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POPULATION DYNAMICS OF ENDANGERED SPECIES *COENONYMPHA OEDIPPUS* FABRICIUS, 1787 (LEPIDOPTERA: SATYRIDAE) ON THE LJUBLJANSKO BARJE (SLOVENIA)

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Abstract – The False ringlet (*Coenonympha oedippus* Fabricius, 1787) is the most threatened European butterfly species. In Slovenia the species lives in extensively managed wet meadows of the Ljubljansko barje and in the vicinity of Grosuplje, as well as in dry scrubby grasslands of the Primorska region. In June and July of 1995 and 1996, we studied the dynamics of the population on the Ljubljansko barje, where one of the last marsh populations of the species are to be found in Slovenia. A mark-release-recapture survey was carried out on study site covering an area of 1.27 ha (1995) and 2.63 ha (1996). Mark-recapture data for each sex were processed separately to estimate population size and density, sex ratio, residence (survival) times and catchability.

KEY WORDS: *Coenonympha oedippus*, population dynamics, population size, sex ratio, survival rate, Ljubljansko barje

Izvleček – POPULACIJSKA DINAMIKA OGROŽENE VRSTE *COENONYMPHA OEDIPPUS* FABRICIUS, 1787 (LEPIDOPTERA: SATYRIDAE) NA LJUBLJANSKEM BARJU (SLOVENIJA)

Barjanski rjavček (*Coenonympha oedippus* Fabricius, 1787) je najbolj ogrožena vrsta med evropskimi dnevnimi metulji. V Sloveniji živi na ekstenzivnih vlažnih travnikih Ljubljanskega barja in v okolici Grosuplja ter na suhih zagrmičenih travnikih na Primorskem. V juniju in juliju 1995 in 1996 smo proučevali dinamiko populacije na Ljubljanskem barju, kjer je življenjski prostor nekaj zadnjih močvirskih populacij vrste v Sloveniji. Z metodo lova, markiranja in ponovnega ulova smo vzorčili na raziskovani površini 1,27 ha (1995) oz. 2,63 ha (1996). Za oceno velikosti

in gostote populacije, spolnega razmerja, stopnje prisotnosti (preživetja) in ulovljivosti odraslih osebkov smo podatke obdelali ločeno za oba spola.

KLJUČNE BESEDE: *Coenonympha oedippus*, populacijska dinamika, velikost populacije, spolno razmerje, stopnja preživetja, Ljubljansko barje

Introduction

The False Ringlet (*Coenonympha oedippus* Fabricius, 1787) is the most seriously threatened European butterfly species (Heath 1981, Balleto & Kudrna 1985, Kudrna 1986, SBN 1987, Chinery 1989, Munguira 1995, Schmid 1996) and one of the seven critically endangered butterfly species in Europe (Swaay & Warren 1998). It is protected by the Appendices of the Bern Convention (Council of Europe 1992) and the Directive of the European Union Council 92/43/EEC (European Communities 1992).

Severe decline of the species over its European range is mainly due to land drainage, the intensification of agriculture, agricultural abandonment and changing management, leading to fragmentation of suitable habitats and isolation of local populations.

At present no practical measures for conservation of species are taken in European countries. Namely, little is known of the ecological needs of the species. Its precise recent geographical distribution is still unknown, especially in Central and Eastern Europe. Few studies of the morphometrics of the specimens in the collections were done, which figure out the appearance of 12 subspecies (Bischof 1968, Krzywicki 1966) inside the European range. The information about biology of pre-adult stadiums is gathered mostly from rearing experiments (breed in captivity). Almost nothing is known of the structure, dynamics and the genetics of the present populations in Europe.

In Slovenia, the species lives on fens and extensive wet meadows of central part of Slovenia (Ljubljansko barje, the vicinity of Grosuplje). In the eastern part of Ljubljansko barje, Slovenia's last marsh populations of *C. oedippus* can be found. The species is also distributed in SW part of Slovenia (from Goriška Brda in the north to the Koper hills and the Dragonja valley in the south, and to the southeast edge of Trnovski gozd, the Karst and Podgorje karst in the east), where it inhabits dry scrubby grasslands on limestone or flysch (Čelik 2003).

