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Estimation of demographic fluctuations within a reproductive roost of *Pipistrellus kuhlii* inferred from capture-mark-recapture data

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Abstract: Despite bats representing one fifth of all mammals, little is known about the ecology and the population status for many species belonging to this order. This is often a consequence of our poor knowledge of population densities and demographic parameters, bats being typically elusive subjects for ecological studies. Capture-mark-recapture studies provide important demographic and ecological data to fill up this information gap. In this study, we monitored animals and gathered data over five years from a reproductive roost of Kuhl's pipistrelle (*Pipistrellus kuhlii* Kuhl, 1817) located in a Natura 2000 site in north-west Italy. One-hundred-thirty-three individuals were captured and demographic parameters collected, including the annual survival probability for both young and adults, the recapture rates for different sex and age cohorts and the adult population size trend. The influence of environmental variables on the population was also assessed, highlighting the relevant impact of winter temperatures and spring rainfalls on individual survival ability. Notably, our study provides for the first time an estimation of the survival rate of adult females of Kuhl's pipistrelle, a crucial information for future design of studies related to this species' ecology and for informing conservation efforts.

Keywords: Kuhl's pipistrelle - bat - CMR - Chiroptera - roost ecology - population modelling.

INTRODUCTION

The order Chiroptera includes more than 1400 species (Wilson & Russel, 2019) being one of the major representative taxonomic group of the mammalian clade. Owing to their biological variability and species' richness, bats have an important role for ecosystems health status, functioning both as bioindicators and being directly involved in many ecological functions such as seed dispersal, pollination and pest control (Kasso & Balakrishnan, 2013; Coutts *et al*., 1973). Despite the economic and environmental benefits deriving from their crucial function within their ecological niche, little is known about bat population status and ecology (Kunz & Fenton, 2005). Bats' nocturnal and elusive habits, coupled with their high vagility, indeed limit data collection from wild animals, negatively impacting on our understanding of their ecology and distribution. Capture-mark-recapture (CMR) data on bat populations represent a valuable tool for addressing this lack of knowledge.

Currently, the development of sophisticated models for the analysis of population dynamics allows to investigate different aspects of a species ecology (Lebreton *et al.,* 1992; Cooch & White, 2001). In the last years, an increasing number of CMR studies were designed to test different ecological hypotheses and to assess important species-specific parameters. This allowed to discover environmental factors negatively affecting the survival of many bat species (Frick *et al.,* 2007), to estimate annual survival rates (Hoyle *et al*., 2001; Sendor & Simon, 2003; Pryde *et al*., 2005; Schorcht *et al.,* 2009; Papadatou *et al*., 2011) and to compare species-specific survival parameters such as growing rates and populational reproductive success (Papadatou *et al*., 2012). Furthermore, given the exceptional longevity of many species of bats, information on the individuals' annual survival and reproductive rates is a crucial information for the correct design of specific-tailored conservation plans (Prévot-Julliard *et al*., 1998).

In this work, we describe an analysis of CMR data on a reproductive roost of Kuhl's pipistrelle (*Pipistrellus kuhlii* Kuhl, 1817) in the north-west of Italy on a five

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years timespan. Kuhl's pipistrelle is an anthropophilic species frequently found roosting in buildings and other artificial structures (Yom-Tov & Kadmon, 1998; Mendelssohn & Yom-Tov, 1999). Females display high philopatry, returning every year back to the same reproductive roost to give birth to 1-2 pups each (Lanza, 2012). These features allowed the study to be conducted on the same colony over time, returning novel information on the survival capacity and reproductive patterns for the species. Furthermore, the analysis revealed the weight of some environmental factors such as temperatures and precipitations affecting the survival ability of the colony for the reproductive season. Taken together, these results provide new information on a *P. kuhlii* colony reproductive dynamics and on the survival capacity of adult individuals, specifically females, in relationship with environmental parameters variations.

