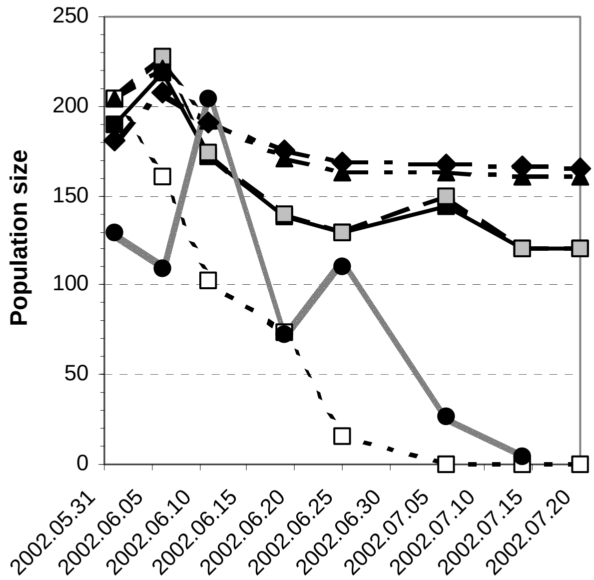
4. *Psophus stridulus*



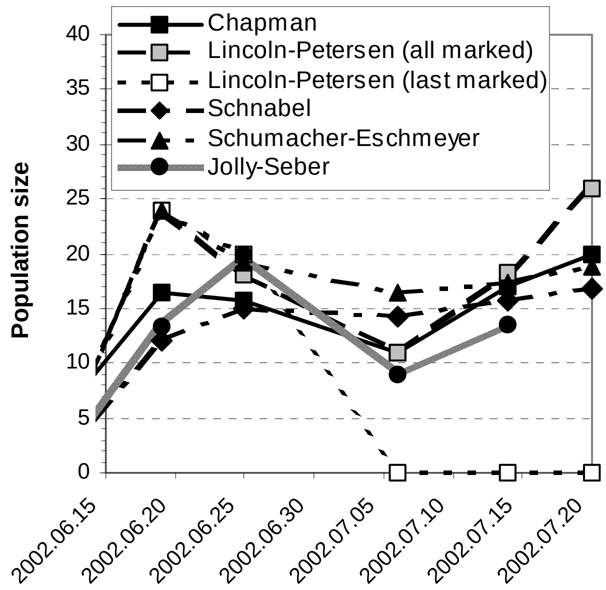
5. *Sphingonotus caerulans*



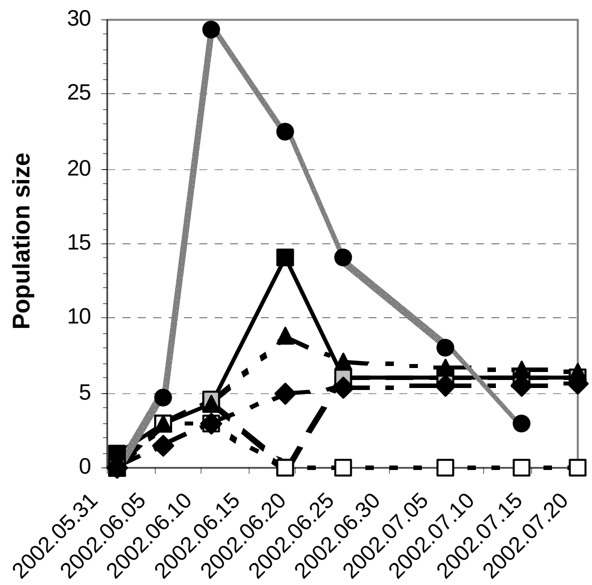
6. *Symmorphus allobrogus*



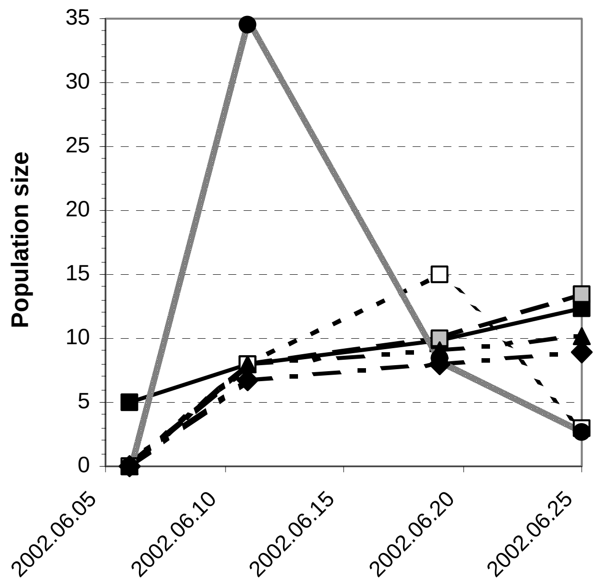
7. *Symmorphus debilitatus*



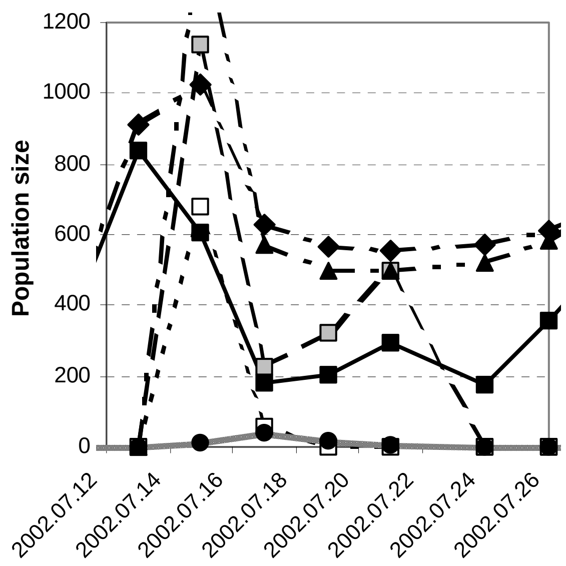
8. *Ancistrocerus antilope*



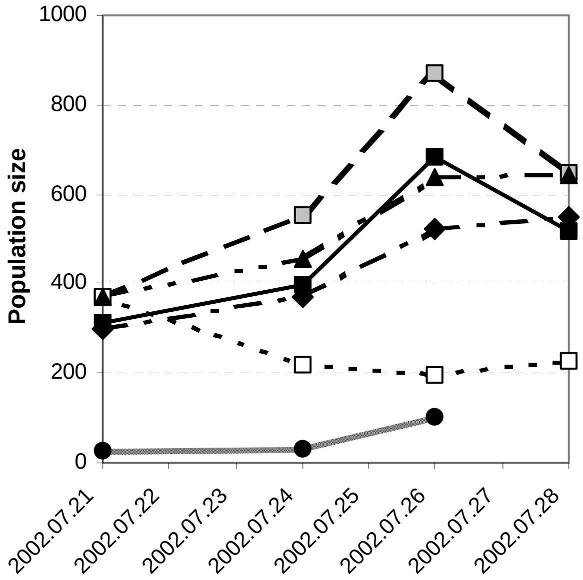
9. *Chrysis purpurata*



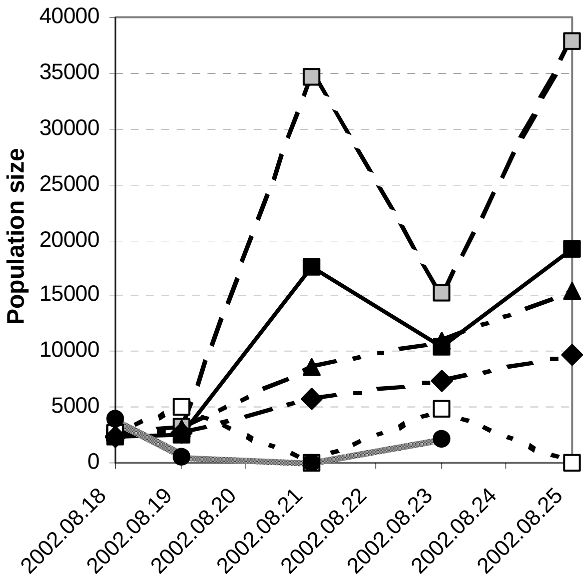
10. *Volucella pellucens*



11. *Cheilosia illustrata*



12. *Hydrotaea ignava*



Figures 1-12. Changes of size estimates (starting from the second or third census) of the model populations of Orthoptera (5 species), Hymenoptera (4 species) and Diptera (3 species), using 5 estimators. For Lincoln-Petersen estimator two values are presented, one with n_1 meaning individuals captured and marked in the previous census (“last marked”), the second with n_1 meaning individuals marked in all earlier censuses (“all marked”).

