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ENVIRONMENTAL CONDITIONS AND PARENTAL CARE IN THE PIED FLYCATCHER

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Noi percepiamo chiaramente che soltanto ora incominciamo a raccogliere materiale attendibile per saldare insieme, in un unico complesso, la somma di tutte le nostre conoscenze; ma, d'altro lato, è diventato quasi impossibile per una sola mente il dominare più di un piccolo settore specializzato di tutto ciò.
Io non so vedere altra via di uscita da questo dilemma (a meno di non rinunciare per sempre al nostro scopo) all'infuori di quella che qualcuno di noi si avventuri a tentare una sintesi di fatti e teorie, pur con una conoscenza di seconda mano e incompleta di alcune di esse, e a correre il rischio di farsi rider dietro.

Tutto ciò a mia difesa.

Erwin Schroedinger, Dublino, settembre 1944

We feel clearly that we are only now beginning to acquire reliable material for welding together the sum total of all that is known into a whole; but, on the other hand, it has become next to impossible for a single mind fully to command more than a small, specialized portion of it. I can see no other escape from this dilemma (lest our true aim be lost forever) than that some of us should venture to embark on a synthesis of facts and theories, albeit with second-hand and incomplete knowledge of some of them — and at the risk of making fools of ourselves.

So much for my apology.

Erwin Schroedinger, Dublin, September 1944

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Riassunto

In questa tesi ho studiato la relazione tra alcuni fattori ambientali e lo sforzo parentale del maschio e della femmina in un piccolo uccello passeriforme, la balia nera (*Ficedula hypoleuca*). In particolare, come misura dello sforzo parentale, ho considerato il numero di visite al nido per portare cibo ai pulli (*feeding rate*), e ho registrato sia la frequenza oraria delle visite da parte di entrambi i genitori che la loro coordinazione temporale. In aggiunta a ciò, ho verificato l'effetto della rimozione sperimentale temporanea di un genitore sul comportamento del partner.

La quantità di cibo fornito ai piccoli al nido dipende dal *feeding rate* e se le condizioni ambientali (qualità e frequenza delle prede disponibili) non sono favorevoli, gli adulti possono essere limitati nella frequenza delle visite al nido. Per questa ragione, nell'analisi del comportamento dei genitori, ho considerato anche alcuni parametri ambientali, sia naturali che di origine antropica, che possono essere associati alla disponibilità di prede. Un fattore ovvio riguarda le condizioni meteorologiche presenti nell'area di studio nei giorni nei quali ho condotto le osservazioni, come temperatura e precipitazioni, e che sono quindi le stesse per tutti i nidi.

I caratteri relativi all'ambiente fisico nella vicinanza del nido, come la distanza dal margine della foresta, il grado di copertura vegetale e la distanza dal più vicino corso d'acqua,

viceversa, differiscono per ogni nido. Tra i fattori antropici ho considerato la distanza dalla strada principale, la distanza dalle strade sterrate che attraversano l'area di studio e la distanza dagli edifici. In aggiunta, sono stati considerati la dimensione della covata al terzo giorno dopo la schiusa e la data di schiusa, dato che il numero di visite normalmente è maggiore quando la nidiata è più numerosa e le condizioni ambientali (qualità delle prede) tendono a deteriorarsi con il procedere della stagione.

La previsione è che la vicinanza ad un corso d'acqua, una folta copertura vegetale, una maggiore distanza dai margini della foresta costituiscano un indice di buona qualità del territorio e che quindi possano essere associati positivamente con le cure parentali. Viceversa, la presenza di strade ed edifici è probabilmente indice di una ridotta qualità del territorio. Temperatura e precipitazioni sono fattori più complessi da valutare per ciò che riguarda la loro influenza sulla riproduzione e il valore ottimale probabilmente varia da specie a specie, con l'eccezione di livelli estremi di temperatura e piovosità, che hanno probabilmente sempre effetti negativi. Lo scopo di questa tesi è stato quindi quello di valutare quali di questi fattori sono maggiormente associati alle cure parentali in questo passeriforme.

I risultati dimostrano che molti dei fattori ambientali considerati sono associati al *feeding rate*, nella maggior parte dei casi secondo quanto previsto teoricamente: ho trovato una correlazione positiva tra la dimensione della covata e il *feeding rate* sia del maschio che della femmina. Per altri parametri, la relazione trovata differisce tra i due sessi: ho osservato una relazione positiva tra *feeding rate* della femmina e data di schiusa, mentre il *feeding rate* del maschio è risultato positivamente correlato con la temperatura e con le precipitazioni del giorno precedente, e negativamente con la distanza dalla strada principale. I viaggi di imbeccata totali dei due genitori sono risultati correlati positivamente con la data di schiusa e la dimensioni della covata. Per ciò che riguarda il grado di coordinazione temporale della coppia nei viaggi di imbeccata, con maggiori temperature si è denotata una maggiore coordinazione della coppia. In contrasto con questi risultati, il *feeding rate* del genitore durante il periodo di rimozione sperimentale del partner non ha mostrato relazioni con nessuno dei parametri indagati. Sono state formulate delle possibili spiegazioni a questi risultati, ma si tratta di conclusioni che richiederanno di essere confermate da studi futuri. I risultati indicano che esiste una relazione tra fattori ambientali e cure parentali in balia nera. Come previsto, il comportamento della femmina è stato meno influenzato da fattori relativi alla sola qualità del territorio o alle condizioni climatiche, indicando che il suo sforzo parentale viene mantenuto elevato anche in condizioni meno favorevoli. Al contrario, il comportamento del maschio si è dimostrato più influenzabile dalle condizioni ambientali che probabilmente influiscono sul costo dello sforzo parentale. Entrambi i genitori hanno aumentato gli sforzi quando era presente una covata più grande, confermando il loro obiettivo primario di crescere il maggior numero di pulcini in buone condizioni. L’assenza di relazione tra fattori ambientali e *feeding rate* di compensazione dopo la rimozione del partner conferma l’ipotesi che, in condizioni particolarmente difficili, i genitori non risentano significativamente di ulteriori fattori ambientali, considerato l’aumentato stato di bisogno della prole determinata dall’assenza di un genitore. È interessante notare che la coordinazione tra i genitori aumenti in condizioni di temperatura più alta, un risultato che suggerisce che le condizioni meteorologiche influiscano sulla capacità dei genitori di ottimizzare il loro sforzo parentale.

Complessivamente, i miei risultati suggeriscono che le condizioni ambientali hanno effetti diversi sul comportamento parentale dei due genitori in relazione al sesso e allo stato di bisogno dei pulcini. È di primaria importanza capire maggiormente le reazioni animali alla variazione delle condizioni dell’ambiente in cui vivono, e per farlo, è necessario analizzare quali fattori abbiano un impatto maggiore sulla stagione riproduttiva e, di conseguenza, sulle popolazioni.

Abstract

The environmental conditions can be considered as all the factors affecting the life of an individual. Both human activities and climate changes share the common potential of being dangerous in the short and long period, for the natural populations of many organisms.

The aim of this thesis is to investigate how some environmental factors affect the parental behavior of a small passerine bird, the Pied flycatcher (*Ficedula hypoleuca*). More specifically, how these factors influence the parental effort (food provisioning) of each of the father and the mother. Additionally, we performed an experimental mate removal to assess how such environmental parameters influence the behavior of the remaining adult when feeding alone. The parental care effort has been measured as the hourly feeding rate (trips to the nest) of each adult and the coordination between the parents' feeding trips. The feeding rate can be influenced by the quality of the territory and hence the availability of prey. The chosen environmental parameters are both natural and human-related. The natural factors divide into meteorological data, that were identical for all the nests in relation to the day of the parental care data recording, like temperature and precipitation, and the spatial data, which differed for each nest, like the distance from the edge of the forest, the tree leaves coverage and the distance from the nearest stream of

water. Human related factors were represented by the distance from the main asphalted road, the distance from the secondary dirt roads and the distance from surrounding buildings. In addition to these, two breeding parameters were added: the hatching date and the brood size.

We expect that flycatcher parents' benefit, in terms of parental effort, from some of these factors like the proximity to the stream of water, a high tree leaves coverage, a further distance from the edge of the forest, and be disadvantaged by the vicinity to buildings and roads. A larger brood size should require more visits by the parents, while a later hatching date (late breeding) should result in prey of lower quality, thus implying more feeds. Temperature and precipitation are more complex parameter to assess, having an optimal interval for every species and being harmful at both negative and positive extremes.

The results showed that many of these factors were associated with the observed level of parental care, mostly in the predicted way. Both female and male feeding rates were positively related to the brood size. While the female feeding rate was also positively related to the hatching date, the male feeding rate was positively related to the temperature and negatively by the distance from the main asphalted road. The total feeding was positively related to the brood size and the hatching date. Both parents increased their effort when they raised a large brood, confirming their response to brood's need. Higher temperatures showed higher alternation score between adults which is expected to provide a more constant supply of food to the nestlings. The results collectively indicate that environmental factors do influence the Pied flycatcher parental care. As predicted, the female behavior was probably maximized according to existing limiting factors. Male behavior was conversely influenced by more factors, suggesting that males increase their parental contribution when conditions impose lower foraging costs.

The compensation feeding rate observed after the removal of the partner was not significantly affected by any of the investigated environmental factors. The absence of effects on the compensation feeding rate further suggests that, when the offspring are likely to face a reduced feeding rate, as a consequence of a parent raising a brood alone, the parental effort is little affected by other environmental conditions. These results confirmed many studies done before, which showed that the male is usually more prone to lower its effort when external conditions impose higher costs to his parental investment. My study evidenced, however, that when males are forced to care the offspring alone, they increase their feeding effort irrespective of the environmental conditions.

It is of the utmost importance that animal reactions to their environment changes are deeper investigated, and to do that, it is important to analyze which factors have a stronger impact on the populations.

1. Introduction

1.1 Introduction to pied flycatcher

The flycatcher is a small (12-13g) passerine bird (see Figures 1 and 2), which breeds in many forested areas of the Palearctic region (Lundberg & Alatalo, 2010). It winters in West Africa during the fall and winter and spends the rest of the year on migration or breeding in Europe. Most of the knowledge about its biology derives from studies conducted during its reproductive period but recent studies on the migration and the wintering period have also been conducted thanks to GPS (global positioning system) tracking devices (Paxton et al., 2017; Wang et al., 2007).

Figure 1: Adult male flycatcher on a branch (courtesy of Juan Carlos Fontanillas, Universidad Complutense de Madrid)
Figure 2: Adult female flycatcher on a branch with nesting material in the beak (courtesy of Juan Carlos Fontanillas, Universidad Complutense de Madrid)

In Western Europe there are two abundant species of flycatcher, the pied flycatcher (*F. hypoleuca*) and the collared flycatcher (*F. albicollis*). Current distribution ranges likely reflect expansions from Pleistocene glacial breeding refuges on the Iberian (pied flycatcher) and the Apennine (collared flycatcher) peninsulas (G. P. Sætre et al., 2001). Areas of sympatric occurrence are present both in central and eastern Europe and on the Baltic Sea islands Gotland and Öland (Figure 3), and hybridization occurs at a low rate within these zones (Alatalo, Gustafsson, et al., 1982; G. -P. Sætre et al., 1999).

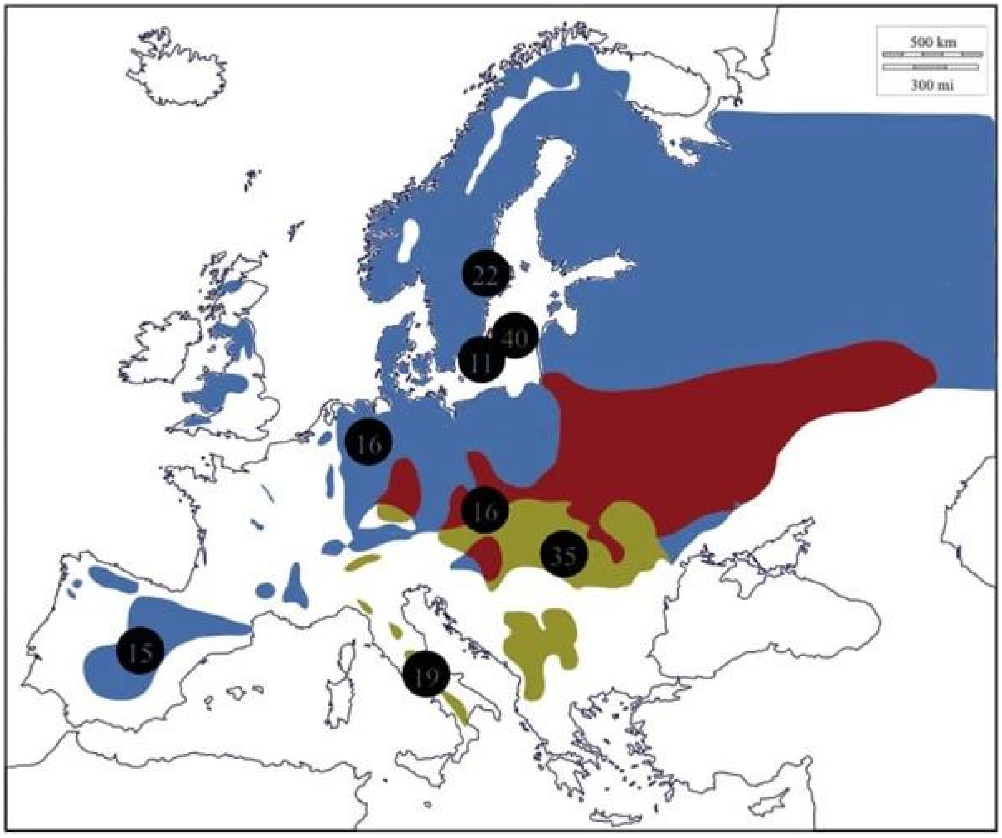


Figure 3: European breeding distribution ranges for the pied flycatcher (Ficedula hypoleuca, light blue), the collared flycatcher (Ficedula albicollis, green), and regions where both species occur together (red).

