Overlapping generations can balance the fluctuations in the activity patterns of an endangered ground beetle species: long-term monitoring of *Carabus hungaricus* in Hungary

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Abstract

1. *Carabus hungaricus* is a ground beetle inhabiting the Pannonian steppes. It is highly endangered by fragmentation and abandonment of its habitat.
2. For five consecutive years, from 2006 to 2010, we used the mark-release-recapture technique in a grid of 270 live-capture pitfall traps to study its population ecology in sandy grasslands on Szentendrei Island in the Northern vicinity of Budapest, Hungary.
3. In total, 3950 individuals of *C. hungaricus* (1874 females and 2076 males) were marked.
4. Population size was estimated at ~2000 individuals per year; the estimates for females were consistently higher than for males. The minimum population size was 1317±60.1 individuals in 2007, while the maximum was 2169.7±108.8 individuals in 2008.
5. Adults older than a year formed ~32-42% of the population, while individuals surviving for three years formed ~10%, and those surviving for four years formed ~2% of the population. Individuals older than four years comprised <1% of the population. Female survival rate was higher than that of male, but the capture rate also differed between sexes.
6. Although the studied population showed considerable fluctuations in the pattern of activity during the five years, its size seemed to be relatively stable, underlining the importance of overlapping generations.

Keywords: *Carabus hungaricus;* long-term monitoring; mark-recapture; sandy grasslands; time series; Natura 2000

Introduction

The dry grasslands of Central Europe support distinct plant and animal assemblages (Medvedev, 1950; 1954; Medvedev & Shapiro, 1957; Petrusenko & Petrusenko, 1971; Eidelberg *et al.,* 1988; Penev, 1996; Putchkov, 2011; Cizek *et al.,* 2012), with many species endemic to the Pannonian biogeographical region (Varga, 1995). Thus, they are considered to be biodiversity hotspots (Cremene *et al.* 2005). Dry grasslands are vanishing rapidly; with less than five percent of the remaining steppe areas being in their natural state and only a fraction of them protected (Mader, 1983; Goriup 1998). Remaining grassland fragments are often too small to support viable populations of more specialized species; many grassland inhabitants are thus endangered and some have become locally extinct (Mader *et al.* 1990). In Hungary, the proportion of natural and semi-natural grassland areas has decreased from 2.7 to 0.7 million hectares since the 19th century (i.e. by 74%) (Hungarian Central Statistical Office, 2010). Most of the productive grasslands were converted to arable land; and the less productive parts such as sand steppes were turned to poplar (*Populus X euamericana*), black pine (*Pinus nigra*), scots pine (*Pinus sylvestris*) and black locust (*Robinia pseudoacacia*) plantations after World War I (Anonymous, 1923). Infrastructural developments, such as road building and urbanization, increased during the course of the 20th century. These processes led to fragmentation of all habitat types and a further dramatic decline in the biodiversity of open habitats (Magura & Ködöböcz, 2007). Moreover, the intensification of agricultural practices, such as ploughing, soil tillage, and fertilizer usage, together with the spread of invasive plant species, such as common milkweed (*Asclepyas syriaca*), resulted in changes in plant species' composition and quality in most of the remaining dry grassland habitats in the Carpathian Basin (Török *et al.,* 2003).