For Orthoptera tentative observations did not show visible decrease of population density during the sampling period, except for *M. bicolor*. The visible abundance of the latter species decreased in August. The observations revealed that *M. bicolor* was very sessile, possibly territorial species: marked stridulating males were recaptured mostly on the same stems of grasses or shrubs as they were earlier released. As result, we had high recapture rate and we could obtain reasonably narrow confidence intervals of Chapman and Schumacher-Eschmeyer estimators of this species population after four censuses (Table 1).
In contrast, *P. stridulus* was highly mobile species: although most of specimens observed in the sampling area could be captured and marked, the subsequent censuses contained low, or even no recaptures, indicating high specimen (mostly male) exchange rate with neighbour areas. As expected, all estimators were sensitive to lack of recaptures in the censuses, however Chapman and Schnabel estimates were reasonable in those cases. *P. stridulus* was the only orthopteran species with Jolly-Seber estimator always giving unrealistically lower population estimates than closed population estimators due to low recapture rates (low m_i and z_i – see Jolly-Seber formula in Material and Methods).
O. caerulescens and *P. albopunctata* were rather mobile as well, but unlike *P. stridulus*, more difficult to capture, thus only part of the observed specimens could be marked during the census. *S. caerulans* was more sessile, connected with sparse vegetation and open sand plots on the sampling area. For *O. caerulescens* and *S. caerulans*, in cases of high fluctuation of recapture rates, Schnabel estimator could provide the narrowest confidence interval, however in all other cases combination of Chapman and Schumacher-Eschmeyer estimators seemed to be more efficient, giving reasonable population estimates after 6-8 censuses (Table 1).
The MRR study confirmed, that the sampling area for Hymenoptera contained small and rather closed populations of wasps: after two or

three censuses the recaptures made more than half of all captured specimens. In this case results of Jolly-Seber estimator were more or less coinciding with those of the closed population estimators. Changes of values of the Jolly-Seber estimator probably reflected the real seasonal change of the imago abundance in the populations of the univoltine wasp species. For all studied these species, having high and stable recapture rates, the Schumacher-Eschmeyer estimator provided the narrowest confidence limits after 4-6 censuses (Table 2).

The studied Diptera provided us with examples of low recapture rates despite the shortest, in comparison with Orthoptera and Hymenoptera, 1-3 day intervals between censuses. As with *P. stridulus*, Jolly-Seber estimator was rather useless, giving unrealistically low values due to low m_i and z_i. Seemingly reasonable estimates were provided by Schnabel and Schumacher-Eschmeyer estimators after 4-5 censuses; Schumacher-Eschmeyer formula giving the narrowest confidence limits (Table 3).

Summarising this first experience of application of the MRR method for insects in Lithuania, we may note that in cases of sufficient number of recaptured specimens, as for *Metrioptera bicolor*, *Symmorphus allobrogus*, *S. debilitatus*, or *Ancistrocerus antilope*, Jolly-Seber estimator provides similar results to those of closed population model estimators. However, in cases of low recapture rate, the estimators based on the closed population model seem to be more efficient.

Conclusions

Lincoln-Petersen estimator was the least adequate, in comparison with the other estimators, and should not be recommended to use.

In cases of high recapture rate the estimators based on closed population model (Chapman, Schnabel and Schumacher-Eschmeyer) provided similar results with relatively narrow confidence intervals, expectedly reflecting the real size of insect population.

In cases of low recapture rate Schnabel estimator was less susceptible to the fluctuation or partial lack of recaptures in the series of censuses, but combination of Chapman and Schumacher-Eschmeyer estimators provided the narrowest confidence interval.

In general, Jolly-Seber estimator, originally designed to assess population dynamics, was little efficient in assessment of the population size of insects with short-living stage of imago, lacking territorial behaviour and relatively high mobility. In cases of low recapture rates it provided much more fluctuating results than the cumulative estimators based on the closed population model, and it often underestimated the probable population size.

Estimators based on closed population model provided little fluctuating results with relatively narrow confidence interval after 4-8 censuses, dependently on the recapture rate.

Acknowledgements

The research was supported by the Lithuanian State Science and Studies Foundation (contract No T-579).

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Received: October 31, 2003.