In this paper, we infer the population dynamics of local population of *C. oedippus* in the SE part of Ljubljansko barje. Demographic parameters, such as population size, density, sex ratio, catchability and residence times are represented at the first time. The present results are only one part of my master thesis (Čelik 1997), which was carried out with the goal of studying population parameters (structure and dynamics of population, imagoes mobility, dispersion, size and shape of imagoes home range) and ecological needs of pre-adult stadiums and imagoes and to suggest the priority actions for conservation of remnant populations of this endangered species on the Ljubljansko barje.

Material and methods

The species

The False Ringlet (*Coenonympha oedippus* Fabricius, 1787) is a palaeartic species with a ponto–caspiansouth siberian–manchurian type of range (Varga 1977). The distribution of the species is disjunct: in Europe, there are isolated populations in France, Switzerland, Liechtenstein, Austria, Italy, Slovenia, Croatia, Hungary, Poland, Russia (Kudrna 2002), Germany (Braü 2003 pers. comm.), Ukraine and Belarus (Swaay and Warren 1998); the species only has more or less continued distribution in the Asian part of its range (southern Russia, northeastern Mongolia and China, northern Korea). In Spain, the species has only been recorded once, in 1988 in Navarre, and it is therefore defined on a national scale as data deficient species (“indeterminate”) (Munguira 2002 pers. comm.). The species is extinct in Belgium, Slovakia and Bulgaria (Lhonore, 1996; Swaay and Warren, 1998; Abadijev 2001).

The False Ringlet lives in the zone of deciduous forests, forest steppes and steppes, where it occurred in the following habitats: rich fens, wet meadows (with purple moor grass and sedges), wet and dry heaths, grassy forest clearings (alluvial forests with willow; forests of oak and birch), light beech forests, overgrown dry grasslands (only in Slovenia, Italy and Croatia), forest steppe and steppe (Čelik 2003).

Adult butterflies emerge in early June and fly until late July. They visit flowers of Cyperaceae and Asteraceae (*Carduus*, *Centaurea*, etc.), rarely Papilionaceae (Helsdingen, Willemse, Speight 1996). In Ljubljansko barje, the only known nectaring plant of the species is tormentil (*Potentilla erecta*, fam.: Rosaceae) (Čelik 1997, 2003) Adults are active, in particular, in the lower level of grassland vegetation, where they also rest (Čelik 1997).

Eggs are deposited on the leaves of the food plant, singly, 5–20 cm above the ground (Čelik 1997). Larvae hatch in July and early August. They feed until the end of September when they start to hibernate on the roots of grassy vegetation. They emerge from hibernation in April or at the beginning of May and are active to the end of May, when they begin to pupate on the leaves of host-plants. The larval food plants are leaves of Purple Moor Grass (*Molinia caerulea*), Sedge (*Carex flava*, *C. hostiana*, *C. panicea*, *C. distans*) (Čelik 1997, 2003), Black Bog-rush (*Schoenus nigricans*), Meadow Grass (*Poa* sp.) (Lhonore 1996) and Cottongrass (*Eriophorum*) (Weidemann 1995).

Study area

The Ljubljansko Barje (centroid: long: 14° 26' 13" E, lat: 46° 15' 54" N), with 12588 ha, is located in the pre-alpine region of Slovenia, at an altitude of 288–289 metres. It is referred to the european CORINE site classification system (code S00000035) (Dobravec et al. 2001). The central plain is exposed to regular flooding, which is one of the most important characteristics of Ljubljansko Barje.

The local population on a wet meadow (centroid: long: 14° 33', lat: 45° 58') near Škofljica (SE part of Ljubljansko barje) was monitored during the flight season in 1995 and 1996.

A mark-release-recapture experiment was carried out on a study area, where a grid of 10 m squares was established. In 1995, only the central part of the population was included in the study area of 1.27 ha. In 1996, we extended study area on 2.63 ha, using data on imagoes mobility in previous year.

The search area was unfertilized wet meadow on clay with prevailing vegetation community *Molinietum caeruleae* subasoc. *Caricetosum davallianae* (Seliškar, pers. comm.). Moist depressions with standing water still in early July predominated there. Marsh conditions permit mowing once a year at the end of July, when depressions are dried enough.