MATERIALS AND METHODS

Study area and marking procedure

The study area was located inside the Natura 2000 protected area "Riserva naturale della palude di San Genuario" a SACs (IT1120007) in the Vercelli province, Piedmont (Italy). Animals were found roosting in bat boxes placed on the external walls of the natural reserve visitor centre building. Individuals have been captured from summer 2014 to summer 2019, by using telescopic landing nests positioned in the proximity of 3 bat-boxes exit hole. Capture sessions were conducted once every year of the study during summer.

Individuals were marked with a subcutaneous Passive Integrated Transponder (PIT tags) of 0.8 mm length as described in Locatelli *et al*. (2019), each PIT tag reporting a single alphanumerical identification number. For each animal, forearm length (in mm, *sensu* Dietz & von Helversen, 2004) and body mass (g) were measured. Animals were classified as young or adults according to the shape and the level of calcification of the phalanx joints (Dietz & von Helversen, 2004). Before each capture session, and every week during summer, a portable PIT tag reader was used to scan the bat box in order to reveal the presence of any marked bats in the roosts, thus allowing to plan the following capture sessions minimising colony disturbance and animal stress.

Capture and handling permits

The capture, handling and marking of the individuals were carried out with all the required permits (Ministero della Tutela del Territorio e del Mare, Aut. Prot. N°: 13040, 26/03/2014). All the main procedural guidelines (Agnelli *et al*., 2004) were used during animal handling to minimise stress. Some of the fieldwork material and instruments were supplied by Prof. Teeling's lab at University College of Dublin.

Modelling analysis

As previously described, the sampling was carried out over a 5-year timeframe. Presence data collected during the same year were pooled together and treated as from a single sample session. The MARK program was used to conduct two different analyses elaborating the same type of model, the Cormack-Jolly-Seber model (CJS model). The first analysis was carried out by modelling the survival and recapture rate separately. Individuals were grouped in males and females and one-variable (time) basic models were elaborated. The recapture rate was examined considering time and sex with survival using the best basic model. The survival rate was calculated including environmental variables in CJS model without partitioning the population in sex classes. Indeed, *Pipistrellus kuhlii* tends to form reproductive roost comprising only adult females (Lanza, 2012). Consequently, only a few males were recaptured, thus being not enough to assess an unbiased male survival rate. The environmental variables were selected among those which could be affecting the most bats' annual life cycle such as hibernation and awakening times in winter and spring respectively (Kunz, 1982). Since low temperatures can represent a serious risk to individuals' survival ability, we retained the number of days with a temperature below 0° C as winter length value and we used the average temperature of the coldest month of the year as a proxy for winter severity. Rainy days in spring can also negatively influence individual survive as they can partially impair the foraging activity (Locatelli *et al*., 2019). Weather data were collected from an open access database (ARPA, www.arpa.piemonte.it). These data were used to calculate the respective seasonal mean value which were used as covariates for the model.

The second analysis was performed by dividing individuals into two age-cohorts, young and adults respectively. Purpose of the investigation was to compare survival and recapture rates between the two age groups, being young individuals typically characterised by lower survival ability (Sendor & Simon, 2003; O'Shea *et al*., 2004; Schaub *et al.,* 2007; Papadatou *et al*., 2009). Since juveniles usually disperse and permanently emigrate from their reproductive roost, the recapture rate was variable among the age cohorts (Hoyle *et al*., 2001; Pryde *et al*., 2005; Papadatou *et al*., 2009; Schorcht *et al*., 2009). The adult population was estimated each year by dividing the number of adults captured during the summer by the recapture rate calculated for the same timeframe. The goodness of fit (GOF) of data for CJS models was calculated in R by using the "R2ucare" package, which verified if the assumption of CJS model were met with test 2 and 3 (Gimenez *et al*., 2017). Respectively, the first test examined whether all individuals had the same probability to be captured, challenging the assumption one of the CJS model (i.e. all individuals have the same probability to be captured), while the second test verified if marked individuals had the same probability to survive in a period between time 0 and t+1. In both analyses, GOF was evaluated for both sexes and age-classes (Gimenez *et al.*, 2017).