Such habitat changes led also to decreases in the area, quality, and connectivity of dry grasslands, resulting in a dramatic decline of their biodiversity, including also arthropods (Rushton *et al.,* 1989; McLaughlin & Mineau, 1995; Magura & Ködöböcz, 2007). The magnitude of changes in arthropod diversity can be estimated by the monitoring of groups sensitive to the above processes (Sieren & Firscher, 2002). Ground beetles (*Coleoptera, Carabide*) have been successfully used as indicators in many ecological studies (Mader, 1980; Lövei & Sunderland, 1996; McGeoch, 1998; Rainio & Niemelä, 2003; Samways, 2005). Despite that, little is known about the population biology/ecology of most species, including the large and attractive habitat specialists of the genus *Carabus* (e.g. Matern *et al.,* 2007). A number of studies deal with their reproduction, life cycle, and movement strategies (e.g. Rijnsdorp, 1980; Sota, 1987; Kobuta, 1996; Weber & Heimbach, 2001; Pokluda, 2012), while others have investigated the size of ground beetle populations (e.g. Greenslade, 1964; Nelemans *et al.,* 1989; Samu & Sárospataki, 1995; Thomas *et al.,* 1998; Holland & Smith, 1999; Griffiths *et al.,* 2005). Population size estimates of *Carabus* species are rare (Grüm, 1975; Hockmann *et al.*, 1992; Vainikainen *et al.,* 1998; Weber & Heimbach, 2001; Matern *et al.,* 2007). None of the papers mentioned above applied a detailed selection procedure to find a proper model for the estimations of population parameters. However, they do provide further details on their life histories and population structures and would be potentially useful for their conservation. In most of European countries, several *Carabus* species are red listed, legally protected, and often endangered (Niemelä, 2001). The European Union has listed several species of community importance - *Carabus hampei, C. hungaricus, C. menetriesi pacholei, C. olympiae, C. variolosus and C. zawadszkii* - in Annexes II and IV of the Habitat Directive (92/43/EEC: European Commission, 1992). *C. hungaricus* is considered to be a stenotopic tall-grass steppe-habitat specialist (Pokluda *et al.,* 2012), occurring mainly in dry calcareous and acidic sand grasslands in lowland areas, and dolomite grasslands on hills (Szél *et al.,* 2006; Bérces *et al.,* 2008). The distribution of *C. hungaricus* is highly fragmented even in Hungary, in its last stronghold (Bérces *et al.,* 2008). The beetle is endangered everywhere across its distribution range; it is almost extinct or critically endangered in several countries (Austria: Müller-Motzfeld, 2004; Czech Republic, Slovakia: Pokluda 2012; Moldova: Neculiseanu *et al.,* 1999; Turin *et al.,* 2003).

To allow for its effective conservation, an extensive monitoring program of *C. hungaricus* was initiated by the Duna-Ipoly National Park, Hungary. Here we present the main results of a five-year study dealing with the temporal changes of major population parameters and analyze the key factors affecting survival of this highly endangered, tall-grass sand steppe specialist, including: (i) seasonal activity patterns; (ii) estimation of the major population parameters, such as population size, between-year survival, and capture probability; (iii) identification of the trends in the capture data by the decomposition of the time series and its components; and (iv) prediction of future trends based on the identified temporal patterns in capture data.

Material and methods

Study area and sampling design

The study was carried out on the Szentendrei Island, a 30 km long, 0.5-3.5 km wide island surrounded by the Danube River, located about 30 kilometers North of Budapest, Hungary. Natural floodplain forests and poplar plantations dominate the shores of the island, while arable lands, human settlements (three villages) and forest plantations such as black locust, black pine and scots pine cover large areas in the core of the island. There are two larger, and one smaller sand dune areas on the island, all belonging to the authority of the Duna-Ipoly National Park, and it is a Site of Community Importance with the appellation of “HUDI20047 Szigeti homokok”. One such area near the village of Pócsmegyer (about 170ha, 100-120 m a.s.l.) comprising 40 ha (see appendix-1.kml) is covered with tall-grass vegetation of the Pannonian sand steppes (*Festucetum vaginatae*) and was selected as the study site. These grasslands are fragmented by patches of black locust plantations (*Robinia pseudoacacia*). Pannonian sand steppe vegetation is characterized by the dominant bunch grasses *Stipa borystenica*, *Chrysopogon gryllus* and *Festuca vaginata*. No management took place at the sampling area during the study period, while the surrounding areas were irregularly mown. Mean annual precipitation is between 550-600 mm, and the mean annual temperature is 10°C (min.: -14°C and max.: +34°C) (Dövényi *et al.,* 2010).

Two hundred and seventy live-capture, non-baited pitfall traps were placed in a 4×4m grid in 10 rows and 27 columns, covering an area of 0.4 ha (see appendix-1.kml). Each trap contained 2 cups, the larger ones (9 cm diameter, with a volume of 0.5 l) were dug into the ground. The smaller cups (with a diameter of 9 cm and volume of 0.3 l) were inserted into the larger ones in order to empty the traps more easily. Cups were perforated at the bottom and covered by a plastic roof to avoid penetration of water. The traps were checked weekly from March to December each year between 2006 and 2010; the sampling thus covered the whole activity period of *C. hungaricus* (Bérces *et al.,* 2008).

Marking the individuals

Beetles were individually marked by numbers, engraved on their elytra with a small drill. After marking, beetles were released, approximately 1.5 m NE of the trap. On release, beetles usually hide among grass/litter on the spot. Handling and marking caused no obvious mortality nor harm to the beetles. The sex and visible injuries or anomalies of each individual were recorded in a database.