Flycatchers belong to the family of Muscicapidae, which contains 9 subfamilies and 107 species, breeding from Africa and Europe in the west, through Asia to the Japan island in the east (Howard and Moore, 1991). The pied flycatcher can be divided into five subspecies: *F. h. hypoleuca, F. h. iberiae,* *F. h. speculigera, F. h. semitorquata* and *F. h. tomensis* (Potti & Merino, 2008).

Note that *F. semitorquata*, which breeds in Southeastern Europe, from the Balkan to Iran, is now considered a separate species (Saetre et al., 2001).

The subspecies investigated in this dissertation project is *F. h. iberiae*, breeding in the central part of Spain. The population considered can specifically be found in the forest area of Valsaín (Segovia).

Male and female do not share the same plumage color during the breeding season (see Figures 1 and 2). The female displays a grey/brown color on the back (Figure 2) with a white front plumage, while the male is black on the back and has a wider white front patch (Figure 1). Not all the males share the same blackness, whose level can vary by genetics or life stage (Siitari, 2002). Blackness is mostly categorized by the covering of black feathers on the back, but it is not the only way to scale it (Drost, 1936; Galván & Moreno, 2009). The male color depends more on the environmental factors than on the condition during the nestling stage (Potti & Montalvo, 2008). The darker male color phenotype is adapted to a typical northern climate and functions as a dominance signal in male–male competition over nesting sites, while the browner phenotypes are favored by a less competitive intraspecific competition with the more dominant male collared flycatchers in areas where the two species co-occur (Lehtonen et al., 2009). Pied and collared flycatchers can

hybridize, but only hybrid males are fertile, thus with an overall reduced population fitness (Backström et al., 2013). Hybridization can be an adaptive strategy if conspecifics are not available, thus producing at least some offspring (Wiley et al., 2009). Hybridization's dynamics are complex and various mechanisms can explain why it sometimes can be the best strategy (Veen et al., 2001).
For the *iberiae* subspecies, older individuals (2 or more years) might display an increasingly reduced blackness (Potti & Montalvo, 2008). It is usually easy to distinguish between sexes, but in areas of sympatry with the more dominant collared flycatcher, male and female colors are quite similar if not indistinguishable (Alatalo et al., 1990).

Among the nearly 10,000 bird species, many can live up to 20-30 years (Wasser & Sherman, 2010) or even more (Mäntylä et al., 2020). However, this is not the case of most passerines, where the maximum lifespan can be longer than 10 years, but most individuals have a much shorter adult lifespan. As most other small species of this order, the pied flycatcher is a relatively short-living bird (Figure 4), with the average age of recaptured individuals being 3.0 ± 1.3 years in our study population. The highest lifespan for a female and a male recaptured in this population is respectively 8 and 9 years old (Alejandro Cantarero, unpublished data).

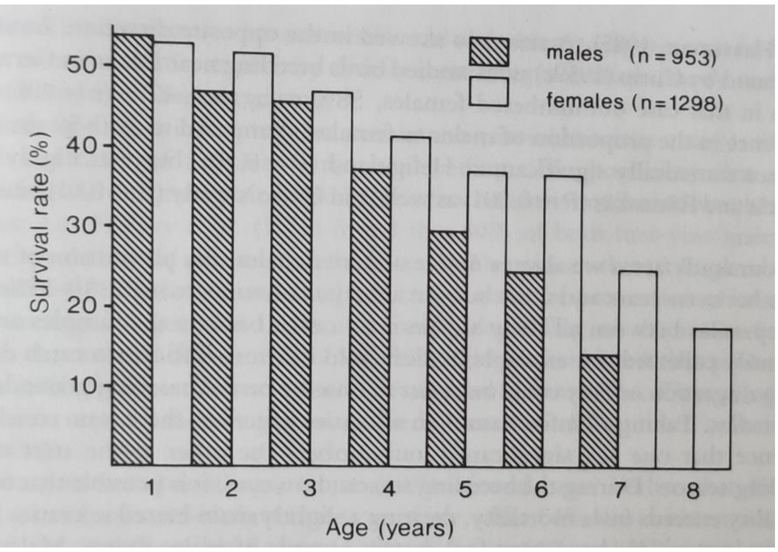


Figure 4: Survival rates of male and female Pied flycatchers in relation to age. Based on data from Lower Saxony, Germany (Sternberg, 1989)

The higher mortality is detectable in the early stages of life in the first days before fledging and in the first year of life, with an estimated survival rate of 50% to the first reproduction (Sternberg, 1989).

Diet

The pied flycatcher is an almost completely insectivorous species, although adults feed substantially on fleshy fruits during their migration stopovers (Hernández, 2009). Lepidoptera (adults and caterpillars) are the most common prey type, followed by Diptera and Coleoptera, that it is found in the nestling diets of different populations (Sanz et al., 1998). Analysis conducted by Nicolaus et al. (2019) shows that diet composition does not vary with date, nestling age, and the parent sex (Nicolaus et al., 2019).

Because caterpillars have a high-quality nutritional profile (Arnold et al., 2010), a higher proportion of caterpillars in the diet should result in better nestling condition, as has been found in great tits (*Parus major*) (Wilkin et al., 2009). However, it was not clear whether this relationship also applied to pied flycatchers (Eeva et al., 2005) until a further study from Burger et al., 2012 showed how the fledgling mass is positively correlated with the proportion of caterpillars in the diet, thus underlining the importance of this prey availability. Caterpillars are not always available, especially in oak forests, where a decline in the abundance of caterpillars in the forest is reflected in the nestlings' diet over the season, particularly in warm years, whereas in colder years, it is less apparent (Burger et al., 2012).

As previously explained, it is important to match the hatching date with the prey's peak of abundance. During the breeding season, especially during the nestling stage, most forest passerines, including flycatchers, are dependent on lepidopteran larvae whose abundance is variable between years and habitats (Lack et al., 1954; Nadolski et al., 2021; Perrins, 2008). Caterpillar outbreaks seem to provide insectivorous birds with especially advantageous conditions to provision offspring (Capinera, 2010; Marciniak et al., 2007). Because of the timing of budburst, the period of peak abundance of leaf-eating caterpillars is usually short in spring (Perrins, 2008; Southwood et al., 2004). Both the timing and the level of peak abundance of caterpillars influence breeding performance and hence populations of insectivorous passerines (Noordwijk et al., 1995; Sanz, 2001a; Visser et al., 2005). It has been commonly recognized that the bird species that feed nestlings chiefly with caterpillars should synchronize the nestling stage of their breeding with the timing of caterpillar abundance and that temporal mismatches are penalized in terms of fitness (Blondel & Aronson, 1999; Tremblay et al., 2004). Thus, early breeders can profit from the caterpillar's peak, whereas late breeders usually cannot, and this effect is exaggerated in warmer years (Burger et al., 2012). It is possible that early breeders are specialists, and the late ones are generalists, regarding the habitat choice. For the individuals that join the breeding area later in the season, pure oak forests are not the obvious choice, and nearby coniferous or mixed ones might be chosen.

Territory quality

In hole-nesting species like flycatchers, the choice of nesting area is the most crucial for reproduction. The higher quality of a chosen area translates into a more successful breeding season (Siikamaki, 1995). After wintering in West Central Africa, the males come back to Europe to breed and arrive before the females. The early arriving allows males to find a better spot to attract a female and build a nest (Potti et al., 2018). In this species the male defends a small territory around the nest position. A favorable feeding area in the nest surroundings may therefore influence the bird's evaluation of the quality of a given territory (Siikamaki, 1995).

Usually, high-quality males (e.g., males in better conditions and more experienced) afford the better nest sites, but it has been shown that a female prefers a below-average male with a good nesting territory rather than a higher-quality male with a worse nest site (Lundberg & Alatalo, 2010). Male quality factors can be related to each other, but singularly isolated from the context, the criterion used by female to choose a male can be displayed in this order, from the most important: territory/nest site quality, male's mating status (already mated or unmated), male's blackness, and age (Alatalo et al., 1986; Sirkiä & Laaksonen, 2009).

1.2 Pair formation and mating

Because of its short lifespan expectation, sexual development occurs fast. There are differences between sexes, with an estimated frequency of 30 – 70 % of females and 25 – 40 % of males breeding at the first year (Grinkov & Sternberg, 2019; Nyholm, 1986).

Females are the choosing sex at pair formation. The mate choice is critical, as the good genes, paternal ability and quality of the resources held by the male can significantly vary between individuals (Both et al., 2017; Nowicki et al., 2002; Sundberg & Larsson, 1994).

Unlike the majority of mammals, most bird species are monogamous (Bart & Tornes, 1989; Black & Hulme, 1996; Wittenberger, 1980), although polygynous, polyandrous, and promiscuous mating systems also occur (Orians, 1969). Selection favors those individuals that leave most surviving offspring to future generations. The strategies and tactics employed to maximize fitness differ not only between the sexes but also between individuals of the same sex. Regarding the mating system, a conflict arises between the sexes: males can sire more offspring by mating with several females, while females usually do not (or to a lesser extent) increase the number of offspring by copulating with several males (Székely, 2014). For this reason, the best strategy for females to increase their reproductive success is generally to increase the contribution in the care of the offspring by the male, so that most or all can be raised to independence (Houston et al., 2005). Thus, there is a conflict between the sexes as to how to produce as many surviving offspring as possible (Barta et al., 2002; Harrison et al., 2009; Székely, 2014). In birds this conflict has most often been settled by a monogamous breeding system, but in our study species, males can become polygynous by attracting more than one female into the same territory in the same season (Stenmark et al., 1988). When two females are attracted by male in a different territory, it is called “polyterritorial polygyny”, and in this case, the females mated to a polygynous male are not aware of each other (Alatalo & Lundberg, 1984). An already mated male will rarely give full parental care to the offspring of the secondary female, and females that choose to mate with an already mated male, are probably deceived by the polyterritorial male strategy (Stenmark et al., 1988). In the pied flycatcher copulations cease when egg-laying starts, and consequently, some males are able to defend a second territory after. Females store the sperm in the so-called "sperm storage tubules"; thus a few inseminations before egg-laying might be sufficient to fertilize an entire clutch (Birkhead, 1988).

The risk of shared paternity is consequently reduced if the male abandons the nest after the start of female egg-laying. The average distance between nests varies from adjacent nests (few meters) (Alatalo & Lundberg, 1990) to very far ones (few kilometers) (Rätti et al., 1994); the range is however underestimated because long-distance movements are less likely to be discovered than short ones. Not all the polyterritorial males succeed in attracting a second female, and polygyny frequencies vary between geographic areas, habitats, breeding densities and nest-holes availability. In general, early arriving males are more likely to mate polygynously whereas late-arriving males more often remain unmated (Canal et al., 2011).

Female choice and male deception

The presence in the territory is important, the more a male sing and shows its presence in an area, the more a female can detect him. The difference between already-mated and unmated males resides in the time spent in the mating territory waiting for a female; an already-mated male spends significantly less time in the secondary territory than an unmated male does in its first territory if a female is not around. When a female is around both unmated and already-mated males are almost continuously present in their mating territories (Lundberg & Alatalo, 2010).

On the other hand, also the female choice is critical. The choice is important itself because it implies the investment of the female's energies, and therefore it directly affects the breeding season success (Harrison et al., 2009). There are many theories about the female's choice, and it has been overall demonstrated that the female chooses actively, sometimes rejecting poor breeding situations, and consequently looking for better ones (Sirkiä & Laaksonen, 2009). Theoretical studies have proposed models for active female choice procedures (Dale & Slagsvold, 1996; Janetos, 1980; Real, 1990). The simplest is the 'threshold tactic' in which the female accepts any male/territory if the quality is above some level set up by the female (Real, 1990). This threshold might differ between females.

Another mate search tactic is what is called 'sequential

comparison'. Here females sample males sequentially and choose based on the last two breeding situations encountered (Dale & Slagsvold, 1996).
A third method is called 'best-of-*n*-tactic' (Janetos, 1980). In this case, females sample a fixed number of males/territories and then choose the best from this sample. The advantage of this tactic is that there is a good chance for a female to find an especially good breeding situation; the drawback is that they may already have become occupied by another female during the first female sampling procedure. These pros and cons go to extremes if the number *n* is large. It is then possible that a female makes her choice before sampling all the *n* sites, if a situation is particularly fitting.

Females can be more-or-less picky, generally depending on the difficulty of the choice. If the choice is easy, females will discriminate between breeding situations, if the choice is instead costly, they will save energy and choose without much hesitation (Slagsvold et al., 1988).

