

Reproduction of the Crag Martin (*Ptyonoprogne rupestris*) in relation to weather and colony size

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From 1994 to 1999, we investigated how climatic conditions influence the laying dates and number of fledged young of the Crag Martin *Ptyonoprogne rupestris*, a poorly studied colonial martin that, like other aerial feeding birds, is supposed to be highly dependent on weather conditions. Laying dates were concentrated in May and the first half of June. The mean annual laying date differed significantly among years; however, probably because of the small absolute difference between early and late years, there was no influence on the clutch size nor on the number of fledged young. Mean clutch size was 4.4 ± 0.9 eggs, the hatching rate was 80.2 percent, and the average number of fledged young was 3.1 ± 1.9 . Temperature and rainfall in the days before laying and during the incubation period did not influence the breeding success, while in the chick rearing period there was a negative relationship between temperature and number of fledged young. It is supposed that high temperature can negatively influence breeding success through the drying up of small rivers where parents find food (mainly aquatic insects). In our study area the Crag Martins nested solitarily or in small colonies (mean 3.5 ± 1.9 nests). Colony size did not influence the laying date, the clutch size or the number of successfully fledged young.

1. Introduction

Climatic (Elkins 1988) and social factors (Brown & Brown 1997) are known to influence the reproduction of birds. The effects of weather on behavioural or life-history parameters (from the number of laid eggs to the survival rate) have been widely documented in many species (Newton 1998). Aerial feeders (Hirundinidae and Apodidae) are particularly good models since their food (aerial plankton) strictly depends on the temperature and other weather parameters like rain, atmospheric pressure and wind (Koskimies 1950, Brown & Brown 1999). There have been reports

of short-term effects of weather on pre- and post-migratory fattening of Barn Swallows *Hirundo rustica* (Pilastro & Magnani 1997) and on pre-breeding roosting behaviour of the Crag Martin *Ptyonoprogne rupestris* (Sackl & Putz 1998). Effects on mortality were observed in adult Cliff Swallows *Petrochelidon pyrrhonota* mainly after cold and rainy days in the early spring (Brown & Brown 1997). Regarding long-term weather effects, it has been shown in Sand Martins *Riparia riparia* that winter aridity in Africa is inversely related to survival (recruitment) to the next reproductive season (Bryant & Jones 1995, Szep 1995).

Considering more particularly the reproductive parameters of aerial feeders, the effect of climate has been detailed on clutch size and chick survival in House Martins *Delichon urbica* (Bryant 1975). Laying dates are also affected by bad weather in Pallid Swifts *Apus pallidus* (Cucco *et al.* 1992, Cucco & Malacarne 1996) and Common Swifts *Apus apus* (Gory 1992). In the Barn Swallow, Loske and Lederer (1987) observed a first-clutch mortality of 16%–20% in a very rainy summer. In species with hatching asynchrony, mortality related to food scarcity and severe climatic conditions is more common in the last-born chick (Malacarne & Cucco 1991, Turner 1984).

Coloniality, with its associated costs and benefits, is known to influence the behaviour and reproduction of birds (Wittenberger & Hunt 1985). In hirundines, several studies have focussed on the relationship between colony size and parasite load, extra-pair paternity, nest parasitism, infanticide, predation, and physiological costs (cfr. Møller 1987). Effects of colony size on reproduction have been particularly well studied in the Cliff Swallow (Brown & Brown 2001), Barn Swallow (Ambrosini *et al.* 2002) and Purple Martin *Progne subis* (Davis & Brown 1999). A positive effect, i.e. an increase of egg hatchability, was found in Cliff Swallows, while there was no correlation between breeding performance and colony size in Barn Swallows and Purple Martins.

The object of our study, the Crag Martin, is a Palearctic species living in temperate climates, mainly in the Mediterranean but also in continental areas. Its biology is not as well described as that of other Hirundinidae (Glutz & Bauer 1985, Cramp 1988). The aim of this study was to characterize on a multi-annual basis the reproductive ecology of small colonies in an area of NW Italy in order to identify the influences of (1) climatic conditions and (2) colony size on the laying date, clutch size and breeding success.