Model selection was performed based on the AIC criterion by selecting the most parsimonious model (characterised by the lowest AIC score), for each analysis (Burnham & Anderson, 1987).

RESULTS

Capture trend

During the five-year study, 133 individuals were captured (Fig. 1): 27 adults (26 females and 1 male) and 106 juveniles (72 females and 34 males) (Fig. 2). 38 recapture events occurred during the sampling sessions; 13 were adult females, 10 were young females and 1 was a young male. Most of the recaptured bats were also recaptured during following summers (Fig. 3).

Modelling survival and recapture rates

The GOF for CJS models, evaluated for both males (= 1.913; P = 0.167) and females (= 8.949; P = 0.347), showed absence of overdispersion. Models for recapture rate were processed by fitting the survival rate constant, being φ(.) p(.) the best basic model. The best model, selected based on the AIC, involved a recapture rate correlated with the sex of the individual while excluding an annual time effect (Table 1). Starting from this estimate, a model to predict the survival rate was designed. Such analysis did not consider any possible influence of sex on the individual's survival given the extremely low presence of male individuals in maternity roosts after birth. In the first model the survival probability was only influenced by the time covariant. The best fit of data, modelled a constant survival rate for individuals along the years of study (Table 1), thus excluding weather variables. The parameters retained in this model were: $\varphi = 0.69 \pm 0.075$, 95% CI = 0.53-0.82; $p_m = 0.05$, 95% CI = 0.01-0.18 ± 0.034; $p_f = 0.38 \pm 0.081$, 95% CI = 0.24-0.54 (p_m= recapture probability of males; p_f= recapture probability of females).

Age models and female adult population size

Results from the GOF inferred on the adult population showed that CJS model fits well the general data (= 2.814) while poorly fits for the juvenile subgroup (= 16.383). More tests were elaborated to address this result and understand which assumption had been violated. Both test 2 and test 3 of the "R2ucare" package include other two tests each: test 2ct, test 3sm, test 2cl and test 3sr. Briefly, test 2ct evaluates if the currently captured individuals have the same recapture probability than

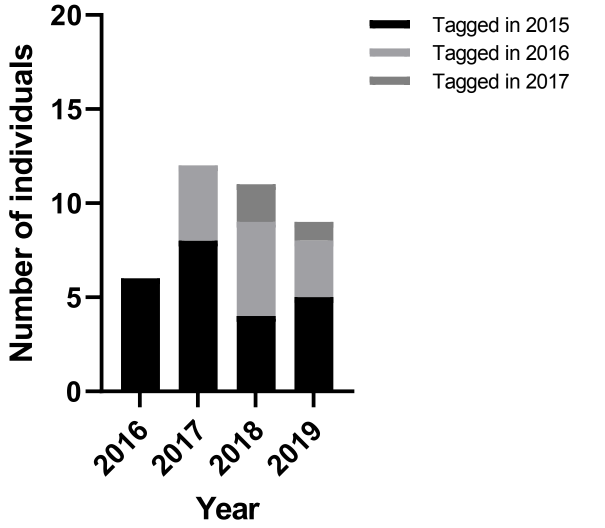

Fig. 1. Number of recapture events during the five years study. The three colours indicate the number of individuals tagged in 2015, 2016 and 2017 respectively. None of the bats tagged in 2018 was recaptured in 2019.

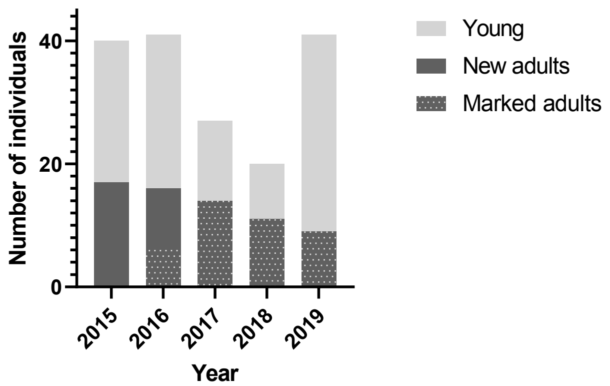

Fig. 2. Youngs and adults captured and recaptured for each year. Youngs were considered marked adults after first year.