Male pairing status is important for female reproductive success and pairing with an already-mated male might lead to a reduced number of offspring (Stenmark et al., 1988). As it has been said before, the most important parameter to consider in the female choice is the quality of the territory and nest, and this assessment is easily achievable. Assessing the male mating status is furthermore not as easy. It is time-consuming for the female to investigate it, and, depending on the female rush to find a mate, it can sometimes be impossible to discriminate the mating status between many males (Alatalo & Lundberg, 1990). Polyterritoriality allows males to make their mating status more difficult to understand, making it costly in terms of time and energy for a female to discover. This situation can be labeled as the 'male deception' (Alatalo & Lundberg, 1984; Stenmark et al., 1988), in which the male takes advantage of the 'environment' variable to hide precious information from the female. Despite the color of the male can be used as a variable to possibly discriminate whether it is already-mated or unmated, females do not distinguish between individuals, also because already-mated males behave like unmated ones (Stenmark et al., 1988). If the female mates with an already-mated male and is consequently left alone in the parental care, it is anyway better for her to continue the attempt rather than quitting and maybe end as a secondary female again, but later in the season (Alatalo, Lundberg, et al., 1982). Delayed breeding might lead to reduced survival prospects for the offspring. Overall, some females even choose an already-mated male because they cannot afford the high cost of searching for an unmated male or investigating the mating status of every male, and this cost is argued to exceed the cost of being a secondary female (Alatalo, Lundberg, et al., 1982).

Courtship feeding and nest building

Males of many animals, including insects, birds, and mammals, provide their females with food from prior to mating until the laying (Galván & Sanz, 2011; Lack, 1940), which is known as courtship feeding (CF).

The pattern of courtship feeding differs between bird species, mostly resulting in when they take place and for how long. In this study species CF takes place mostly during the pre-laying and laying periods up to the incubation (incubation feeding) (Lifjeld & Slagsvold, 1986), when the females have the highest resource requirements relating to egg formation (Ledwoń & Neubauer, 2018).

This behavior seems to improve female nutrition rather than influence female choice (Cantarero et al., 2014). Improving the female nutrition status has benefits for the breeding success, with a positive correlation between female body weight and offspring's body weight (Lifjeld & Slagsvold, 1986).

Polygynous males are able to recognize the female's nutrition status and shift their effort on the female with a poorer one (Slagsvold & Lifjeld, 1989).

Nest building in the pied flycatcher is performed mainly by the female although males also provide materials (Martinez-de la Puente et al., 2009). When the male has attracted a female, she soon starts building the nest. Depending on the arrival date of the female, the nest-building will take place immediately or after few days (Moreno et al., 2008). Early arriving females will have more time to choose a nest-site carefully while the late ones will have less time to do it.

The pied flycatcher nest consists of two layers, an exterior bottom one, composed of packing material and an inner interior one, composed of more fibrous material (Stjernberg, 1974). The nest material used varies considerably according to what is available. However, the bottom layer is commonly made up of such material as pine and birch barks, dry pine and heather twigs, and dead leaves. In our study area pied flycatchers incorporate strips of bark of laurel-leaf cistus (*Cistus laurifolius*), pine (*Pinus sylvestris*) barks and dry grass as nest material (Moreno et al., 2009). The inner layer and the nest cup are almost always composed of dry grass, animal hair, root fibers, and shafts of moss (Stjernberg, 1974).

Egg laying

Females that arrive earlier in their breeding grounds have the possibility to wait before mating. This waiting might be the consequence of evaluating more males and territories before taking a mating decision or might be influenced by the weather (Siikamäki, 1996). The minimum necessary time to start laying eggs is five days, in which the oocytes grow (von Haartman, 1990). Late females often start laying eggs soon after this minimum time. Eggs size of the pied flycatcher rage between 10 and 20 mm, and they are blue (see Figure 5), whose brightness has been demonstrated, can display the quality of the female (Moreno et al., 2005), and induce the male to enhance his parental care effort (Moreno et al., 2006).

Figure 5: Complete clutch of six eggs, Valsaín (2022)

Egg laying occurs once per day, between 5.30 and 7.00 AM. After thirty minutes from the laying, the female leaves the nest and does not come back until the weather turns cold, to incubate the eggs for the night (Lundberg & Alatalo, 2010). The size of laid egg increases with laying sequence, but only in early and big clutches, and it's caused by a greater level of albumen, thus meaning that only the level of water increases during the sequence, while dry matter remains constant (Ojanen, 1983). Egg size can also be affected by the temperature about one week before laying, so that in warmer weather conditions egg volume increased. This effect probably occurs because higher temperatures positively affect insects' abundance (Noordwijk et al., 1995).

In many birds, including the pied flycatcher, hormonal control of the breeding cycle is geared to annual photoperiodicity, modified by weather conditions (Bissonnette, 1937).

As the temperature rises, the weather becomes more favorable for egg laying, and consequently, more females will start laying leading to a breeding synchrony (Siikamäki, 1996). As the egg laying is positively related to the temperature, it is critical to consider how a relatively warm and stable temperature is needful for a successful breeding season. Abrupt changes may cause many problems such as: egg cooling down faster and the possibility that the low temperature kills the embryo; lack of prey, which can influence the egg formation (resources shortage) and limits the possibility to feed all the chicks sufficiently; unsuitable temperatures for the newborns, that can bring them to death (George et al., 1992; Glądalski et al., 2020; Marques-Santos & Dingemanse, 2020; Musselman, 1939).

An indirect effect of early cold snaps is that they affect food availability. Caterpillars' (*Operophtera brumata*) growth and development takes place more than one month before flycatchers use them to feed their nestlings; the lack of young leaves in oaks due to cold snaps prevents the caterpillars to feed properly, causing a significant reduction in the population quantity, as they specifically reproduce and feed on this tree species (Moreno et al., 2015). The capability of *O. brumata* can also use non-oak host plants, as described recently (Vanbergen et al., 2003), but the lack of other tree species in the forest, does not allow the population to adapt on other hosts. With the impossibility to shift on other tree species, the population dynamics of the *O. brumata* depend on the quality of the oaks' leaves. Abrupt and extreme events like cold snaps appear to occur much more frequently in the future, thus endangering the whole chain (Moreno & Møller, 2011).

As incubating birds, flycatchers regulate their eggs' temperature by direct heating. Females can increase their body temperature to compensate for heat loss from the eggs to the nesting material at times of falling temperatures (Nord & Nilsson, 2012). Incubation starts when the female gradually increases the time spent in the nest covering the eggs. Full incubation of the females starts with the penultimate egg or earlier (Ruiz De Castañeda et al., 2012). Females start to incubate up to 3 days before completing their clutches, this being accompanied by hatching spread. Incubation temperature varies during the incubating period, the optimal temperature is around 37-38°C, and it shows an increase over time (35-35°C on days 3, 4; 35.5-36°C on days 6, 7) (Nord & Nilsson, 2012). Females who start incubation before completing the clutch tend to be in better condition and to lay larger clutches than those that postpone incubation until the clutch is complete (Potti, 1998).

Incubation can last between 13 and 16 days, depending on the clutch size, the weather conditions, and the time of the year. Females can spend up to 75% of the active part of the day incubating. The percentage of time spent incubating increases when the temperatures are lower.

The laying dates differ between areas and populations. The average first laying of the season of the Valsaín's population is the 8th of May, based on the 2011-2021 data, with the earliest being the 2nd of May in 2011 and the latest being the 15th of May in 2012. The 2021 first laying occurred the 7th of May (Alejandro Cantarero, unpublished data). As laying dates are related to preys' abundance, the laying period influences the breeding success. In most birds breeding in the temperate zones, the clutch size decreases with the progress of the breeding season (Klomp, 2002). The reasons might be that birds that breed later are of lower quality or the deteriorating conditions for breeding through the extremely short breeding season, with the reduction of caterpillars' availability. After the caterpillars' abundance peak is reached, the presence of this prey slowly decreases during the season.

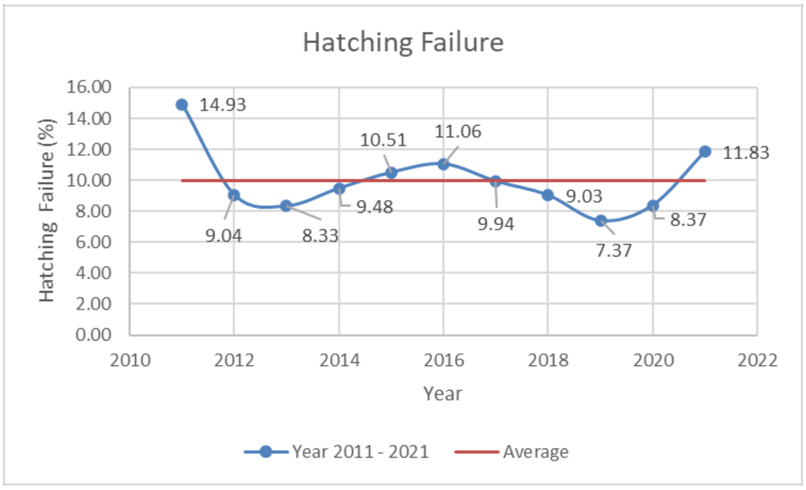
Less prey translates into a clutch size reduction and a decreased likelihood of an egg to produce a fledging and a fledging to be recruited into the population (Noordwijk et al., 1995).

Prey's abundance is not the only factor influencing the breeding success, the other factors to take into consideration are saturated population (intraspecific competition), day length (positive correlation), nest predation (negative correlation), costs of reproduction, and adult mortality (Bissonnette, 1937; Doligez & Clobert, 2003; Griggio et al., 2005; Slagsvold et al., 1988).

Clutch Size

The pied flycatcher was one of the first species chosen for research aiming to solve the problem of variation in clutch size (Lundberg & Alatalo, 2010). Clutch size of altricial birds can be limited by the amount of food that parents can bring to their nestlings, nest dimensions, egg-heating capacity, predation (Briskie & Sealy, 1989); overall every species lay the number of eggs that maximizes the number of surviving offspring (Lack et al., 1954). Usually, flycatchers with good breeding prospects will be the ones laying larger clutches, and the parental survival may be improved by a more favorable environment. Environmental factors are not only essential for the parental survival, but also for the breeding success (Sanz, 1995; Siikamäki, 1996). Flycatchers usually raise only one brood each season, and early nest losses might lead to renesting, but double brooding may occur under determined circumstances (Mazgajski & Dubiec, 2011).

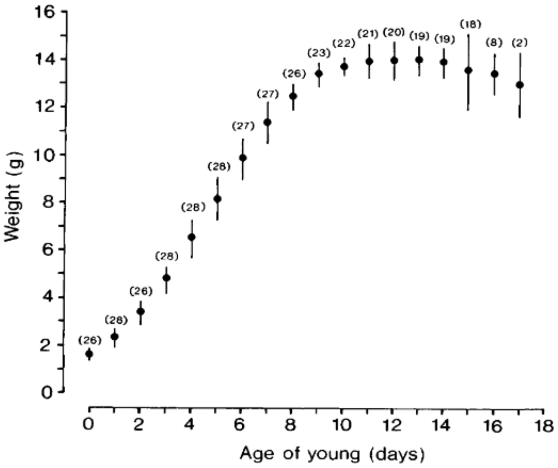
Hatching of the eggs occurs over a short period of time. The hatching order follows the laying sequence though there is much variation (Ylimaunu & Järvinen, 1987). Hatching failure can sometimes occur due to infertile eggs, dead embryos, or embryos unable to hatch. The percentage of hatching failure in the 2021 season in Valsaín (see Graph 1) was about the 11.83%, nearly 2 percentage points over the average of the 2011-2021 series of 9.99%. It is the year with most hatching failure since 2011.



Graph 1: Hatching failure based on the 2010 - 2021 data

Nestling growth

The young are naked and blind (Figures 6 and 7) and weigh about 1.5 g. The form of the growth curve is typical of each bird species (Ricklefs, 2008) and in this one, the growth rate is 1-1.5 g each day until they are 10 days old (see Graph 2), when the weight increase levels off (Jaervinen & Ylimaunu, 1986).



Graph 2: Pattern of weight increase in Pied flycatcher broods during the nestling stage. Data from L. Hillstrom. (Number figures given in parentheses show numbers of clutches weighed)

At about five days after hatching the first body feathers become visible on the back, and on the following day the eyes are opening.

The feeding starts early in the morning, between 6-7 AM and finishes between 9-10 PM, with an overall total estimated of 14-16 hours (Alejandro Cantarero, personal observation). The mean nestling period varies between 15 and 18 days, time when they abandon the nest, and they don't return. The nestlings are fed by the adults some days after the nest abandonment until they are able to obtain preys by themselves (Järvinen, 1990).

Figure 6: 1-day nestlings, still naked and blind and begging for food (Valsaín, 2022)
Figure 7: Nestling being weighted (Valsaín, 2021)

Philopatry

For young nestlings, it takes approximately one year to develop the sexual maturity (Nyholm, 1986), usually it coincides with the time in which most of the young return to their native area; this fidelity to the breeding or natal area in successive seasons, called philopatry (Sanz, 2001b). Not all the yearlings come back to that area, as they can settle many kilometers far away from. This is due to the familiarity with the area, along with the fact that the area was favorable for almost one full brood development. The nest is not necessarily in the same point as the year before, both because of external factors like occupied or destroyed nest, area changes, and population factors such as a too dense population which pushes the individuals in finding new spots and the presence of relatives in the area, which could cause inbreeding (Alejandro Cantarero, personal observations). There is also the possibility that the old area is skipped with the purpose to find a better spot to build a new nest.

The native area is learned in the first 60 days (Löhrl, 1959) and at least two weeks (2 weeks) of experience in an area are necessary to be able to return (Lundberg & Alatalo, 2010).

1.3 Parental care

The feeding rate is the parameter that better describes the parental care effort. The feeding rate is practically the action of actively bringing food to the nest, to feed the chicks.