Field methods

The search site was visited daily, weather permitting, during the flight season of *C. oedippus* in 1995 (22.6. – 20.7.) and in 1996 (14.6. – 19.7.). Within study area, standard transect was performed at each visit. Butterflies were netted and marked with individual number on the underside of the left hindwing with a thin point permanent pen (Schwan Stabilo OH Pen 841S) and immediately released at the location of their capture. On initial capture the following data were recorded: the (1) individual code, (2) sex, (3) position of capture (number of square 10x10m), (4) time and date.

Data analysis

Mark-recapture data for each sex were processed separately to estimate population size and density, sex ratio, residence (survival) times and catchability.

Demographic parameters (daily population size, estimated sex ratio, daily residence rate) were estimated using Jolly – Seber method as applied to open populations (Seber 1982, Krebs 1989).

Estimates of daily adult numbers (N_i) were calculated separately for males and females.

Total daily adult numbers is the sum of the independent estimates for both sexes ($= N_{i\sigma} + N_{i\varphi}$).

Peak butterfly density is the maximum daily N_i estimate observed in a sampling date, divided by the site area.

Average butterfly density is the sum of all N_i estimates in a site, divided by the product of the site area and the number of testable sampling days.

The term “residence” is used rather than “survival” because emigration and death cannot be separated in this study (see Watt et al 1977).

The daily residence rate Φ_i estimates the fraction of animals from day i which will remain in the population on day $i+1$. Daily residence rates were calculated by three different methods: (1) Scott's (1973) Method 1 (Φ_s), (2) variance-weighted averaging (Φ_v) (Tabashnik 1980) and (3) recapture decay plotting (Φ_r) (Watt et al. 1977). The first two methods generate weighted averages of the daily Jolly Φ_i , and base res-

idence on all animals marked. In the third method, number of days in residence (x) is plotted against the logarithm of the number of animals in residence x days or longer; the slope of this plot is $\ln(\Phi)$. A recapture decay plot thus bases residence only on those animals recaptured at least once (excluding same day recaptures).

Mean expected residence times are: $-(\ln \Phi)^{-1}$ as in Cook et al (1967).

Total number of animals present in the brood is: $(1 - \Phi)\Sigma N_i$ (Cook et al 1967, Watt et al 1977).

Capture sex ratio (CSR) is defined as the number of male captures on day i , divided by the number of female captures on day i . If the same male (female) is captured x times, this counts as x male (female) captures (Tabashnik 1980).

Catchability refers to the relative probability of being captured. We used two techniques to determine whether males and females were equally catchable: (1) joint residence-catchability test (JRC) and (2) CES test: capture sex ratio (CSR) vs. estimated sex ratio (ESR) (Tabashnik 1980). The JRC test plots the natural logarithm of the recapture probability ratio against time so as to distinguish between effects of unequal residence times (between sexes) and of unequal catchabilities on recapture probability. The CES test estimates relative catchability of males and females for single sampling date, and gives an average estimate of relative catchability for a set of sampling dates.

Results

Capture statistics

The number of sampling days were 14 in 1995 and 15 in 1996. In both flying seasons *C. oedippus* exhibited a bias toward males compared to females marked and recaptured (Table 1).

Table 1: Capture statistics for *C. oedippus* in 1995 (22.6. - 20.7.) and 1996 (14.6. 19.7.) on Ljubljansko barje.

	1995			1996		
	♂♂	♀♀	♂♂+♀♀	♂♂	♀♀	♂♂+♀♀
No. of marked individuals	166	107	273	286	175	461
No. (%) of recaptured individuals *	50 (30)	26 (24)	76 (28)	140 (49)	83 (47)	223 (48)
No. of captures	236	138	374	546	337	883
No. of recaptures **	70	31	101	260	162	422
Average no. of captures per individual (captured individuals)	1.4	1.3		1.9	1.9	
Average no. of captures per individual (recaptured individuals)	2.4	2.2		2.9	3.0	
Maximum no. of captures per individual	5	4		7	7	

* Records for recaptured individuals, which were recaptured only on marking day, providing at least 30 min had elapsed since initial capture, are combined with those for daily recaptured individuals.

** Records for same-day recaptures (=10% of total), providing at least 30 min had elapsed since initial capture, are combined with those for daily recaptures.