Data analysis - Estimating the demographic parameters of the studied population

Demographic parameters of the *C. hungaricus* population were estimated using constrained linear modeling (CLM), which applies the framework of generalized linear modeling (glm: Lebreton *et al.,* 1992). This approach provides high flexibility in the estimation of parameters and the opportunity to compare the models based on information theoretic approaches (i.e. AIC, AICc).

The *C. hungaricus* population was considered as an open population, due to fact that capture occasions (i.e. years) were distant in time and mortality and births occurred between them

(Baillargeon & Rivest, 2007). Cormack-Jolly-Seber and Jolly-Seber models have been fitted for the open populations (Cormack, 1985; 1989) followed by a loglinear approach to estimate survival (Φ) and the number of new units entering into the population (B) between the studied years. Capture rate (p) and population size (N) were estimated for each year of the study. Total number of individuals inhabiting the survey area (*Ntotal*) was also estimated for each year. Two types of Poisson regression models using the glm approach were fitted in order to consider properly the temporal effects in the mark-recapture data; 1) an open model with unconstrained capture probabilities (varying between years), and 2) an open model with equal capture probabilities (common value for capture probabilities between years). In the first case it was not possible to estimate the requested parameters for the first and last capture occasions (i.e. years). Models were fitted on the whole population (full data matrix), and separately for females and males. The mark-recapture survey followed a robust design, thus the data matrix was converted to primary session data (i.e. years) with the consideration of the secondary sampling sessions (i.e. number of sampling occasions within a year). Models were compared based on their deviance, degrees of freedom and AIC values. The goodness of the model fit was tested by the deviance of the standard model based on the Pearson residuals against the number of captures. Large residuals indicated bad fit of the data. Thus they were removed and the models were re-fitted, compared and tested again.

Estimating trends in time

The identification of overall trends in long-term datasets requires techniques that are able to distinguish between seasonal differences and global trends. In our studies we followed the protocol suggested by Zucchini & Nemadić (2011). The decomposition of time series was applied through a non-parametric regression technique for the capture data between 2006-2010. This method performed a seasonal decomposition of a given time series (X_t) by determining the trends (T_t) using local polynomial regression and calculating the seasonal component (S_t) (and residuals) from the differences X_t-T_t (Cleveland *et al.,* 1990; Zucchini & Nemadić 2011). To predict the possible number of captures in the population for the following year, ARIMA [autoregressive integrated moving average, which is the generalisation of autoregressive moving average (ARMA) models] time series models were fitted to the capture data (or Box Jenkins approach, Brockwell & Davis, 1996; Ripley, 2002). This modeling process takes advantage of associations in the sequentially lagged relationships that usually exist in periodically collected data. The formula of the ARIMA model is:

$$\Delta 1Zt = \Phi_{1Zt-1} + ... + \Phi p_{Zt-p} + a_t - \theta_1 a_{t-1} - ... - \theta_q a_{t-q}$$

where:

$\Delta 1Zt$ – differenced time series (i.e. Zt-Zt-1)

Zt – set of the possible observations on the time-sequenced random variable,

a_t – random shock term at time t

$\Phi_1 \ldots \Phi_p$ – autoregressive parameter of order p

$\theta_1 \ldots \theta_q$ – moving average parameter for order q.

Sample autocorrelation and partial autocorrelation functions were used to identify the ARIMA model in the appropriate order. The model's estimates were obtained using a maximum likelihood method and diagnostics included the Akaike Information Criterion and the residual analysis by Ljung-Box. Since the residuals of a well-fitted model are distributed randomly (Box & Pierce, 1970; Ljung & Box, 1978) the statistics examined the null of the independently distributed residuals. Thus, the final model was the result of several iterations of identifications, estimations and diagnostic processes based on the conventional criteria for the model's adequacy. All analyses were carried out in R 2.13.1 (R Development Core Team, 2011) using the package Rcapture for capture-recapture analysis (Baillargeon & Rivest, 2007).

Results

Major activity patterns

During the five years we marked 3950 *C. hungaricus* individuals (1874 females and 2076 males). Twenty five - thirty three percent of individuals were recaptured in the year after marking, and <10% of individuals were recaptured later (i.e. in the second, third or fourth year after the year of marking); the main decline in the recaptures appeared after the second year (Table 1).