Both males and females help to feed the nestlings, at a different ratio, in response to each other's behavior (Houston et al., 2005). The feeding rate depends on many factors such as brood size (Ylimaunu & Järvinen, 1987), temperature (Burger et al., 2012), age of the nestlings (Lundberg & Alatalo, 2010), partner's feeding effort (Houston et al., 2005), and availability of food. Quantity and quality of food depend among couples, but the overall dry weight is almost the same (Lundberg & Alatalo, 2010).

Not all broods are attended by two parents, and this is especially the case among late broods. Most single parents' nests are held by females, only 2-5% of single parent nests are cared by a male (von Haartman, 1969). Polygynous males give priority to their first female, thus causing the second female to care usually alone (Alatalo & Lundberg, 1990).

Several studies have shown that when a parent is experimentally removed, the other can entirely compensate for the rate of the feeding (Pilastro et al., 2001), almost doubling the effort in the early stages of the chicks (Lundberg & Alatalo, 2010). This was firstly demonstrated by R.V. Alatalo (1988) in an experiment of mate removal where at day 7-8 the female and male feeding of a monogamous couple were respectively 18.8 ± 4.69 and 16.5 ± 4.3 feeds per hour, becoming 31.6 ± 7.57 and 35.7 ± 12.91 feeds per hour after the removal as single parents (Alatalo et al., 1988). Close to fledging, the feeding rate of assisted and unassisted parents become more similar, though single parents feed more often than the single individual of a two-parents nest (Smiseth et al., 2005). Another factor influencing reproductive success is the weather during the breeding season, with a positive correlation between temperature and fledging success. All the stress factors negatively affect not only the fledging success but also the overall present and future parent health condition (Barta et al., 2002; Houston et al., 2005).

Breeding in natural cavities

This study species prefers natural cavities to nest boxes when both are available. Suitable nesting holes for flycatchers are scarcer today than they were in the primeval forests of the past. Natural holes are scarcer in coniferous than in deciduous habitats, and in young compared to old forests (Lundberg & Alatalo, 2010). Natural cavities' origins are mainly the result of falling branches or similar damage to the trunk, such that the trunk had become hollowed out either through decay or by excavation by tits. The second most common nest type, in relation to origin, was old woodpeckers' nests (Alatalo & Lundberg, 1990). The Pied flycatcher tend to use holes with rather narrow entrance holes (about 30mm) and situated high up in trees. Natural tree holes of good quality are probably quite scarce due to deforestation and the immaturity of the forests, also because they're sometimes occupied by tits, which breed earlier and can choose the nest location first (Slagsvold, 1975). The direct consequence is that if nest boxes are provided, they are often preferred to natural nest-sites. The choice of a narrow entrance and the metallic net all over the box are taken to avoid the predation by woodpeckers, while the height is necessary to avoid weasels and stoats, other important predators. With the always more cleaned forests, where usually old branches are removed, it is predictable that many species, as well as the Pied flycatcher, will gradually be less present. The deforestation problem is not the only one, changing the habitat of the endemic species will cause changes in the population dynamics (Saether et al., 2004). If it is not always possible to leave the forest immaculate, using nest boxes to attract these birds is an active action that can provide good results. Nest boxes can also be used to enlarge a population, attract individuals to new areas where the presence is now reduced or absent, and once the nest boxes are set, it is possible to contribute to this species populations management and conservation.

1.4 Environmental or anthropological threats to the reproductive success

Wild fauna is influenced by many factors. Some can affect the individual's behavior, influencing the population growth and stability.

Overall, each individual needs to grow, sustain itself and breed. Food and water availability are the basis of survival, and thus are of crucial importance. The availability of hiding places and the possibility to carry out the mating interactions are other important factors to consider.

The natural habitats are dynamic and complex, and there are many factors that can affect the survival success.

The study was conducted in a forested area, mainly composed by montane oaks (*Quercus pyrenaica*) of Valsaín, in the province of Segovia, a mountain village where human activities are secondary to the greatness of nature, but where the human presence is anyway undeniable. It is a small village, 176 people in 2016 ("Instituto Nacional de Estadística. Spanish Statistical Institute)," n.d.) located in central Spain (40°52′42″N 4°01′39″W), in the region of Castille and León, approximately 14 kilometers from Segovia and 75 kilometers from Madrid, at an altitude of 1200 m (*Valsaín - Wikipedia, La Enciclopedia Libre*, n.d.).

Biotic factors

There are many natural factors possibly affecting animal life, we have investigated both spatial and physical ones.

Birds can choose their territory, but there are factors that change over time, like temperature and precipitations. The variations within these two variables must be faced, as they cannot be avoided by simply moving away, at least during reproduction when young offspring have a limited or no dispersal capability, as in the case of altricial birds. Every species has an optimal temperature for its biological activity and can still be efficient in a range around it. There are extreme temperatures, both low and high, that can significantly affect the survival of the individuals. The temperature then, influence all the species in the ecosystem, thus not only affecting our study species but also the species with which it interacts, prey included.

As we are focusing on parental care and therefore, the animal behavior, we are looking for slight changes that can influence it.

The precipitations affect the water availability and the prey availability, other than possibly being disrupting in extreme conditions.

Other factors can differ based on the nest position, like the tree coverage, the distance from the nearest stream of water, or the distance from the edge of the forest.

The tree coverage can influence the hiding efficiency from predators and the presence of more prey.

The distance from the nearest stream of water directly influences the water availability and consequently the food availability; it can also stimulate temperature changes nearby, proportionally on its dimensions. The stream of water of the study area is subject to dry out during droughts and hot seasons, as it is not of large dimensions (in summer, average width ~1.5 meters, average depth ~5 centimeters).

The larger distance from the edge of the forest is related with a more resilient ecosystem (Aragón et al., 2015).

Another factor investigated is the hatching date. It depends on the date the female is fertilized and subsequently on the day she starts to incubate. The hatching date is then predictable, but the exact day can only be an esteem. The importance of having the hatching date in a specific period is a consequence of the variable prey availability during the season. Prey density peak occurs in the oak forest, as for the one considered, and it is overall ascertained that the prey availability decreases as the season progresses. It is expectable that a hatching date around the peak of abundance makes it easier for the parents to feed the newborns, thus making the process more efficient and enhancing the fitness of the parents. Ultimately, the hatching date represent an esteem for the quantity of prey available.

Abiotic factors

Artificial factors can be as dangerous as the natural ones, and possibly more. Usually, the presence of these factors is associated with a disturbance, which entity can dramatically change based on the activity itself. Here we considered the distance from the nests to the buildings and the streets. The buildings are a general display of many possible human activities, in this case, the buildings are represented by houses and stables. The streets can be source of disturbance because of the traffic related to these preferred paths; in the main street, all types of vehicles are allowed, and they create a huge noise disturbance, other than being involved in bird's fatalities, leaving an overall disturbed ecosystem. Birds are usually more influenced by the traffic disturbance (noise, lights, pollution, traffic motion) rather than the traffic mortality; noise, in particular, may interfere with the songbirds' activities (Osbrink et al., 2021). In addition to the direct effects, habitat loss and impact on the prey are factor to consider when discussing about how roads can influence the population dynamics. Nonetheless, road presence can sometimes be a positive factor; if the population density of the predators of the study species are negatively affected by the road presence, the predation can drastically be reduced (Fahrig & Rytwinski, 2009). Secondary roads are less impacting on the habitat, being only crossed by humans, bikes and horses, and not strongly modifying the habitat itself. Secondary roads are still taken in account as their presence is not natural and can possibly modify the ecosystem structure.

1.5 Aims, hypotheses and predictions

This study considers the possible relations between environmental factors and parental behavior. The goal of this research is to investigate various factors, biotic and abiotic, to check whether they can influence the parental care of the study species, the pied flycatcher. This study might then represent a specific example of the more general topic, as adverse environmental conditions are becoming more frequent as human activity increasingly deteriorates, directly or indirectly, the habitat quality. The results might then help explaining other populations dynamics.

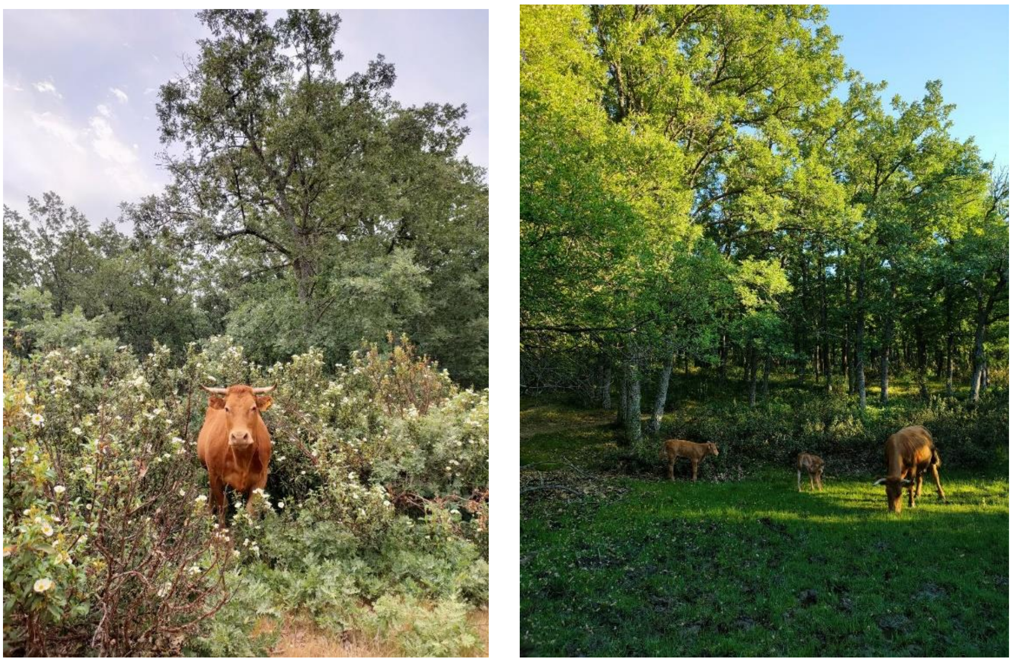
I therefore predict that 1) natural factors as the water presence, the integrity of the forest and a high-density leaves coverage are positively correlated with territory quality; 2) anthropic elements, like the buildings or the streets, are detrimental and are related to a scarce quality of the ecosystem around, making it more difficult for the species to forage and breed; 3) temperature and precipitation, which can have a more complex (i.e. non-linear) effect on environmental conditions experienced by birds, as extreme temperatures and rainfall values have negative effects.

Valsaín's forest is relatively undisturbed, with a scarce presence of people and human activities. The disturbance of the anthropic factors should not be as obvious to spot as possibly imagined, and it is complex to assess. As far as the ecosystem is well-preserved, possible results might even be more interesting to further develop.

2. Materials and Methods

2.1 Study area

The study area is situated in the forest of Valsaín, Segovia, Spain (*further information at page 35, 36*). The forest is characterized by the presence of different species of plants and animals (Figures 8 and 9). The vegetation is mainly composed by trees (*Q. pyrenaica* and *P. sylvestris*) and bushes (*C. laurifolius*).



Figures 8 and 9: Typical view on the field, with the first representing the bushes (C. laurifolius) area, and the second showing the oaks with a short-grass basement. The cattle are allowed to use both types of habitats.

While for the animal species, there are farm animals, like cows and horses, that are free ranging in the area, where there are also wild boars, foxes, wolves, roe deer, snakes and many insects and birds, from small passerines to mediumlarge raptors. Other birds' species that can be found in the nest boxes are great tits (*P. major*), blue tits (*Cyanistes caeruleus*), rock sparrows (*Petronia petronia*), eurasian wrens (*Troglodytes troglodytes*), and nuthatches (*Sitta europaea*); other animals that can occupy the boxes are bats (Figure 10) and hornets/wasps.

Figure 10: Bats' colony in a nest box (Rights reserved on Davide Longhin)

2.2 Nest

As the nest predation is common among birds, the choice of a safe nesting site is crucial. It is also important to find a strategic location for the nest, which is the fulcrum of the bird's life during this season. The location's choice takes in consideration not only the feeding possibilities for the adults, but also the feeding of the nestlings and the presence of competitors, both of the same species and of other species with similar ecological niches.

Nest-sites and Nest boxes

The pied flycatcher is a cavity-nesting bird. Predation is the most important factor reducing reproductive success, and so birds prefer nest-sites with low predation risks. The nest boxes used in the study area are built to give passerines a safe environment where they can breed. There is a total of 300 nest-boxes in the study site where passerines birds breeding in them have been studied since 1991. These nest boxes are placed on the oaks' branches thanks to a hooked wire, at about 3-5 meters of height above the ground (Figure 11). A good healthy branch is of critical importance, also to reduce the chances of the box falling. The orientation of the entrance is randomly chosen.

Figure 11: The nest is located on a relatively high branch and to control its content it is necessary to take it down with a stick (In this photo, Davide Longhin is taking down a nest box)

They are made of pine wood, with a wall thickness of 15 mm, a height of 17.5-19.5 cm, a width of 11.5 cm and a depth of 13 cm (Moreno et al., 2006). The nest box is composed by two parts: the 5-sides box and the "door". The door is crucial to open the box when needed, and it is sticked firmly on the box thanks to a metal wire. The door has one circular 35 mm diameter hole, to allow the adults entrance (Moreno et al., 2006). A 40 mm tube is placed on the hole to discourage predators from entering it. A metal net is placed all around the nest box, covering the wood area, to protect the nest from woodpeckers and to avoid dismantling caused by damages (Figure 12). On the roof, one hook is present to allow to hang it on tree branches.