Daily numbers and densities

The estimates of daily numbers (N_i) for *C. oedippus* on Ljubljansko barje during 1995 and 1996 are given in Fig. 1 (year 1995) and Fig. 2 (year 1996). Continuous sampling in June and July 1996 was prevented because of cold and rainy weather with temperatures between 13° and 20°C.

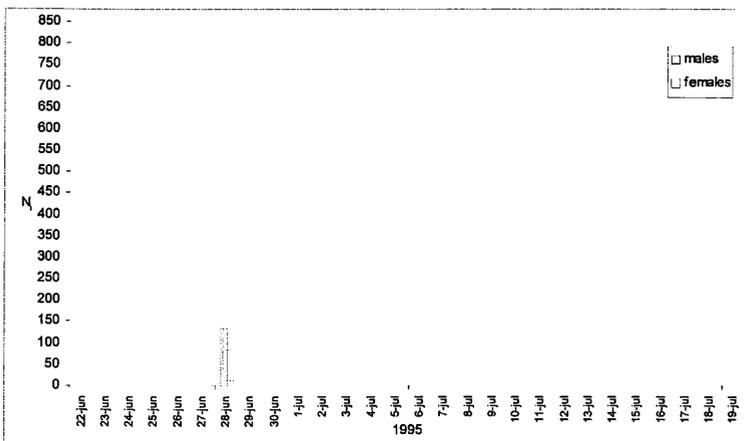


Fig. 1: Daily population sizes (N_i) for male and female *C. oedippus* during 1995 on Ljubljansko barje. Vertical lines are confidence intervals of N_i .

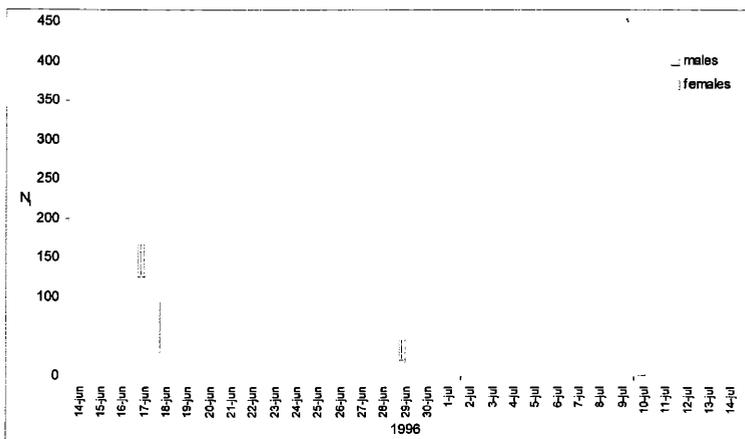


Fig. 2: Daily population sizes (N_i) for male and female *C. oedippus* during 1996 on Ljubljansko barje. Vertical lines are confidence intervals of N_i .

Peak 1995 flight was on 3 July (177 adults). The estimated peak numbers were 169 for males (3 July) and 64 for females (10 July). For 1995 the estimated peak densities were 133 males/ha and 50 females/ha.

In 1996 the population peaked on 19 June (288 adults). The estimated peak numbers were 223 for males (19 June) and 71 for females (5 July). The estimated peak densities were 85 males/ha and 27 females/ha.

The average daily male density was 53 ha⁻¹ (1995), and 31 ha⁻¹ (1996), while for females the density was 16 ha⁻¹ (1995), and 17 ha⁻¹ (1996).

The maximum population density was 139 adults/ha (1995) and 109 adults/ha (1996).

Total numbers per brood

The total number of adults present ($(1 - \Phi) \sum N_i$) in 1995 is estimated at: 625 (by Φ_s); 723 (by Φ_v); and 571 (by Φ_r). For the 1996 population of *C. oedippus*, the total number of adults is estimated at: 850 (by Φ_s); 847 (by Φ_v); and 898 (by Φ_r).

Total brood size is an important population parameter in conservation programme including continuous monitoring of population.

Sex ratio

Daily changes in capture sex ratio (male/female) show the population dynamics through the flight period. The sex ratio (male/female) of marked individuals was the same for both years: 1.6 : 1.