2. Methods

The study was carried out from 1994 to 1999 in a 15 × 20 km mountainous area of the Apennines (NW Italy: central lat. 44°39', long. 9°03', altitude 300–700 m a.s.l.). We searched extensively

for nest sites along the Borbera, Sisola and Vobbia rivers, three natural watercourses with 3–10 m wide riverbeds. Crag Martins usually build their nests on vertical cliffs along rivers or on the roof of bridges, and we selected the sites where the nest contents could be safely inspected from the ground by means of a mirror placed on a long telescopic pole (water in the riverbed no more than 60 cm high, nests from 2 m to 6 m high). In the study period, altogether 70 nests were inspected almost weekly in the egg laying and incubation periods, and then every three days during the chick rearing. Hatching rate was calculated for each nest as the ratio between hatched and laid eggs. Chicks leaving the nest after about 25 days (Cramp 1988, pers. obs.) were considered successfully fledged.

We assessed the colony size for each site by counting the total number of nests containing eggs or young. In a few cases in which the nest contents could not be inspected from the ground, we considered the nest to be utilized if adult Crag Martins regularly attended it.

The climate in the study area is temperate continental (Mennella 1967). Rainfall reaches a maximum in May and again in November. From June to September the weather is generally favourable, with high temperatures and few rainy days. Meteorological data were obtained from the Poplar Institute of Casale (20 km north of the study area). To investigate the influence of climatic variables on breeding parameters, we considered for each nest the mean temperature (°C) and rainfall (mm) recorded during seven 10-day periods (decades), i.e. the two decades before egg laying, the laying decade, the two decades of the egg incubation period, and the first two decades of the chick rearing period. To avoid confounding effects of low or high temperatures experienced respectively by early or late breeding attempts, a subsample of 49 nests with eggs laid in the main laying period (from 1 to 31 May) was selected. For the analysis, we calculated single correlation tests (temperatures and rainfall values during the seven 10-day periods) and employed the appropriate Bonferroni-adjusted significance level.

Because data were not normally distributed, throughout statistical analyses we used the non-parametric Kruskal-Wallis' test for analyses of variance, and the non-parametric Spearman's test for correlations.

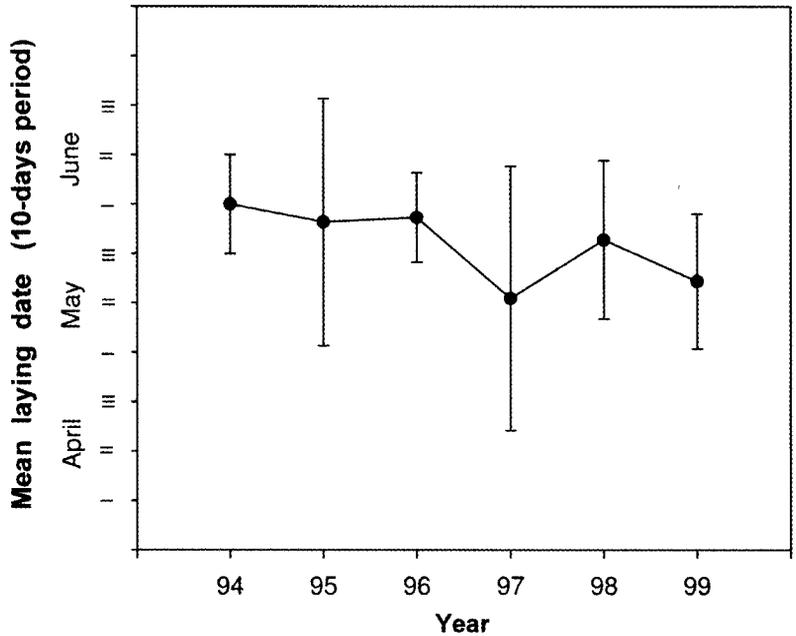


Fig. 1. Among years differences in the mean (\pm SD) laying dates.