The activity pattern showed distinct periodicity (Fig. 1) characterized by two activity peaks within a year. During the first activity peak (from mid-May and mid-July), females were more active than males. The second peak was characterized by high activity of males from early August to October. Larvae were caught from the end of October to the early May.

Estimation of population parameters

For females, models with unconstrained capture probabilities provided better fit (smaller deviation) and lower estimates than models with equal capture probabilities (Table 2). The two model types provided similar estimates for males. In order to compare the differences among years, we considered the results of models with equal capture probabilities, which provided estimates for all the years studied. Estimated survival rates varied between 32-42%, and were the highest in 2007 and 2008, with significant between-year variation. Survival rates for females were usually higher than that of males (except in 2007-2008, see Table 3). The number of newly-marked individuals varied between ~600-1000 per year, the highest being between 2007-2008 (Table 3). The number of new entrants per sex showed variation between periods, also showing the highest estimates in 2007-2008. The capture probabilities of males were higher than those of females, especially in 2007 (Table 4, Fig. 2A). The estimated population size ranged from 1317 (±60.1) to 2169.7 (±108.8) individuals per year, with the number of females being consistently higher than that of males (Table

4). The population size decreased between 2006 and 2007, reaching the highest abundance during the study period in 2008 and decreasing thereafter monotonously towards 2010 (Fig. 2B).

Trends and seasonality

A clear and distinct seasonal pattern has been found in the capture data based on the decomposition of time series. A bimodal pattern was found with an earlier and a later activity peaks (Fig. 3). A between-year pattern showed a slight increase in the number of captures in 2006 and a strong decrease in 2007. The second high activity period was characterized by an activity peak in 2008, with a slight decline in 2009. In 2010, this overall pattern (high activity in every other year) was intended to return (Fig. 3). We found that the optimum ARIMA model was the most useful, with (2,2,5) for the captures (log likelihood = -517.82, AIC = 1051.63). The residuals indicated small variation around the mean zero; none of them was greater than the double standard deviations, thus this model fitted best. The autocorrelation of the residuals was not significantly different from zero as a set, and had a constant variance, thus confirming the adequacy of the model (Box-Pierce test, $X^2 = 0.017$, df = 1, p = 0.89). The observed mean (with S.E.) of captures was 78.93±12.82. Based on the models the expected mean value of the captures for the following three years were 79.11±59.18. The portrayed number of captures with the predictions indicated a slight decrease in the number of captures in the subsequent three years (Fig. 4).

Discussion

No data on the population ecology of *C. hungaricus* have been published prior to this study. Our long-term “mark-recapture” study proved that an abundant population inhabited the sandy grasslands of the Szentendrei Island. Although there was considerable variation in activity during the five-year study, the population size of *C. hungaricus* seemed relatively stable. The high proportion of beetles surviving for more than one year seemed to reduce fluctuations in population size between the years, and might be the key for persistence of isolated populations of this species.

Activity patterns

The seasonal activity has been divided into two main activity regimes in the studied population. Matern *et al.* (2007) found similar bimodal activity pattern for a typical spring breeder, *Carabus variolosus*. The activity pattern of *C. hungaricus* can be explained by its phenology, which starts with adults emerging in June causing the first peak of activity. After a short aestivation in July and the first half of August, the high male activity detected corresponded to the breeding season, similarly to other species (eg. Brunsting, 1981; Kegel, 1990; Kennedy, 1994; Drees & Huk, 2000). The activity of the adults had almost ceased by the end of reproduction. Larvae appeared at the end of October and they were active during the winter period. Second and third instar larvae developed in spring (March-May); low (peculiar) activity of overwintering adults could be observed during this time (Szél *et al.,* 2006; Bérces *et al.,* 2007).

One of the most important results of our study was that a large proportion of the individuals (32-42% estimated) contribute to reproduction in the following year. Although this phenomenon had already been described for other carabids (Schjøtz-Christiensen, 1965; den Boer, 1971; Thiele, 1977; Sharova *et al.,* 2005), its magnitude was unknown. Based on the above-mentioned facts, we suppose that many *C. hungaricus* individuals are able to spread the risk of encountering unsuitable conditions (e.g. dry or cold) over several years, thus reducing fluctuations in population size and the chance of sudden extinction due to stochastic and other reasons (den Boer, 1971).