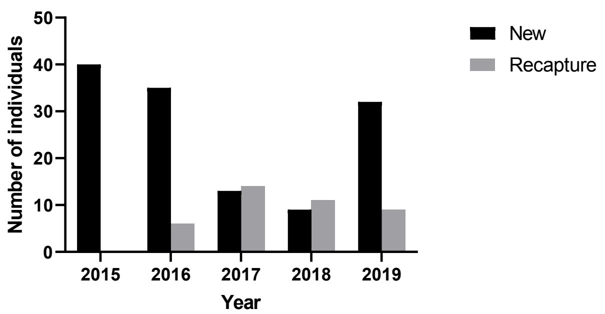

Fig. 3. Number of captured and recaptured individuals for each of the five years. Black columns represent the new individuals captured, grey columns represent the numbers of individuals recaptured.

Table 1. Model ranking obtained from the first analysis. ϕ(.) = is set as constant survival during the various years of the study. ϕ(time) = is set with survival ability varying during time. p(g) = recapture probability is set different between sex. p(g+time) = recapture probability is set as different between sex and varying over time with an additive effect between them. p(g*t) = recapture probability is different between sex and varies over time, with an interaction effect between the two variables. p(.) = recapture rate is set constant during the various years of the study. p(t) =recapture rate is set as varying during years.

Model rank	Parameters in the model	AIC	ΔAIC	N° of parameters
Basic model				
1	φ(.) p(.)	226.1351	0	2
2	φ(.) p(t)	230.9463	4.8112	5
3	φ(t) p(.)	232.4856	6.3505	5
4	φ(t) p(t)	234.1197	7.9846	7
Modelling recapture				
1	φ(.) p(g)	213.0964	0	3
2	φ(.) p(g + time)	217.4785	4.3821	6
3	φ(.) p(g*t)	222.5152	9.4188	9
4	φ(.) p(.)	226.1351	13.0387	2
5	φ(.) p(t)	230.9463	17.8499	5
Modelling survive				
1	φ(.) p(g)	213.0964	0	1
2	φ(time) p(g)	219.3702	8.931	2

missed individuals; test 3sr evaluates if newly captured individuals have the same chance to be found in following capture sessions than individuals previously marked; test 3sm and 2cl assess if the time for new and previously captured individuals is the same. Test 3sr was significant (= 15.447, p-value= 0.001), while test 2ct (= 0; p-value= 1), test 3sm (= 0936; p-value= 0.626) and test 2cl (= 0; p-value= 1) were not significant. The model result indicated that juveniles permanently emigrate from the reproductive roost, providing statistical evidence supporting a previously observed behaviour for the species.

In the best model, the survival rates for juveniles and adults were constant throughout all the years of the study while the recapture rate varied over time for juveniles only. The juveniles' recapture rates of the last three years of the study were not estimated since limited data were available. The parameters of the best model obtained were: φ_A= 0.82 ± 0.083, 95% CI= 0.60- 0.93; φ_J= 0.19 ± 0.054, 95% CI= 0.11- 0.32; p_A= 0.38 ± 0.087, 95% CI= 0.22- 0.55; p_J= 0.51 ± 0.23, 95% CI= 0.15- 0.86 (where φ_A= adult's survival rate, φ_J= juvenile's survival rate; p_A= adult's recapture rate; p_J= juvenile's recapture rate). All models elaborated are shown in Table 2 while the trend of the adult population size is reported in Fig. 4.

DISCUSSION

This study provides novel data on female adult population dynamics and survival parameters for *Pipistrellus kuhlii*. Specifically, this represents the first longitudinal study for the population found in the reserve of San Genuario. Results are coherent with our current knowledge of the species' ecology (Lanza, 2012). Most of the individuals captured were young females. As expected, no adult male was captured, the sampling area being located within a maternity roost (Greenwood, 1980; Lanza, 2012). Intriguingly, fewer male than female juveniles were captured, despite the sex ratio of new-borns is typically 1:1 (Lanza, 2012).