Figure 12: Nest box structure from the front, the metal fence all around it gives more protection to the nest

The nest boxes are numbered and hanged in strategic positions. The geographic coordinates are marked and put on a nest map (Figure 13), used afterwards to orientate in the field.

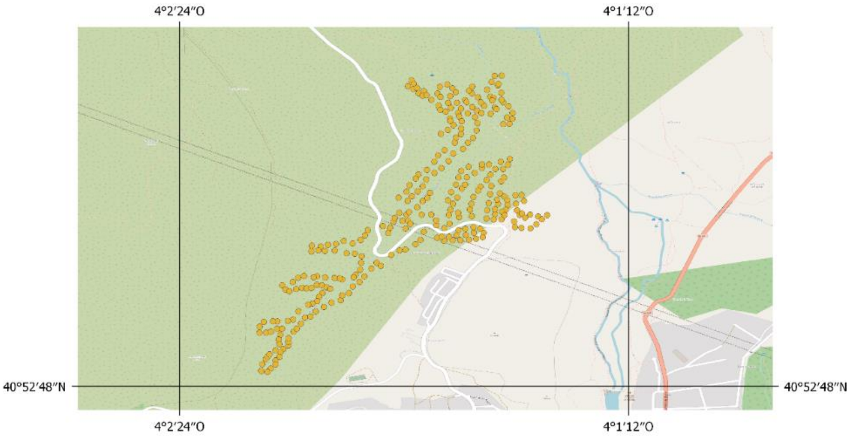


Figure 13: Nest-boxes map area, made with QGIS

2.3 Study species

The Pied flycatcher was firstly described by Linnaeus in 1746 in his book “Fauna Svecica”, and since then, has been intensively studied because of its abundance (population size in Europe estimated at around 5.250.000) (Backström et al., 2013) and its predisposition to breed in nest boxes (Stjernberg, 1974). Additional features making it suitable for research include their relative tameness, which makes them easy to catch, their reluctance to abandon a breeding attempt after having been caught and handled (Lundberg & Alatalo, 2010), and sexual dimorphism, which makes them individually recognizable in the field by plumage characters. On the other side, they are small (12-13g) and spend much of their time in the canopy, which makes them difficult to follow and identify when foraging or moving in the area.

All the flycatchers breeding in Europe spend the winter months in central-west Africa. The population studied breeds in central Spain where the first males usually start to arrive in the middle of April (Alejandro Cantarero, personal observation) and, as in most migratory passerines, males arrive ahead of females (López et al., 2013).

2.4 Routine at the field

The field season generally starts in late March, and it extends until late July, depending on the year. There are two areas in Valsaín where nest boxes are investigated: the low forest area (40°53'12.0"N 4°01'50.5"W) where 300 nests are set (Figure 14), and the mountain area of Valdeconejos (40°51'55.5"N 4°03'51.2"W) where another 150 nests are set (Figure 15). For this experiment, only the low forest area was taken in account.

Figures 14 and 15: On the left a scorch from Valsaín and on the left a view on the Valdeconejos slopes

To simplify, when referring to this area, only the name of the main town "Valsaín" will be used (Figure 16).

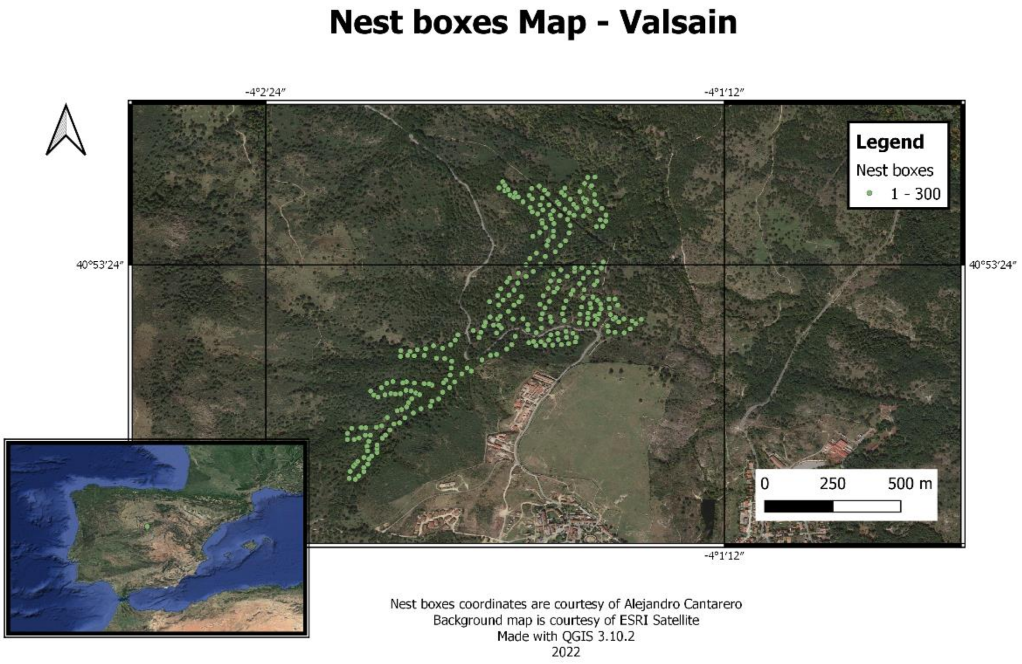


Figure 16: Nest-boxes map of Valsaín

The routine at the field varies per day, week, and month, and as every day new information is added to the breeding season development of bird nesting around, it is impossible to plan the work more than one day before. In the first period, all 300 boxes are checked every four or five days (Figure 17). At each visit, the information about the occupancy status is recorded for each box: empty, with a nest in construction (different stages are noted), with a complete nest, with a complete nest with eggs, with animals that are not birds (bats, hornets).

Figure 17: The revision being performed while substituting old or broken nest boxes. (In this photo, starting from the left: Samuele Tusini, Davide Longhin, Alejandro Cantarero)

As previously introduced (see *page 42*), the boxes also fit the needing of other birds' species, that can use them to build their nest. Based on the nest composition it is possible to distinguish between species, with the exception of blue tits and great tits that build very similar nests. It is important to record if the nest building stops, that can be an indication of nest abandoning. When a nest is complete, it is checked more frequently to get the exact laying date.

Following the protocols at the field, it is possible to correctly predict the laying date. For example, if a nest hasn't been checked in 4 days and 2 eggs are found, the laying date was the day before the last control. After 8 days from the laying date, the nest is again checked to count the final number of eggs; 7 days after clutch completion, the incubating female is captured by hand and the ID (wrote on a ring) is noted if the female is already ringed, or a ring is applied to the tarsus of the female; 11 days after clutch completion the nest is checked to see if the nestlings hatched. If on that day no egg hatched, the control of that specific box is made the day after, until at least one chick hatches. At the third day from hatching (hatching date = day 1), the brood size is checked, because it is possible that a clutch does not hatch simultaneously. After day 3 no further egg hatching is expected, and unhatched eggs are counted. 6 days after hatching (day 7), both the parents are captured when they visit the nest to feed the nestlings, measured and the male ringed, if necessary, as the female has been already controlled. The measurements comprehend the tarsus and the wing length (to the nearest 1 mm), and the weight (to the nearest 0.1 g).

To capture the adults, am automatic trap (see Figure 18) is set on the internal part of the entrance of the nest-box, and it is placed in a way that it should not be noticed from the outside. As the adult enters, the trap closes the entrance and the observer takes the nest down and, after placing a net around the box, opens the front and carefully grabs the bird with the hand.

Figure 18: On the left, the trap open and ready to be set. On the right, the trap closed after an adult join.

When the adult is removed from the net, the trap is eventually set up again to capture the other adult; if the other parent has already been captured, the trap is removed, and the nest-box is hanged on the original branch. The trap is placed for at most one hour, if the capture fails the trap is removed and the capture is postponed to the following day. Adults captured (Figure 19) usually take some minutes to rest after the release and then come back resuming the feeding. The chicks are ringed and measured at day 13 from hatching. Chicks are still not able to fly, so as the nest is brought down, the chicks are put in a cotton bag and then singularly ringed and measured and put back in the nest one by one.

Figure 19: Bird handling, measurement tools on the background.

Field methods of flycatcher monitoring, trapping, measurements of adults and chicks

Since this species spends much of its time in the canopy, it is difficult to spot it in the forest. When a flycatcher nest-box is spotted, anyway, it is possible to see the adults around, multiple times per hour, depending on the phase of reproduction. It is possible to do observations from a distant point, depending on the canopy shape, at about 15-20m if the area is covered, or more if there are no places to hide. To observe this bird, a basic binocular is enough. There are different instruments needed for trapping. A long stick is necessary to bring down the nest; in our case a hooked stick (max length 4 m) was used. To open the nest-box a screwdriver might be needed to force the wire. The trap (see Figure 18) is composed by two metal parts with the shape of a rectangular, placed one on another and taken together by a thin wire; the two metal parts have different dimensions, with the bigger one having a circular hole to allow the birds to enter. The holed part is hanged on the nest box door from the inside, thanks to two or more pins. Once the trap is set, the smaller metal part is supported by the wire, making it a movable part; once the bird enters, it operates the wire that allows the metal part to fall on the bigger one, thus closing the trap. When the bird is inside the nest box and has no exit ways, the nest is brought down with the stick and a holed net is placed all around it. The bird in the net is carefully taken, extracted, and brought to the measurement camp. The measurement camp, usually placed at least 50-100 m from the nest, is provided with a caliper, to measure the tarsus length, a ruler, to measure the wing length, a weight scale, and a tube, to take the body mass of the bird, and a plier with the rings, to eventually ring the individual. The bird is placed in the hand to be measured; its paws are steadily kept avoiding it from escaping. If the bird is unringed, one coded ring is placed in the right or left paw, indifferently, using the smaller hole of the plier. Tarsus is measured with the caliper; the average length is 17.52 ± 0.54 mm for females and 17.36 ± 0.55 mm for males (based on the 2011-2021 Valsaín's data). Wing is measured with the ruler; the average length usually measures 77.72 ± 2.02 mm for females and 79.51 ± 1.93 mm (based on the 2011-2021 Valsaín's data). Before releasing the bird, the weight scale is calibrated with the tube on it, and the individual is placed inside the tube and weighted; usually the weight averages around 12.31 ± 0.66 g (based on the 2011-2021 Valsaín's data). If a male is captured, the blackness is also estimated as the percentage of black feathers on the back of the male. To measure the nestlings, the trap is not needed; the chicks are placed in a cotton bag and measured one by one with the same instruments. The sex is undistinguishable on the chicks.

Mate removal experiment

To assess how such environmental parameters influence the behavior of the remaining adult when feeding alone we performed an experimental mate removal. Before the capture, one 1-hour video recording is made to record the feeding rate of the couple. To do that, digital video cameras (Sony Dcr-sr190) were placed on the ground underneath the nest-boxes at least 10 m from the nest and framing the front of the nest-box and its immediate surroundings. Cameras were set in the first hours of the morning (7:00-11:00 h), which is the daytime with the highest activity. After the video is taken, the capture starts. Once an adult is captured and placed in a cotton bag, after 1 hour interval that it is estimated to allow the remaining adult to notice the absence of the partner (usually many visits are performed per hour), a further 1-hour video is recorded to estimate its feeding rate after the partner removal. The second adult is then captured and measured by placing the nest trap after the second video recording. All the data were extracted manually from these videos. I have watched all the videos and scored down every visit, the time of the visit, the sex of the adult. For the current experiment, 2095 visits were counted on 51 nests.

2.5 Data

The variables describing the parental care focused on the parents' feeding rate, which are summarized on Table 1. A more detailed description of parent feeding behavior is given below.

Variable	**Description**
Male feeding rate	The times that the male visited the nest to feed the chicks, here expressed in times per hour
Female feeding rate	The times that the female visited the nest to feed the chicks, here expressed in times per hour
Total feeding rate	The sum of male feeding rate and female feeding rate
Compensation feeding rate	The feeding rate of the ”deserted” parent in the removal experiment, here expressed in feeds per hour
Alternation score	The pair coordination index, expresses the active alternation between male and female in the feedings (see page 54 for further information)

Table 1 Responsible variables used in the present dissertation

The environmental factors chosen are both natural and artificial, the expected effect on the bird’s behavior is is summarized on Table 2. A more detailed description of the variables is given below.

Factors	**Description**	**Purpose of investigation**
Temperature	Average daily values. These parameters vary within time but not within the study area. It influences life itself, but dynamics among species are complex.	Temperature trends will change drastically in the near and far future, affecting life in different ways.
Precipitation		The precipitation events are going to be less balanced, becoming very rare or much more frequent, being more frequently extreme. Reactions to the precipitation events trend might differ between species.
Tree coverage	It is the leaves coverage, expressed in percentage, and it represents the density of the forest.	The human decision on the woodlands and the green areas of the planet will inevitably change many ecosystems. Many species will suffer from this habitat damage or loss.
Edge distance	It is the minimum distance from the nest box to the edge (the end) of the forest. Bigger values mean a more pristine environment.	
River distance	It may represent a parameter useful to track the fertile area, as a source of water, useful if not necessary for direct supplying.	This specific river does not change the ecosystem itself, as it is more a stream (wide ~1m) than a proper river. The water availanility is anyway a crucial factor.
Main street distance	The distance from the nests to the main street, the secondary roads and the buildings represents the stress factors related to human activities; the main street is an asphalted street connecting Valsain to La Granja de San Ildefonso and then Segovia. The secondary roads are dirt roads within the study area. The buildings investigated are the nearest buildings (houses or stables).	In a future where human ownings and artifacts will surely increase, it is important to try to understand how it could affect animal's behavior; the purpose of these factors is to estimate how significantly they can affect and influence such critical behavioral patterns as the parental care.
Secondary roads distance		
Buildings distance		
Brood Size at Day 3	Dimension of the brood at the third day since hatching. It expresses how many chicks the parents have to feed.	This parameter takes in account the biological needs of the chicks, and whether or not the parents will be influenced by it.
Hatching Date	Date when the first egg hatched. It overall expresses the stage of the season in which the parents have to feed the chicks.	Depending on the season stage, different quality and quantity of prey are available. This can bring to different feeding strategies.