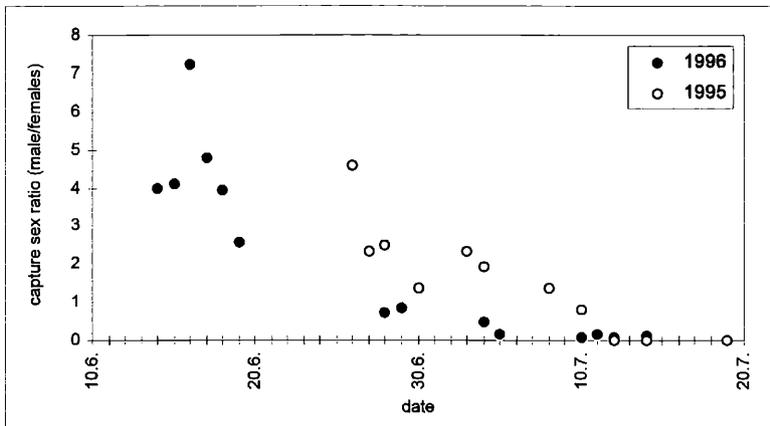


Fig. 3: Daily changes in capture sex ratio (male/female) of *C. oedippus* during 1995 and 1996 on Ljubljansko barje.

The daily numbers estimates for both years suggest that males emerge before females (protandry). Males outnumbered females substantially in the early stages of a brood (max. capture sex ratio: 4.6 on 26 June 1995; 7.3 on 16 June 1996), but not at the end of each brood (Fig. 3). In both years capture sex ratio was approximately 1 (one) in the second half of the flight season, when numbers of males declined and females peak numbers occurred.

Residence times and catchability

Fig. 4 and Fig. 5 present the recapture decay plots for both sexes in year 1995 and 1996. In both years residence follows a constant loss rate ($1 - \Phi_r$) (year 1995: ♂♂: $k = -0.44$, $F_{1,8} = 606.5$, $P < 0.001$; ♀♀: $k = -0.62$, $F_{1,4} = 80.5$, $P < 0.001$; year 1996: ♂♂: $k = -0.29$, $F_{1,15} = 365.8$, $P < 0.001$; ♀♀: $k = -0.21$, $F_{1,23} = 409$, $P < 0.001$).

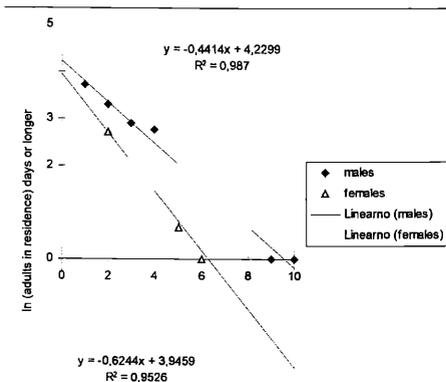


Fig. 4

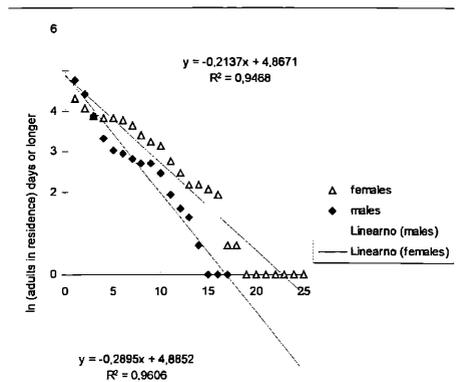


Fig. 5

Fig. 4: Recapture decay plot for *C. oedippus* on Ljubljansko barje in 1995. Slope (k) of regression line is: $k = \ln(\Phi_r)$. Residence rate Φ_r is $-\ln(k)$.

Fig. 5: Recapture decay plot for *C. oedippus* on Ljubljansko barje in 1996. Slope (k) of regression line is: $k = \ln(\Phi_r)$. Residence rate Φ_r is $-\ln(k)$.

Table 2 shows residence statistics for both sexes in 1995 and 1996. There is more variation among the estimates of daily residence rates (Φ_s , Φ_v , Φ_r) in 1995 because lower percentage of individuals were recaptured (1995: 28%, 1996: 48%). The higher are differences between the estimates of daily residence rates, the wider is range of values for estimated residence times.

Table 2: Residence of *C. oedippus* on the study area on Ljubljansko barje in 1995 and 1996. The ranges of values for estimated residence times are based on the lowest and highest estimates of daily residence rate. See Material and Methods for details.