The observed unbalance in the sex ratio of young individuals may arguably been explained by the fact that young males tend to emigrate from the reproductive roost as soon as they learn to fly, usually within the first month of life (Lanza, 2012). Capture sessions were indeed carried out during August - September, when the juveniles were already able to fly. The recapture rate modelled in the first analysis depicts a different use of reproductive roost between the two sexes. The only male recaptured during the five year-observation was a young individual tagged earlier the same summer. A different recapture probability was also observed between young and adult male individuals, indicating the presence of a transience effect, with young males rarely returning to

Table 2. Ranking of the age models. Y. = constant juveniles' parameter. A. = constant adult parameter. Y_T = young parameter varying during time. A_T = adult parameter varying during time. p(.)/p(T) = recapture probability equal for two groups.

Model rank	**Parameters in the model**	**AIC**	**ΔAIC**	**N° of parameters**
1	φ (Y./A.) p (Y_T/A.)	206.2626	0.70806	4
2	φ (Y_T/A.) p (Y_T/A.)	209.5153	0.13924	6
3	φ (Y./A.) p (.)	211.0512	0.0646	3
4	φ (Y./A_T) p (Y./A_T)	212.2265	0.03589	7
5	φ (Y_T/A.) p(.)	213.1578	0.02253	5
6	φ (Y./A.) p (Y./A_T)	215.5977	0.00665	7
7	φ (Y_T/A_T) p(Y_T/A.)	215.7359	0.00621	9
8	φ (Y./A.) p (T)	215.9704	0.00552	6
9	φ (Y_T/A.) p(Y./A_T)	217.2411	0.00292	9
10	φ (Y./A_T) p (.)	217.3168	0.00282	6
11	φ (Y_T/A.) p(T)	217.6422	0.00239	8
12	φ (Y_T) p(Y_T/A_T)	218.3100	0.00171	11
13	φ (Y_T/ A_T) p(.)	219.6609	0.00087	8
14	φ (Y_T/ A_T) p(Y./ A_T)	221.8808	0.00029	11
15	φ (Y_T/ A_T) p(T)	222.0595	0.00026	10

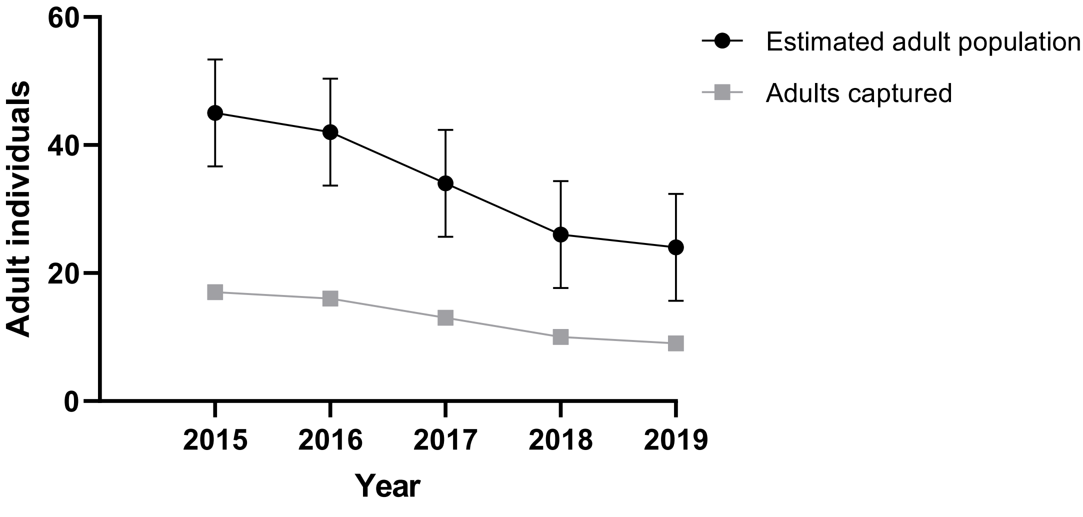

Fig. 4. Number of individuals captured over the five years study (grey line) plotted with estimations of adult population size with 95% CI (black line).