Estimated population parameters and size

A relationship between the activity and capture probability, corresponding to the fact that higher activity leads to higher captures (e.g. Thomas *et al.,* 1998; Konvicka *et al.,* 2005; Matern *et al.,* 2007) was detected in the studied population of *C. hungaricus*. Females had lower capture rates than males, while their survival rate was higher. This suggests that higher male activity during the mating season might lead to an increased mortality, due to e.g. predation. A similar observation was made for *Pterostichus melanarius* where males' daily dispersal distance was considerable higher than that of females, resulting in more males caught (Thomas *et al.,* 1998).

The estimation of the population size showed that a stable population of ~2000 individuals inhabited the studied sandy grassland in Hungary. The highest difference in population size between years was ~850 individuals. The observed fluctuations in the size of the population studied over the five years were thus rather low. Especially considering that insect populations typically exhibit strong fluctuations (Samways, 2005), and the fluctuation of carabid populations can change by a factor of five (Grüm, 1986), and even ten, as observed for *C. arvensis* during a nine-year study (Turin *et al.,* 2003). Lower fluctuations are more likely to appear in the populations of forest-dwelling *Carabus* species (Weber & Heimbach 2001; Günther & Assman 2004; Matern *et al.,* 2007). For example for an isolated *C. variolosus* population consisting of ~200 individuals, Matern *et al.* (2007) suggested that the population was large enough to maintain a viable population with evolutionary potential, based on the 50/500 rule by Franklin (1980). The studied population thus exhibited rather low fluctuations and seems viable in the long term.

Decomposition of time series and predictions

The decomposition of the time series data proved that there was a considerable trend in the five-year capture data suggesting a high activity regime every other year. There are only a few studies published on the long-term monitoring of ground beetles (Sieren & Fisher 2002; Scott & Anderson, 2003; Desender *et al.,* 2007), but these concern the assemblage level, the use of different techniques and approaches. Although Scott & Anderson (2003) suggest that six- or seven-year data should be sufficient to find trends in datasets, their paper was based on data from 19 sites in the UK, and the spatial differences could be the responsible factor for the lack of clear trends in their data.

Hunter & Price (1998) found that time series analysis was a powerful tool for understanding insect population dynamics, especially for *Hymenoptera*. This could also help in forecasting agricultural pest densities in arable lands (Szentkirályi, 2002). Matern *et al.,* (2007) suggest that the long-term monitoring of the endangered *C. variolosus* may contribute to identifying the fluctuation in the population dynamics and the critical points of its phenology.

Conclusions

The long-term monitoring of C. hungaricus suggests that the size of the studied population was relatively stable, and seemed large enough to ensure long-term survival. Overlapping generations contribute to the stability of the studied population. Due to fragmentation and habitat size, the population remains susceptible to management, and monitoring should continue. This is also consistent with the fact that Hungary is in the “high biodiversity responsibility class” due to the high ratio of unique habitat types and endemic species, especially of invertebrates (Schmeller et al., 2008) in Europe.

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Table 1. The number of *Carabus hungaricus* individuals marked on Szentendrei Island, Hungary between 2006-2010, and their recaptures over those years. The first line shows the number of individuals newly marked each year. Below, the number (and percentage) of beetles recaptured after a given period.

	2006	*2007*	*2008*	*2009*	*2010*
no. of newly captured adults	1008 (100)	559 (100)	1053 (100)	743 (100)	587 (100)
	2006-2007	2007-2008	2008-2009	2009-2010	
Alive after 2 y	256 (25.4)	185 (33.1)	276 (26.2)	188 (25.3)	
	2006-2008	*2007-2009*	*2008-2010*		
Alive after 3 y	104 (10.3)	50 (8.9)	13 (2.3)		
	2006-2009	*2007-2010*			
Alive after 4 y	21 (2.1)	13 (2.3)			
	2006-2010				
Alive after 5 y	4 (0.4)				

Table 2. Model diagnostics and total population (*Ntotal*) size of *Carabus hungaricus* on Szentendrei Island, Hungary between 2006 and 2010.

Models	*Deviance*	*df*	*AIC*	*Ntotal* ± *S.E.*
Overall				
unconstrained "*p*" model	22.16	15	155.47	4881.54 ± 139.26
equal "*p*" model	31.62	19	171.28	5968.47 ± 208.77
Females				
unconstrained "*p*" model	15.96	17	143.14	2734.19 ± 132.11
equal "*p*" model	26.07	21	158.7	3143.62 ± 157.86
Males				
unconstrained "*p*" model	26.27	17	149.7	2682.71 ± 93.96
equal "*p*" model	29.30	19	149.67	2954.071 ± 121.86

Table 3. Estimated survival(*Φ*) and number of births (*B*), with standard error for *C. hungaricus* on Szentendrei Island, Hungary between 2006-2010. The column "Est." denotes the estimated parameters by the models.