Year	Sex	Estimated daily residence rate			Estimated residence time (days) - $(\ln\Phi)^{-1}$	Maximum residence seen (days)
		Φ_s	Φ_v	Φ_r		
1995	♂	0.580	0.543	0.643	1.6 – 2.3	10
1995	♀	0.557	0.423	0.563	1.2 – 1.6	6
1996	♂	0.773	0.799	0.749	3.5 – 4.5	17
1996	♀	0.802	0.764	0.808	3.7 – 4.7	25

The joint residence-catchability tests (JRC test) for both flying seasons are shown in Fig. 6 (year 1995) and Fig. 7 (year 1996). The y-intercept (n) of the linear regression, an estimation of catchability, is not significantly different from zero in both years, indicating that males and females within each flying season were equally catchable. Fig. 6 shows that slope (k) of the linear regression of the natural logarithm of the recapture probability ratio is not significantly different from zero, demonstrating the equal residence rates for both sexes. In 1996 females have a significantly greater residence rate than males.

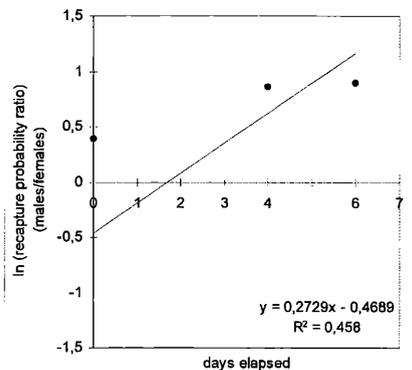


Fig. 6: Joint residence-catchability test, males vs. females, for *C. oedippus* on Ljubljansko barje in 1995. Linear regression of the natural logarithm of the recapture probability ratio on days elapsed between release and recapture. The y-intercept (n) is not significantly different from zero ($n = -0.47$, $t = -0.98$, $P > 0.4$, $\alpha_0 = e^{-0.47} = 0.6$). The slope (k) is not significantly different from zero ($k = 0.27$, $F_{1,5} = 4.23$, $P > 0.1$, $\lambda_0 = e^{0.27} = 1.3$).

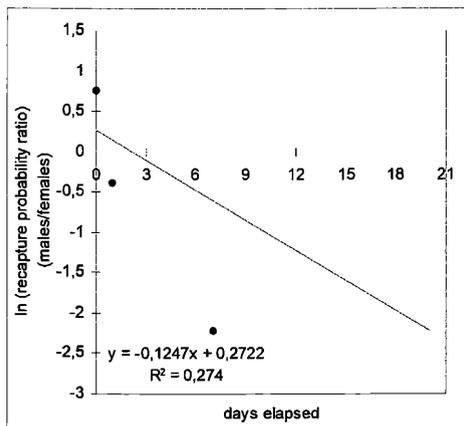


Fig. 7: Joint residence-catchability test, males vs. females, for *C. oedippus* on Ljubljansko barje in 1996. Linear regression of the natural logarithm of the recapture probability ratio on days elapsed between release and recapture. The y-intercept (n) is not significantly different from zero ($n = 0.27$, $t = 0.52$, $P > 0.6$, $\alpha_0 = e^{0.27} = 1.3$). The slope (k) is significantly different from zero ($k = -0.13$, $F_{1,14} = 5.28$, $P < 0.05$, $\lambda_0 = e^{-0.13} = 0.88$).

Daily Jolly's Φ_i can be calculated independently for each sex within flying season for separate time intervals between successive sampling days. Comparison of Jolly Φ_i for 6 intervals in 1995 indicates the equal residence for both sexes. For 4 of these 6 intervals the male Φ_i is higher than the female Φ_i , but only for one interval the difference is significant ($P < 0.001$). The female Φ_i is higher for 2 intervals, with a significant difference for one interval ($P < 0.001$). Comparison of Jolly Φ_i for 9 intervals in 1996 suggests, that males suffered highly loss rate ($1 - \Phi_i$) than females. Only for 3 of these 9 intervals the male Φ_i is higher than the female Φ_i , with a significant difference for two intervals ($P < 0.01$). The female Φ_i is higher for 6 intervals, with a significant difference for 5 intervals ($P < 0.01$).