the roost where they were born. Permanent emigration of male juveniles from the maternity roost is indeed a common event among many species of bats (Hoyle *et al.,* 2001; Sendor & Simon, 2003; Papadatou *et al.*, 2009; Schorcht *et al.*, 2009). Some extrinsic factors, such as adult roost switch in the same area, might also have negatively affected these animals' philopatry estimation. Survival rate was modelled based on the recapture data from all individuals. Results indicated a good survival ability of the individuals of the colony studied. Our findings show that weather variables did not exert a strong influence on the population life span as the anthropophilic nature of *P. kuhlii* allows these animals to find shelter in buildings, therefore decreasing the negative effects of weather conditions on survival (Lanza, 2012). Typically, the number of rainy days negatively affects health condition of Kuhl's pipistrelle (Locatelli *et al.*, 2019) as the foraging activity is perturbed (Audet,

1990). However, for our population the effect of rain was marginal, arguably due to the site-specific characteristics of the foraging area.
The second analysis explored the most important factors impacting on survival ability among the ones we selected. To avoid biases, the male population was excluded due to low statistical representation. The female survival rate for the studied Kuhl's pipistrelle population was in line with that expected for a long-lived mammalian species, likewise for many other species belonging to the Chiroptera (Yoccoz & Ims, 1999; Schaub & Vaterlaus-Schlegel, 2001). As for the survival rate, the Kuhl's pipistrelle population analysed displayed similar values when compared with those of other European bat species, such as the common pipistrelle (*Pipistrellus pipistrellus*, 0.80 ± 0.05 survival parameter, SP) and the brown long-eared bat (*Plecotus auritus*, 0.68 - 0.98 SP) (Papadatou *et al*., 2011). Coherently, all these species share a comparable body size, diet and ecological plasticity (especially for the species belonging to the genus *Pipistrellus* which are characteristically anthropophilic), all factors contributing in increasing survival rates (Lanza, 2012; Fisher *et al.,* 2012). Finally, the survival rates for these species are also higher than in other migrating species (e.g. Leisler's bat, *Nyctalus leisleri*, 0.73-0.76 SP), suggesting they might benefit from not consuming energy in long distance flights or from being less exposed to predation or other ecological factors associated with the different environmental niche. A stationary life paired with a well sheltered hibernation strategy seems to be a good survival strategy for these European bat species.
As expected, the survival rate in juveniles was remarkably lower compared to the same observed for adult females. Even when accounting for underestimation biases deriving from the transient effect, the observed low survival rate of young individuals could be linked with inexperience and more difficulties in tackling threats such as predation and harsh winter condition (Sendor & Simon, 2003). Finally, since the studied population often switched roost within the study area, some of the tagged individuals were probably not detected in all capture sessions, leading to an underestimation of recapture rates and, consequently, an overestimation of adult population size.
Overall our data suggest that Kuhl's pipistrelle has a great survival capacity, likely thanks to its small body size, diet variety and stationary-philopatric habits. The anthropophilic attitude is also an advantage for the species to tackle adverse winter condition and other extrinsic mortality threats such as predators' attack. The estimation of recapture parameters allows to better understand the ethology of the species in maternity roosts and model both the movements of juveniles from these sites and female adults' philopatry. Our data reportedly indicate the roosts harboured in the San Genuario reserve as crucial reproductive sites for the species, being characterised by high annual fidelity by many pregnant females as an elective area to give birth to pups.
Other population studies might be designed in nearby sites used by the species to better understand the health condition of *Pipistrellus kuhlii* in the area and assess yearly weather variation on the species survival ability.

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AUTHORS CONTRIBUTIONS

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by AL, RT and AGL. The first draft of the manuscript was written by AL and all authors commented on previous versions of the manuscript. All author read and approved the final manuscript.

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