3. Results

3.1. Influence of weather

Laying dates were concentrated in May and the first half of June (77% of 70 cases). The mean laying date (decades) differed significantly among years (Fig. 1. Kruskal-Wallis ANOVA; $H_{6,70} = 11.0$; $P < 0.05$). The mean annual laying date was not influenced by rainfall in May ($n = 6$ years: 1st decade: $r_s = -0.27$, $P = 0.66$; 2nd decade: $r_s = 0.61$, $P = 0.25$), nor by temperature in the first decade of May ($r_s = -0.04$, $P = 0.99$), but was negatively related to temperature in the second decade of May ($r_s = -0.83$, $P < 0.05$). On average, Crag Martins delayed the laying date by about 3 days for each one-degree decrease in temperature in the 2nd decade of May.

Average clutch size was 4.4 eggs (± 0.91 SD; $n = 70$; range 1–6). There were only small, non-significant variations of clutch size among years (Kruskal-Wallis $H_{6,70} = 6.3$, $P = 0.28$), and neither the mean annual laying date ($r_s = 0.54$, $n = 6$, $P = 0.31$) nor temperature or rainfall in the different decades of May influenced the mean annual clutch size (all $r_s < 0.49$, $P = 0.36$).

The mean hatching rate was 80.2 percent; thus the average brood size at hatching was 3.5 nest-

lings (± 1.8 ; $n = 64$, range 0–6). There were only small, non-significant variations of brood size among years ($H_{6,64} = 5.3$, $P > 0.20$).

The mean number of fledged young was 3.1 (± 1.9 ; $n = 64$, range 0–6). There were only small, non-significant variations of fledging number among years ($H_{6,64} = 7.2$, $P = 0.21$).

Climatic conditions in the period before laying and during incubation were not related to the breeding success (r_s values for temperature and rainfall in 5 decades ranging from 0.02 to 0.24, $n = 49$; P ranging from 0.36 to 0.99 after Bonferroni correction). However, high temperatures during the first decade of chick rearing were negatively related to the number of fledged young (Fig. 2, $n = 49$; $r_s = -0.38$, Bonferroni-adjusted $P < 0.05$).

3.2. Influence of colony size

In our study area the Crag Martins nested solitarily (20.3% of nests) or in small colonies (mean 3.5 ± 1.9 nests, range 1–7). Colony size did not influence the laying date (Kruskal-Wallis ANOVA; $H_{6,70} = 3.4$, $P = 0.64$), clutch size ($H_{6,70} = 2.9$, $P = 0.72$) or number of successfully fledged young (Fig. 3, $H_{6,64} = 3.2$, $P = 0.67$).

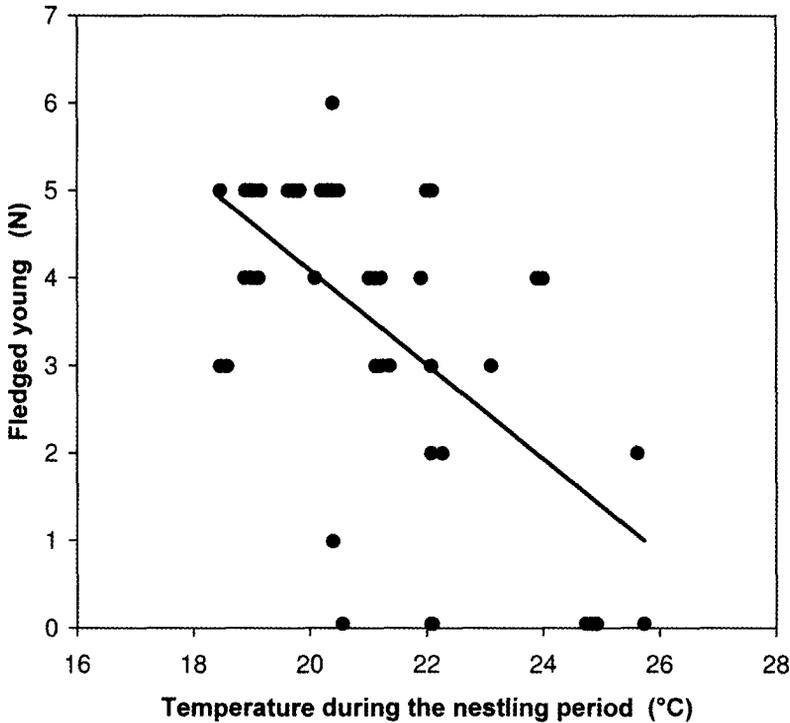


Fig. 2. Relationship between temperature during the first phase of chick rearing and the number of fledged young (the regression line: $y = 14.8 - 0.53x$, is also shown).