Observable residence time is the number of days between first and last capture of individual. Beside Jolly's Φ_i , observable residence time takes into account only recaptured individuals. Observable residence time for the males compared to the females in 1995 also suggest that there is no significant difference in residence between sexes ($Z = -0.18$, $P > 0.8$). The female observable residence time is higher than male observable residence time in 1996, the difference is significant ($Z = -4.18$, $P < 0.001$).

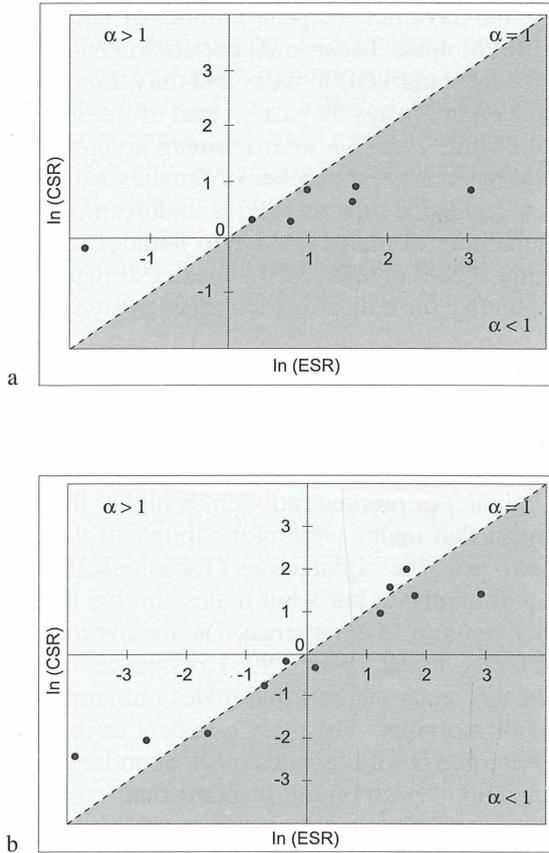


Fig. 8: CES test: capture sex ratio (CSR) vs. estimated sex ratio (ESR) for *C. oedippus* on Ljubljansko barje in 1995 and 1996. $\alpha_{oi} = 1$, ♂ catchability = ♀ catchability; $\alpha_{oi} > 1$, ♂ catchability > ♀ catchability; $\alpha_{oi} < 1$, ♂ catchability < ♀ catchability. **a:** year 1995: $\alpha_{o \text{ average}} = 0.6$, $Z = -1.15$, $P > 0.3$. **b:** year 1996: $\alpha_{o \text{ average}} = 0.9$, $Z = -0.18$, $P > 0.9$.

Observable residence time for the males in 1995 compared to the males in 1996 is not significantly different ($Z = -0.18$, $P > 0.8$). The female observable residence time in 1995 is lower than female observable residence time in 1996, the difference is very significant ($Z = -3.22$, $P < 0.001$). Lower observable residence time of females in 1995 compared to females in 1996 (equal, compared to males in 1995) is the consequence of untimely mowing in 1995. The west part of study area in 1995 was mowed on 11th July, the day after the peak number of females. The untimely mowing was not so harmful to males because its population had already decreased. After the 11th July 1995, fresh (unmarked) females and only three marked females (marked before 11th July and caught always on eastern part of the study area) were caught on the eastern part of the study area. So, after mowing no more old females from western part were caught. It means that number of females with long survivals is under-represented and their residence time in 1995 is underestimated.

The average catchability of males relative to females ($\alpha_{o\ average}$), estimated as the mean capture sex ratio (CSR) divided by the mean estimated sex ratio (ESR), shows again an equal catchability for both sexes within each flying season (Fig. 8 a and b).

Discussion

Sex ratio

Sex ratio (male/female) of marked individuals higher than 1 and equal catchability of both sexes mean that males were more abundant than females in both flight seasons. There are two possible explanations (Tabashnik 1980): (1) male and female adults emerge in equal numbers, but adult males survive longer than adult females; (2) males outnumber females at emergence. Data show that adult males had lower (year 1996) respectively equal (year 1995) residence rates than adult females. Therefore, results of this study suggest that males outnumber females at emergence due to lower pre-adult mortality. The daily numbers estimates for both years show that most of males emerged before females' peak abundance occurred. Sex ratio was close to 1 only at the end of each brood. It seems that females develop more slowly and consequently may suffer higher pre-adult mortality than males. Males emerge before females (protandry) in many species of Lepidoptera. This is the optimal reproductive strategy for both sexes (Ehrlich 1989): presence of numerous males at the mass emerging time of females increases a male's chances of finding receptive female and successfully mating, and minimises the female's pre-reproductive energy use and risk of predation.