Table 2: Dependent variables used in the present dissertation

Video analysis

The videos have been analyzed manually using the VLC software. VLC (previously known as VideoLan Client) is a free, open-source multimedia player.

The feeding rate was extracted for every nest, counting every parent visit. Two videos per nest were checked, one with the couple (male + female) feeding rate and one with the mate removal (only male or only female).

Of the 300 nests in the study area, 51 of them hosted a flycatcher couple and then, were analyzed. Videos' duration ranged between 52 and 76 minutes but feeding rates have been normalized for the length of one hour.

The male and the female feeding rate were scored from the first video, where both parents were present. The total feeding rate equals the sum of these feeding rates. The compensation feeding rate was scored from the second video recording, where one parent was removed.

The last investigated parameter, the alternation score, was calculated based on these data (see below).

Alternation score

Johnstone et al. (2014) proposed that sexual conflict may promote a form of conditional cooperation between the parents when provisioning offspring. The evolutionarily stable strategy was a turn-taking rule (Johnstone et al.,

2014) where male (M) and female (F) parents actively alternate their feedings.

From the sequence of nest visits scored from the video recordings, I calculated parental turn-taking behavior. I defined alternated visits as visits of one individual that followed a visit of its mate. I expected different amounts of alternation to arise by chance in a sequence of visits depending on the proportion of visits by the two parents. If, for instance, one parent makes either all or none of the visits in a sequence, no alternated visits can occur. Conversely, when parents feed the offspring at similar rates, the proportion of alternated visits I expected by chance increases. To account for this effect, I used an alternation score (Baldan et al., 2019) to measure the deviation of the observed amount of alternation from that expected given the relative contributions (provisioning rates) of the two parents as follows:

$$\text{Alternation score} \quad = \log\left(\frac{\text{Observed no. alternated visits}}{\text{Observed no. nonalternated visits}}\right)$$

$$- \log\left(\frac{\text{Expected no. alternated visits}}{\text{Expected no. nonalternated visits}}\right) \; .$$

Negative and positive values of alternation score mean that, respectively, the observed alternation is lower or greater than expected by chance, while the “0” value stands for an alternation as expected by chance.

Temperature and precipitation source

Temperature and precipitation data were extracted from Meteosolana.net, a forecast web page providing information of the weather in many states of both North and South America and Spain, and earthquake information for the whole Europe. The reference station is the meteorological station of Segovia, provided by the *Agencia Estatal de Meteorología* (AEMET). The weather station (Segovia, station no. 2465, coordinates: 40°56′43″N, 4°7′35″W) is located 9 km from the study area and at the same altitude. Mean temperature and precipitation of the day were extracted; daily wind direction and intensity, relative humidity and maximum/minimum temperature were also available.

QGIS

QGIS (Quantum GIS) is a professional open-source Geographic Information System (GIS) application. It allows users to analyze, edit, extract, and manage spatial data and information. QGIS supports multiple formats, and it can display graphical maps, both based on real maps and images from satellite, and maps created specifically to display variables chosen by the user. QGIS integrates with other open-source GIS packages (*Discover QGIS*, n.d.).

The version of QGIS used for this project is QGIS v3.10 La Coruña. This software has been used to extract, manage, elaborate, and display data. More specifically, the tree coverage (%) was extracted by the "Tree Cover Density 2018 - Copernicus Land Monitoring Map" and associated with the nest locations; the distance from the main and the secondary street crossing the study area have been calculated based on the "Stamen satellite map"; the building distance and the edge distance have been calculated based on the "Google satellite map"; the river distance was calculated based on a field map developed by Alejandro Cantarero. Temperature, precipitation, and brood size were extracted and/or elaborated without QGIS.

Copernicus

Copernicus is the European Union's Earth observation program. It offers information services that draw from satellite Earth Observation and in-situ (non-space) data. Vast amounts of global data from satellites and ground-based, airborne, and seaborne measurement systems provide free and openly accessible information (*About Copernicus | Copernicus*, n.d.). The tree coverage information has been taken from this site, in the section "High resolution layers/ Forests/ Tree cover density". The High-Resolution land cover map for the 2018 reference year was used. The Tree Cover Density (TCD) raster product provided information on the proportional crown coverage per pixel at 10m spatial resolution and ranges from 0% (all non-tree covered areas) to 100%, whereby Tree Cover Density is defined as the “vertical projection of tree crowns to a horizontal earth’s surface”.

2.6 Data elaboration

Qgis

The environmental factors investigated in this project were mainly extracted, elaborated, and displayed on QGIS (see Figure 20). The tree coverage on the nest locations were extracted overlapping the “nest boxes map” to the “Tree Coverage map”. The street distance from main and secondary street was calculated through a more complicated action; the “Stamen map” (available in QGIS via the Stamen tool) displaying the streets was a dynamic image in which objects were not selectable, thus multiple lines were drawn on the Stamen map and used as the reference lines to calculate the distance from the nests. Two different multiline were created to be able to distinguish main and secondary streets.

A similar pattern was followed on the building distance and the edge distance; as the “Stamen map”, the “Google map” (available in QGIS via the Google tool) did not provide dynamic and selectable objects, forcing to create different polygons and then calculate the distance. The edge perimeter was extremely difficult to identify, so it was drawn by identifying the densest area observable on the map. The river distance was obtained overlapping the “river map” and the “nest boxes map”.

The tools used (except the one used to visually display the data) are here listed:

Zonal stats – As QGIS describes: This algorithm calculates statistics of a raster layer for each feature of an overlapping polygon vector layer.

Rasterize – allows you to rasterize a vector file. It is useful to work on vector files with tools that only recognize raster files.

Proximity – allows you to calculate the distance between elements of two separate maps. As QGIS describes: The proximity algorithm generates a raster proximity map indicating the distance from the center of each pixel to the center of the nearest pixel identified as a target pixel. Target pixels are those in the source raster for which the raster pixel value is in the set of target pixel values.

Raster to polygons – allows you to convert raster objects into vector polygons. It is useful since some tools only work with vector files.

Merge attribute by position - allows you to merge data from two different maps based on their spatial location. As QGIS describes: This algorithm takes an input vector layer and creates a new vector layer that is an extended version of the input one, with additional attributes in its attribute table. The additional attributes and their values are taken from a second vector layer. A spatial criterion is applied to select the values from the second layer that are added to each feature from the first layer in the resulting one.

New vector – allows to create new geometries (lines, polygons, multilines, multipolygons) from scratch. It has been used when dynamic objects needed to be created based on a visual map.

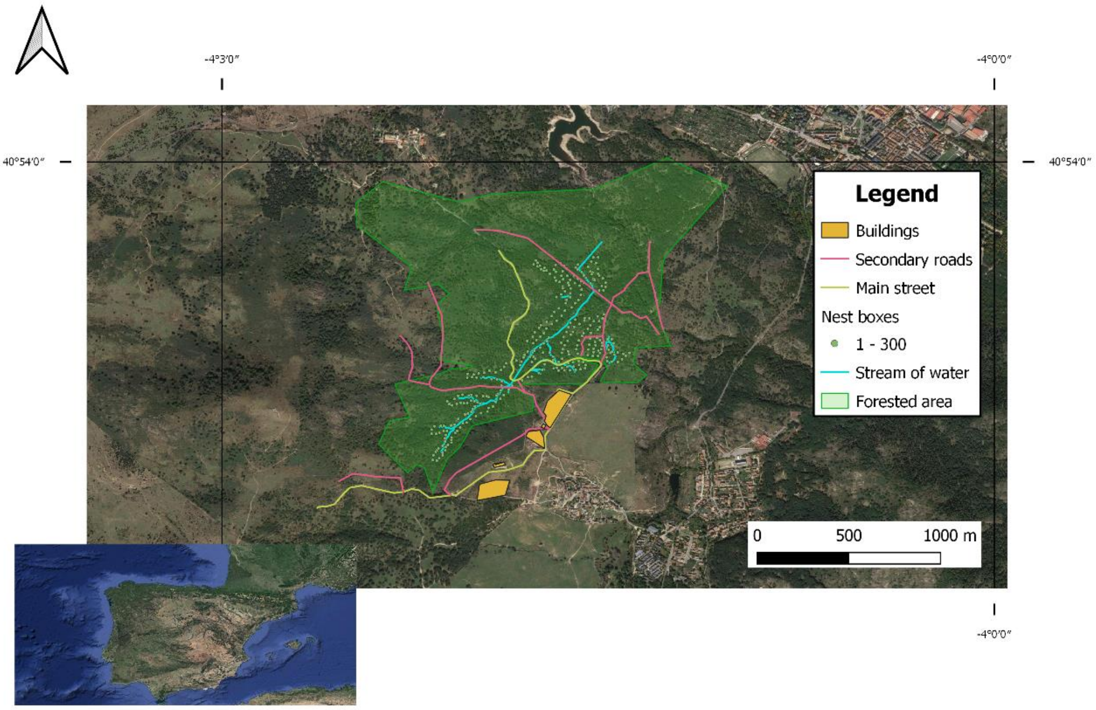


Figure 20: All the spatial environmental factors displayed in a single map, done with QGIS

Microsoft: Excel

Microsoft: Excel is a spreadsheet developed by Microsoft, released for the first time in 1987 and updated since then. It is used to organize numbers and data with formulas and functions.

It has been used to track all the data extracted from the videos and as a tool to elaborate data gathered from QGIS. Excel has been also used to create files used as the input-files for the statistical analysis in RStudio. It has been used not only for the data management and organization, but most importantly as a connection tool among the more technical software.

2.7 Statistical analysis

To evaluate the association between the environmental variables and the parental behavior, I used different sets of linear models. Using male and female feeding rate, total feeding rate, feeding rate during the compensation phase and alternation score as response variables (see Table 1). As explanatory variables, I used the environmental factors derived from the GPS mapping and weather data (see Table 2).

From these full models, I used a backward removal procedure, starting with the full models containing all the main effects and the interaction terms, then dropped the predictor (the interaction terms were tested first) with the highest P value in each step until only significant effects remained in the final models. All the variables investigated (see Table 1) except the alternation score, have been log transformed to improve normality of model residuals.

To test whether parental behavior could also be spatially distributed within our field site, I used a measure of spatial autocorrelation called Moran's I test (Cliff, 1973). This analysis uses the geographical information of the nests (latitude and longitude coordinates) and the behavioral data (male and female feeding rate, total feeding rate, feeding rate during the compensation phase and alternation score) of the parents. Moran's I-test then compares the behavioral data of each nest with adjacent nests within a specified distance. In this analysis, we interactively ran Moran's I tests by specifying different distances (from 200 m and 1000 m) to progressively include more neighboring nests in the comparison.

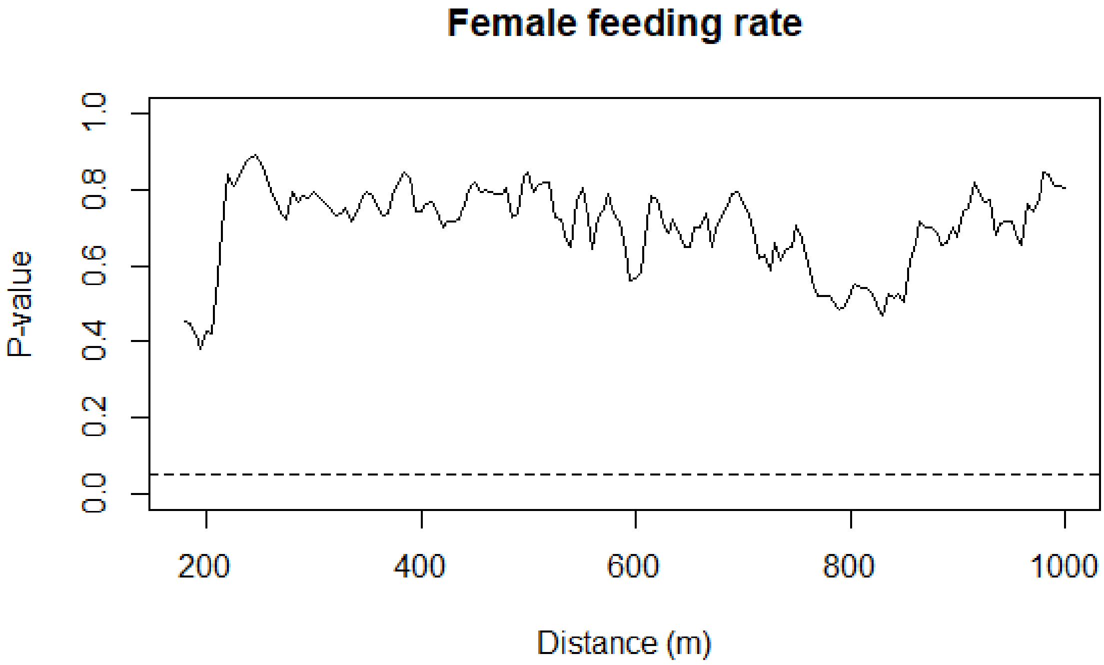
Statistical analyses and plotting were performed in R () using the open-source software RStudio. Linear models were carried out with the function *lm()*, whereas the Moran's I tests were performed within the R package "spdep" v1.0–2 (Bivand & Wong, 2018).