Models	*Est.*	*2006-2007*	*2007-2008*	*2008-2009*	*2009-2010*
overall unconstrained "*p*" model	*Φ*	0.33±0.04	0.41±0.04	0.29±0.03	NA
	B	NA	1301.8±135.7	1028.4±125.2	NA
overall equal "*p*" model	*Φ*	0.35±0.02	0.42±0.03	0.32±0.02	0.39±0.02
	B	680.8±50.9	1614.8±98.3	1072.8±54.8	826.4±46
female unconstrained "*p*" model	*Φ*	0.44±0.05	0.34±0.04	0.41±0.05	NA
	B	NA	666.5±95.4	737.9±125.4	NA
female equal "*p*" model	*Φ*	0.4±0.03	0.41±0.03	0.37±0.03	0.42±0.04
	B	388.7±39.2	849.6±66.3	532.2±45.2	420.1±39
male unconstrained "*p*" model	*Φ*	0.35±0.03	0.42±0.05	0.36±0.04	NA
	B	NA	733.3±78.5	858.1±116.9	NA
male equal "*p*" model	*Φ*	0.33±0.02	0.44±0.04	0.31±0.02	0.40±0.03
	B	308.6±31.6	815.6±61	543.5±35.1	410±29

Table 4. Estimated capture probabilities (p) and overall population size (N) with standard error for *C. hungaricus* on Szentendrei Island, Hungary between 2006 and 2010. The column "Est" denotes the estimated parameters by the models.

Models	*Est.*	*2006*	*2007*	*2008*	*2009*	*2010*
overall unconstrained "*p*" model	*p*	NA	0.48±0.05	0.68±0.05	0.68±0.08	NA
	N	NA	1541.4±126.5	1942±131.9	1596.4±176.1	NA
overall equal"*p*"model	*p*	0.59±0.03	0.59±0.03	0.59±0.03	0.59±0.03	0.59±0.03
	N	1773.8±95.6	1317±60.1	2169.7±108.8	1787.7±94	1533.5±89.6
female unconstrained "*p*" model	*p*	NA	0.41±0.05	0.59±0.07	0.40±0.05	NA
	N	NA	902.4±116.2	977.6±110.8	1144.3±153.6	NA
female equal"*p*"model	*p*	0.49±0.03	0.49±0.03	0.49±0.03	0.49±0.03	0.49±0.03
	N	953±73.8	769.9±56.1	1172.5±84.5	973.3±69.9	831.3±65.2
male unconstrained "*p*" model	*p*	NA	0.59±0.05	0.69±0.06	0.43±0.05	NA
	N	NA	669±53.4	1015.6±86.9	1226±124.4	NA
male equal "*p*"model	*p*	0.65±0.04	0.65±0.04	0.65±0.04	0.65±0.04	0.65±0.04
	N	876.4±55.9	604.2±32.8	1083.6±65.3	882±54.9	765.7±53.1

Figure legends:

Fig 1. One-year activity pattern of *C. hungaricus* based the captures from 2008. The lines indicate the trends in the captures based on the simple moving average for three neighbouring points. Sampling occasions' dates: S1, S2-first and second sampling occasion respectively, the two-digit number after the occasion denotes the month as a number (e.g. 03 = March). Legend: line with full circle – captures for males; line with empty circle-captures for females; solid line-trend for males; dashed line – trend for females.

Fig 2. Estimated capture rate (A) and population size (B) for *C. hungaricus* on Szentendrei Island, Hungary between 2006 and 2010. These estimations based on the equal *p* model per sexes.

Fig 3. Seasonal decomposition of time series data for *C. hungaricus* on Szentendrei Island, Hungary between 2006 and 2010. The data denote the original structure of time series data, the seasonal indicates the within-year variation patterns, while the trend denotes the global (between-year) patterns in the dataset. The remainder shows unexplained variances.

Fig 4. Observed capture data (solid black line) along the forecast by ARIMA models (dashed line denotes standard errors of the predicted values) for the next three years for *C. hungaricus.*