4. Discussion

Our multi-annual data reveal two main influences of weather conditions on Crag Martin reproductive biology: indeed, laying date was delayed by low temperatures, and high temperatures during chick growth lessened their fledging success. The postponement of laying due to low temperature is a typical feature of reproduction of aerial feeders (Bryant 1975, Cucco *et al.* 1992). In our study area, the laying dates were significantly delayed by low temperatures in the main laying period, the second decade of May, but were unrelated to temperatures observed in the previous decade. Probably, the effect of low temperature in early May is only transitory, and females are able to recover quickly to a proper breeding condition when cold occur in this period.

The negative effect of high temperature on breeding success is unusual in hirundines and has rarely been reported for other birds; on the contrary bad weather is usually linked to low temperature and high rainfall (Lack 1968). According to this rule, in the Cliff Swallow, females are in a better condition and able to produce the clutch faster in warm seasons, in which food availability

is greater (Brown & Brown 1999). In northern populations of our study species, the feeding rate is less than average in cold, dull or windy weather (Cramp 1988). The typical decline of breeding success as the season progresses can be reversed when the usual temperature trend is reversed, as reported for the House Martin in the case of a rainy July and sunny September (Christe *et al.* 2001).

A negative effect of high temperature on breeding success has been less frequently reported. In our study area, the negative effect could be related to the fact that too hot summers lead to the drying up of small rivers, and thus a decreased supply of insects in the valleys where our Crag Martins search for food and reproduce (Fenoglio *et al.* 2002, Hall *et al.* 2003). Indeed, it has been observed that this species feeds on insects not far from the colony (less than 1 km: Cramp 1988, pers. obs.), and that most of the food delivered by parents to the nestlings consists of aquatic insects (Diptera, Plecoptera, Trichoptera) (Guitian Rivera *et al.* 1980).

In Mediterranean habitats, hot summer temperatures and drought conditions favour early breeding by birds (Isenmann *et al.* 1990). Summer drought is a problem since the ground becomes dry and sun-baked (Elkins 1988). Another

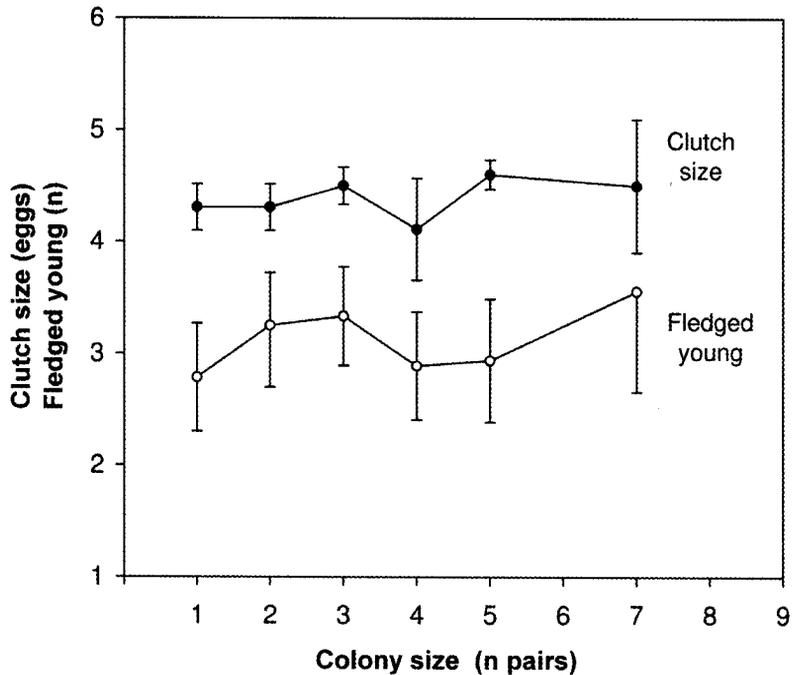


Fig. 3. Relationships between colony size and clutch size (filled circles; mean \pm SD) or number of successfully fledged young (open circles).

effect of high temperature is because young chicks are unable to thermoregulate efficiently and are dependent on the brooding of their parents. Nestlings are very vulnerable to overheating (Webb 1987). The harmful effects of low temperatures can potentially be moderated by parents through increased food provisioning, allowing nestlings to increase energy expenditure, but such is not the case for high temperatures. Thus, increased chick mortality might occur both at high and low temperatures (Redpath *et al.* 2002).