3. Results

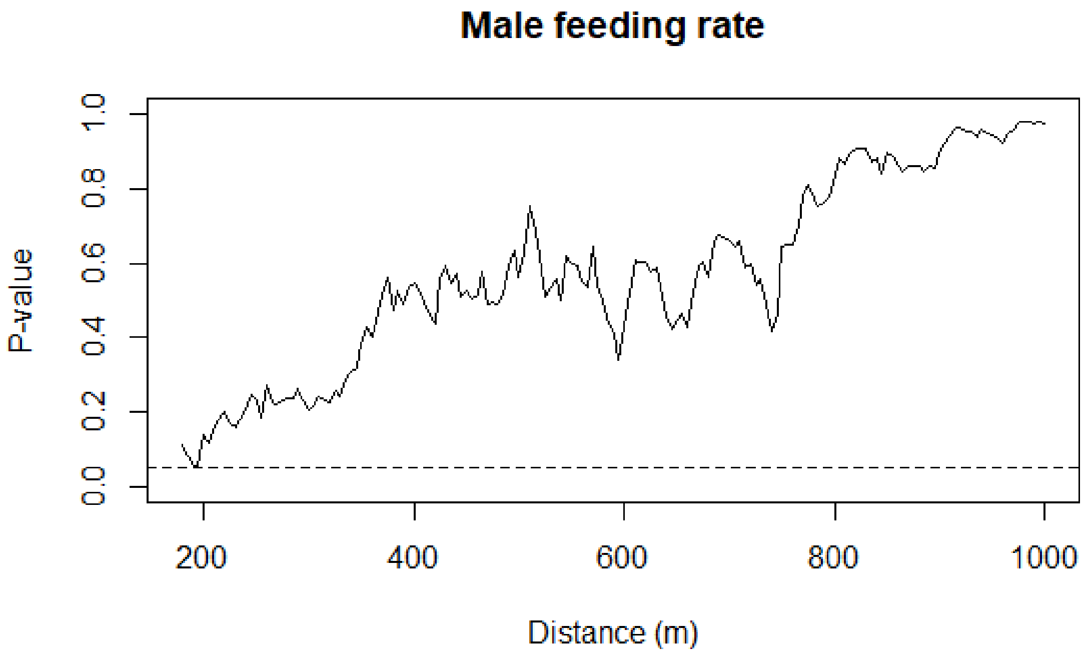
The variables extracted to be deeper investigated in this project include the **feeding rate of the male**, the **feeding rate of the female**, the **total feeding rate**, the **compensation feeding rate** and the pair coordination by two parents, called **alternation score**. The linear model used to analyze these variables has been supported by a spatial autocorrelation with the Moran's I test. For the linear model all the environmental data have been used except for the distance from the buildings, which was too statistically similar to the distance-from-the-edge-of-the-forest parameter. The investigated factors are: *distance from the main street, distance from the secondary streets, distance from the river, distance from the edge of the forest, temperature of the very day, precipitation of the very day, precipitation of the day before, tree coverage percentage*, *brood size at the day 3, hatching date*. For the compensation variable, the sex of the parent compensating was added to investigate any sex difference regarding it. On this model, the backward elimination has been used to progressively select the more significant parameters. To improve the results fidelity, the Akaike Information Criterion has been used.

The spatial autocorrelation

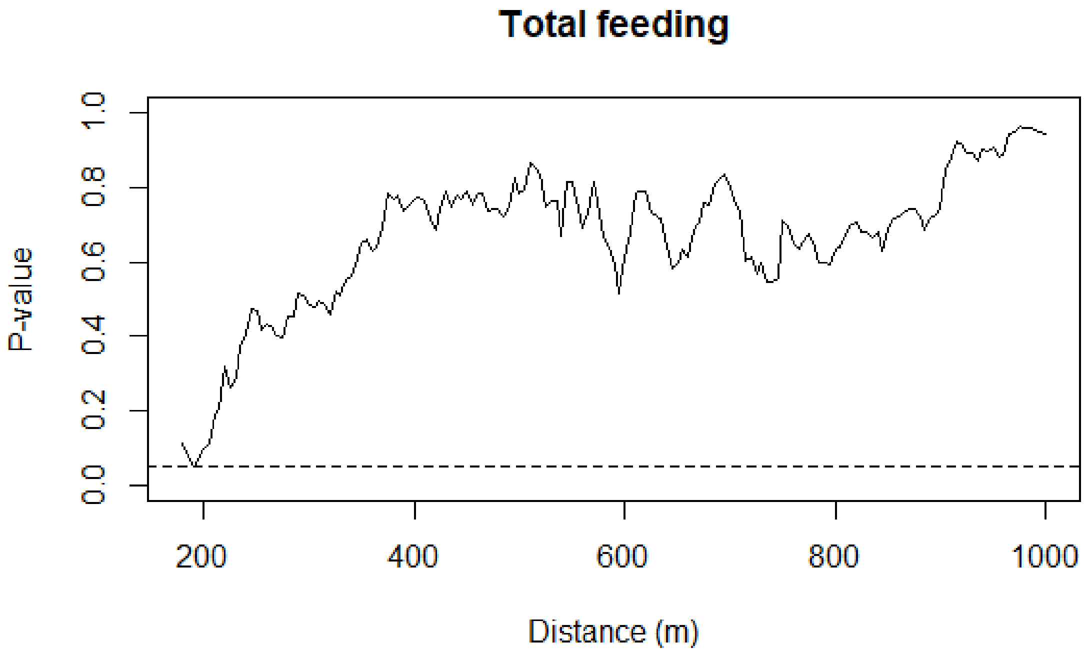
The Moran's I test shows a spatial autocorrelation in the male and total feeding rate (see Graphs 4 and 5). The significance is observable in the range of 200 m. There is therefore a similarity in the male and total feeding rate within the 200 meters range. For the other variables, no such correlation was found (see Graphs 3, 6 and 7), meaning that there are no significant similarities in any range from 200 to 1000 meters.



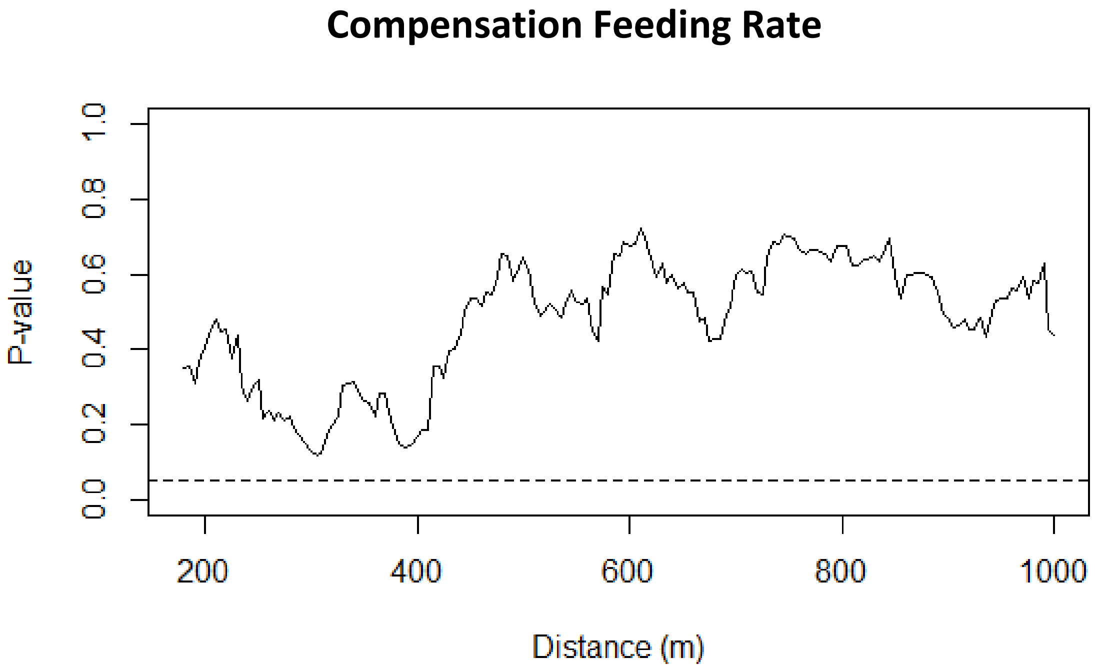
Graph 3: Spatial autocorrelation on the female feeding rate (distance from 200m to 1000m tested)



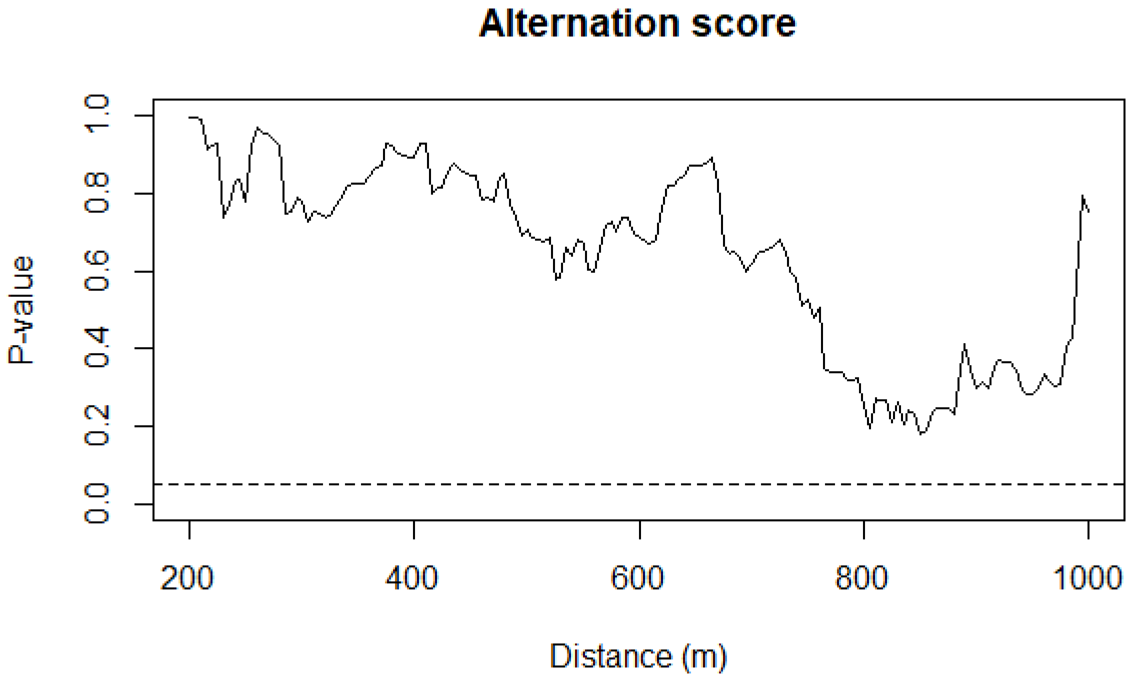
Graph 4: Spatial autocorrelation on the male feeding rate (distance from 200m to 1000m tested)



Graph 5: Spatial autocorrelation on the total feeding rate (distance from 200m to 1000m tested)



Graph 6: Spatial autocorrelation on the compensation feeding rate (distance from 200m to 1000m tested)



Graph 7: Spatial autocorrelation on the alternation score (distance from 200m to 1000m tested)

3.1 The relations between environmental factors and parental care

Brood Size at Day 3

The relationship between the brood size at day 3 (BS3) and the feeding rate is here observable. BS3 is positively correlated with both female and male feeding rate (see Tables 4 and 6), and consequently, the total feeding rate (see Table 3). A bigger brood results in a higher number of visits per nest from the parents, when both present. The brood size did not affect neither the pair coordination (see Table 5) nor the compensation feeding rate (see Table 7).

Hatching Date

It is possible to find a correlation between the hatching date (HD) and two investigated variables: the female feeding rate (see Table 4) and the total feeding rate (see Table 3). The two variables were in both cases positively related, thus meaning that later hatchings in the season involved a more frequent feeding for the female, and overall, in the total count of the parents' visits. Other variables were not related to this parameter ($p > 0.05$).