Population size and density

Population size and density are results of abiotic factors and different biotic interactions between individuals in population and between populations of different species. Estimated population size of butterfly species over one flight period (gener-

ation) is only a brief information if we know nothing about dynamic of changes in abundance over time. Ecological researches of *C. oedippus* in 1995 and 1996 on Ljubljansko barje were first studies of population ecology of this species. To imagine the sizes of estimated population parameters for *C. oedippus*, we compared the results of population studies of three butterfly species: *Coenonympha tullia* (Satyridae), *Maniola jurtina* (Satyridae) in *Euphydryas editha* (Nymphalidae) (Table 3).

C. tullia has discontinuous distribution with isolated populations in Europe. It inhabits wet, grassy habitats, especially in bogs, mires, fens, moors, heaths and wetland margins. Threat status: vulnerable – SPEC 3 (Swaay & Warren 1998). *M. jurtina* is one of the most common and widespread European butterfly species. *E. editha* is rare endemic and highly endangered resident of grasslands on serpentine soils in USA (Murphy et al. 1986).

Table 3: Comparison of estimated population sizes, maximum densities and daily residence rates for *Coenonympha oedippus*, *C. tullia*, *Maniola jurtina* and *Euphydryas editha*.

Species	Locality	Year	Site area (ha)	Total number per brood	Maximum density (no. of individ./ha)	Estimated daily residence rate	Reference
<i>C. tullia</i>	GB Wales Cardiganshire	1961	40.0	500-600		0.70	Turner, 1963
<i>M. jurtina</i>	GB England Hightown	1976	1.4	1960-2590	550-650	0.92	Brakefield, 1982b
		1978	1.4	154-175	63	0.82	Brakefield, 1982b
<i>E. editha</i>	USA California Jasper Ridge	1981	2.5	541-1386	123	0.58-0.87	Murphy et al., 1986
<i>C. oedippus</i>	SLO Ljubljansko barje Škofljica	1995	1.3	571-723	139	0.42-0.64	Čelik, 1997
		1996	2.6	847-898	109	0.75-0.81	Čelik, 1997

Estimates of maximum population density for *C. oedippus* in both flying seasons are comparable only considering aggregated microdistribution of imagoes in both years (Čelik 1997). In 1996, 65% of all captures were made on study area of previous year. It means that maximum density in 1996 on area 1.27 ha was 145 individu-

als/ha. Similarity of estimates for population densities in 1995 and 1996 (on study area of 1995) suggests that abundance was also roughly similar in both years.

Residence rate and lifetime of adults

The mean lifetime of adult is 5-10 days for most butterfly species (Warren 1992 in Vogel 1996). The mean expected residence time of adult *C. oedippus* was 3-5 days. The maximum residence seen was 17 days for males and 25 days for females. Estimates of residence time are lower than maximum residence seen because most of the population never attains maximum lifespan, due to constant loss occasioned by weather, predation, etc. (Watt et al 1977).

Cook, Frank & Brower estimate that modal residence rate for diurnal Lepidoptera with more or less colonial population structure in temperate regions may be 0.80 (Brakefield 1982b). In comparison with this the estimates for *C. oedippus* are quite similar (year 1996). In 1995 the estimated daily residence rate was lower due to greater emigration of imagoes according to improperly defined boundaries of study area.

The lower daily residence rates for males (0.749-0.799) compared to the females (0.764-0.808) in 1996 are consequence of greater emigration or (and) briefer lifespan due to the males' greater mobility and activity during the day. Probability for emigration was lower for females because of their sedentary behavior (Čelik 1997). Greater mobility of males indicates the briefer lifetime of individuals. Males are smaller and have shorter ontogeny than females. Because of greater activity they lose the energetic stores much faster and so they live a shorter period of time than females.

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