This study shows no effects of coloniality on Crag Martin reproductive parameters. This result is different from the one reported for the Cliff Swallow, where there was an increase of egg hatchability with colony size (Brown & Brown 2001), but is similar to those reported for the Barn Swallow and Purple Martin (Davis & Brown 1999, Ambrosini *et al.* 2002). Our study species is a facultative colonial with, at most, 10–20 loosely clustered nests, and instances of pairs nesting solitarily are usually reported (Cramp 1988, pers. obs). Probably, differences in reproductive parameters related to colony size are more likely to be found in species with a larger range of colony sizes, such as the Cliff Swallow. However, even if our study does not provide any indication of costs or benefits

associated with coloniality, as would have been indicated by a variation in reproductive success with colony size, more data on other aspects of the life-history (e.g. survival, parasite load, physiological costs; Møller 1987, Alves & Bryant 1998, Szep & Møller 1999) are necessary to definitively assess this point.

In conclusion, the results of our study may also have useful implications for the management and conservation of breeding populations of Crag Martin. For the conservation of Crag Martins living near small rivers, water resource planning should take into account aspects of both the quantity and quality. Water resource sharing should consider the demands of the various water users, but also the need of a minimum flow in any section of the river. This may require that the water resource sharing problem be reformulated so as to increase the water flow in the river to avoid the negative effects of drought.

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Selostus: Pesimäajan säätilan sekä koloniakoon vaikutus kalliopääskyn pesimämenestykseen

Pesimäaikaisella säätilalla on oletettavasti suuri vaikutus kalliopääskyn ja muidenkin ilmasta ravintonsa hankkivien lintulajien pesimämenestykseen. Artikkelin kirjoittajat tutkivat pesimäkauden säätilan ja koloniakoon vaikutuksia kalliopääskyn muninnan aloitusajankohtaan sekä poikastuottoon Apenniinien vuoristoalueella Italiassa vuosina 1994–1999. Tutkimusalueen kalliopääskyt pesivät joko yksittäin tai pienissä kolonioissa (noin 3,5 pesää per kolonia) jokivarsien kalliorannoilla. Koloniakoolla ei havaittu olevan vaikutusta kalliopääskyjen muninnan aloitusajankohtaan, munamäärään tai lentopoikasten määrään. Kalliopääskyjen muninta ajoittui pääosin touko-kesäkuun vaihteeseen. Muninnan aloitusajankohta vaihteli vuosien välillä. Kylminä keväänä muninnan aloitus myöhästyi. Munamäärässä tai lentopoikasten määrässä ei havaittu eroja vuosien välillä. Kalliopääskyjen pesissä oli keskimäärin 4,4 munaa, munien kuoriutumisprosentti oli 80 ja lentopoikasia tuotettiin keskimäärin 3,1. Munintaa edeltävien päivien ja haudonta-ajan lämpötilalla sekä sademäärällä ei ollut vaikutusta kalliopääskyn pesimämenestykseen. Sen sijaan pesäpoikasajan korkeat lämpötilat alensivat kalliopääskyn lentopoikastuottoa. Kirjoittajat päättävät, että pesäpoikasajaiset korkeat lämpötilat kuivattavat jokia, joiden varsilta kalliopääskyemot hakevat poikasilleen ravintoa. Kuumina kesinä pääskysille tarjolla olevaa hyönteisravintoa on ilmeisesti vähemmän saatavilla. Tämä voisi olla syy lämpötilan ja lentopoikasten määrän väliseen negatiiviseen korrelaatioon. Kalliopääskyn suojelemiseksi jokiuomien kuivumista tulisi ehkäistä.

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