Total feeding rate (feeds/h)				
Explanatory variables	*Estimate*	*Std. Error*	*t-Value*	*p-Value*
Full model				
Brood Size Day 3	6.36E-02	1.65E-02	3.845	0.000423 ***
Tree Coverage (%)	8.46E-04	1.47E-03	0.577	0.566999
Hatching Date	6.46E-03	4.85E-03	1.332	0.190343
Distance from the edge (m)	1.01E-04	8.88E-05	1.137	0.262185
Distance from the river (m)	-7.98E-05	3.17E-04	-0.251	0.802762
Distance from the main street (m)	-1.74E-04	1.11E-04	-1.566	0.125245
Distance from the secondary roads (m)	1.13E-04	1.73E-04	0.652	0.51784
Temperature (°C)	8.05E-03	8.12E-03	9.91E-01	0.32787
Precipitation (mm)	8.02E-03	7.77E-03	1.032	0.308146
Precipitation of the day before (mm)	7.85E-03	6.35E-03	1.238	0.223107
Final model				
Brood Size Day 3	0.062966	0.014719	4.278	8.94E-05 ***
Hatching Date	0.010047	0.003476	2.89	0.00576 **

*Table 3: Full model with all the explanatory variables tested and the final model, with only the variables that show a significant relation with the total feeding rate. Asterisks indicate P values. *P < 0.05; **P < 0.01; ***P<0.001*

Female feeding rate (feeds/h)				
Explanatory variables	*Estimate*	*Std. Error*	*t-Value*	*p-Value*
Full model				
Brood Size Day 3	5.35E-02	2.09E-02	2.565	0.0142
Tree Coverage (%)	7.26E-04	1.85E-03	0.393	0.6963 *
Hatching Date	7.03E-03	6.11E-03	1.15	0.2571
Distance from the edge (m)	1.53E-04	1.12E-04	1.362	0.1809
Distance from the river (m)	-1.34E-04	4.00E-04	-0.334	0.7403
Distance from the main street (m)	-3.58E-05	1.40E-04	-0.255	0.7999
Distance from the secondary roads (m)	7.87E-05	2.18E-04	0.362	0.7194
Temperature (°C)	-3.06E-03	1.02E-02	-2.99E-01	0.7665
Precipitation (mm)	8.43E-03	9.79E-03	0.861	0.3946
Precipitation of the day before (mm)	4.84E-03	8.00E-03	0.604	0.5492
Final model				
Brood Size Day 3	0.051233	0.017991	2.848	0.00646 **
Hatching Date	0.010259	0.004249	2.415	0.01961 *

*Table 4: Full model with all the explanatory variables tested and the final model, with only the variables that show a significant relation with the female feeding rate. Asterisks indicate P values. *P < 0.05; **P < 0.01; ***P<0.001*

Temperature

The average temperature of the very day has a significant, positive relation, to the male feeding rate (see Table 6) and the alternation score (see Table 7); as the temperature increases so do the male feeding rate and the pair coordination. Other variables were not related to this parameter (p > 0.05).

Alternation Score					
Explanatory variables	*Estimate*	*Std. Error*	*t-Value*	*p-Value*	
Full model					
Brood Size Day 3	2.27E-03	7.35E-02	0.031	0.9755	
Hatching Date	-1.53E-02	2.15E-02	-0.713	0.4802	
Tree Coverage (%)	-3.05E-03	6.51E-03	-0.468	0.6421	
Distance from the edge (m)	-4.14E-04	3.95E-04	-1.05	0.3	
Distance from the river (m)	9.39E-04	1.41E-03	0.666	0.5093	
Distance from the main street (m)	2.81E-05	4.95E-04	0.057	0.955	
Distance from the secondary roads (m)	2.86E-04	7.67E-04	0.373	0.7114	
Temperature (°C)	8.67E-02	3.61E-02	2.40E+00	0.0211	*
Precipitation (mm)	-4.37E-03	3.45E-02	-0.127	0.8998	
Precipitation of the day before (mm)	4.01E-02	2.82E-02	1.422	0.1627	
Final model					
Temperature (°C)	0.06527	0.02987	2.185	0.0337	*

*Table 5: Full model with all the explanatory variables tested and the final model, with only the variables that show a significant relation with the alternation score. Asterisks indicate P values. *P < 0.05; **P < 0.01; ***P<0.001*

Distance from the main street

The only negative relation between a factor and a variable comes with the distance from the main street. It negatively impacts on the male feeding rate (see Table 6), thus meaning that the closer to the street the nest is situated, the higher the feeding rate of the male is. No other variables were affected by this factor (p > 0.05).

Precipitation of the previous day

There is a significant relationship between the average precipitation occurred the day before the video recording and the male feeding rate (see Table 6). There is a trend between this factor and the compensation feeding rate (p = 0.09). In both cases the relation is positive, thus meaning that the more rain dropped the day before the recording, the more times the male and the left alone adult fed. All the other variables were not related to this factor (p > 0.05).

Male feeding rate (feeds/h)				
Explanatory variables	*Estimate*	*Std. Error*	*t-Value*	*p-Value*
Full model				
Brood Size Day 3	7.39E-02	1.90E-02	3.894	0.000365 ***
Tree Coverage (%)	8.95E-04	1.68E-03	0.532	0.597328
Distance from the edge (m)	5.86E-05	1.02E-04	0.576	0.568059
Hatching Date	4.96E-03	5.56E-03	0.892	0.377589
Distance from the river (m)	-4.23E-05	3.64E-04	-0.116	0.908023
Distance from the main street (m)	-2.93E-04	1.28E-04	-2.292	0.02722 *
Distance from the secondary roads (m)	1.13E-04	1.98E-04	0.573	0.569841
Temperature (°C)	2.03E-02	9.32E-03	2.182	0.035007 *
Precipitation (mm)	8.39E-03	8.91E-03	0.942	0.351743
Precipitation of the day before (mm)	1.11E-02	7.28E-03	1.529	0.13409
Final model				
Brood Size Day 3	0.0765046	0.0164932	4.639	2.92E-05 ***
Distance from the main street (m)	-0.0002383	0.0001026	-2.323	0.02466 *
Temperature (°C)	0.0242645	0.0081356	2.983	0.00456 **
Precipitation of the day before (mm)	0.0157748	0.0052114	3.027	0.00404 **

*Table 6: Full model with all the explanatory variables tested and the final model, with only the variables that show a significant relation with the male feeding rate. Asterisks indicate P values. *P < 0.05; **P < 0.01; ***P<0.001*

Distance from the edge

The last relation found is slightly non-significant, between the distance from the edge of the forest and the compensation feeding rate (see Table 7). The trend is positive and stands for higher feeding rate when the nest is located further from the edge of the forest. No other relations were found with this factor (p > 0.05).

Compensation feeding rate (feeds/h)				
Explanatory variables	*Estimate*	*Std. Error*	*t-Value*	*p-Value*
Full model				
Brood Size Day 3	-5.87E-03	3.27E-02	-0.18	0.85846
Tree Coverage (%)	-1.95E-03	2.87E-03	-0.678	0.50164
Distance from the edge (m)	-4.37E-04	1.92E-04	-2.276	0.02839 *
Hatching Date	-1.30E-02	9.69E-03	-1.34	0.18792
Distance from the river (m)	7.42E-04	6.49E-04	1.143	0.26006
Distance from the main street (m)	3.43E-05	2.19E-04	0.157	0.87621
Distance from the secondary roads (m)	-4.73E-05	3.38E-04	-0.14	0.88939
Temperature (°C)	-1.06E-02	1.53E-02	-0.696	0.49047
Precipitation (mm)	2.90E-02	1.25E-02	2.314	0.02604 *
Precipitation of the day before (mm)	9.49E-03	1.63E-02	0.582	0.56398
Sex of the compensating parent	-1.01E-01	6.28E-02	-1.613	0.11485
Final model				
Precipitation of the day before (mm)	0.015336	0.0088762	1.728	0.0905 .
Distance from the edge (m)	-0.0002214	0.0001313	-1.687	0.0982 .

*Table 7: Full model with all the explanatory variables tested and the final model, with only the variables that show a significant relation with the compensation feeding rate. Asterisks indicate P values. *P < 0.05; **P < 0.01; ***P<0.001*

The other parameters investigated

All the other parameters studied did not show any significant relation to the investigated variables (p > 0.05). These parameters are: tree coverage, distance from the river, distance from the secondary roads, precipitation of the very day and sex of the compensating parent (only accounted in the compensation feeding rate).

4. Discussion

In this study I investigated the association between parental care and a set of environmental factors. The observed results did not always match the predicted ones, although the unexpected results might be explained by different assumptions.

The relationship found between the brood size (BS3) and the feeding rates (male, female, total) was not surprising. A higher number of nestlings, which actively require food, are expected to solicit more food from the parents and hence more frequent feeding trips. This result is aligned with the findings of Moreno et al. (1995), even though their study was based on experimentally manipulated brood sizes (4, 6 and 8 nestlings) and the contrasting results found in the larger broods (8 nestlings) may be explained by the unnaturally large brood size. In contrast, although a higher pair coordination is expected to be particularly beneficial in the case of large clutches, no significant correlations between these two variates were found.

The compensation feeding rate was not affected by the BS3, possibly because deserted parents maximize their effort also for a small brood. Because of the evolutionary adaptation of the brood size, the parental effort might not be raised over certain levels as it may badly affect adult survival and future reproduction. According to Ylimaunu and Järvinen (1987), in enlarged broods it is observed that rather the nestlings will suffer due to the lack of food than the parents subject themselves to a survival reduction.

The hatching date was positively related to the female and total feeding rate, indicating that, as the season progressed, the female fed more often the (males did not show this temporal trend). The seasonality of the area is important; as there is a peak of favorable preys, females try to adjust their breeding season to it (Nadolski et al., 2021; Noordwijk et al., 1995). After the peak, a slow decline of the prey quality is expected. To compensate for the reduced prey quality, a higher feeding rate might be required; alternatively, if lower quality territories are chosen by late reproducing females, the increased number of feeding trips may be associated with differences in territory quality, rather than by a seasonal decrease in prey quality. This would agree with the results of the autocorrelation analysis, that demonstrated that females in closer territories (that are likely more ecologically similar) tend to have more similar feeding rates.

The fact that only the female feeding rate is affected might be caused by the fact that females always feed at high rates, nearly at the maximum possible based on the prey quantity, while the male feeds at high rates only when needed, and consequently might not adjust their feeding rate according to environmental conditions. Of course, one potential explanation for the lack of relationship between male effort and hatching date is that our measure of visit rate (the most widely used metric of parental effort) does not accurately measure workload, as males make less feeding trips than females and one-hour sampling may have a higher statistical error for males than for females. Birds could vary workload through variation in meal size, foraging distance, or the size or quality of prey (Stodola et al., 2010; Wright et al., 1998). As for the brood size, the coordination and the compensation feeding rate were not affected by the time of the season.

I found a significant correlation between the temperature and male feeding rate and pair coordination. For the male feeding rate, one possibility is that with the higher, warm temperature, there is a more intense biological activity (O'Connor & Hicks, 1980), and consequently males feed more times, however, if this was related to the species, we should have also noticed it for the females. Nonetheless, there is also the possibility that the male is more susceptible to the warm temperatures. If the positive correlation between male feeding rate and the temperature was caused by the more pronounced activity of the prey, in the same way also the female feeding rate should have been affected by that, unless there is food-niche partitioning between the sexes, possibly to reduce intersexual food competition (Cauchard et al., 2021).

The most reasonable interpretation of this result, however, is that male feeding rate is lower in the cold days, when providing preys may be more costly, thus resulting in a positive correlation with the temperature.

The pair coordination was positively affected by the temperature. With higher temperature, and consequently an overall better situation, the parents may be less constrained in their foraging options and may have the opportunity to optimize their parental care by temporal coordination with the partner. With lower temperatures, parental foraging success may be less predictable, and temporal coordination with the partner may be constrained.
The other measures of parental effort were not associated with the temperature.

The distance from the main and secondary streets did not affect parents' provisioning effort, except for the male feeding rate. The original prediction was that the distance from the main street, as a disturbance factor, would have been positively related to the feedings. However, this was the only negative relation found in this study; in particular, the nearer to the main street the nest was, the higher the male feeding rate was. The fact that only the male is associated with this environmental variable may be sought in the difference in prey type between the parents. Usually male and female bring the same amount of dry food, but males use to feed less frequently than females with large preys (Moreno et al., 1995). It is possible the roads can attract large insects which are the male's preferred prey. This is just a speculation, and more observations would be necessary to confirm this hypothesis.

The male feeding rate was positively correlated with the rainfall in the day before the video were recorded. If, in the study area, swarms of insects are more frequent the day after raining, also the female feeding rate and consequently the total feeding rate should increase. As previously explained, however, females may tend to maximize their feeding effort and hence may be less sensitive to temporary fluctuations in prey availability.
The compensation feeding rate has no significant relation with the precipitation of the previous day but shows a slight trend ($p = 0.090$). This possibly means that in the days after the rain, the prey availability was somewhat greater, making both the parents' compensation easier to perform. The other parameters were not affected by the precipitation if the previous day.

A second trend was found between the distance from the edge and the compensation feeding rate. Compensation requires a high parental effort to be performed, and an undisturbed area might slightly favor the parents compensating. The prey availability and quality might be greater in the inside of the forest.

Regarding all the explanatory variables, the compensation feeding rate was the only one not significantly related to any of the environmental parameters considered. The reason might be that in tough times, when a parent deserted, died, or simply disappeared, the remaining individual maximized its efforts on feeding regardless of the environment conditions. Increasing the level of care in response to a reduction in a mate's effort may imply costs in reduced survival prospects (Jönsson et al., 1998; Santos & Nakagawa, 2012). In any case, no significant differences were evidenced between male and female compensation feeding rate.

From the other environmental parameters considered, there was no significant relation with the parental effort. These parameters were: tree coverage, distance from the river, distance from the secondary roads, rainfall in the same day and sex of the compensating parent (only accounted in the compensation feeding rate).

The tree coverage expressed in percentage-of-leaves cover has been extracted from a raster map. Raster maps base their structure on pixels, pixels have a specific area of influence. In this case, each pixel was equivalent to a square of about 10m x 10m. The tree coverage map was taken by satellite and owes its precision to an algorithm used to extract the values from the satellite's images themselves. Overlapping this map with a satellite's image (source: google satellite maps) may result in many critical issues, both on the position of the coverage and on the percentage given by the raster map. It is therefore possible that the data used were not precise enough to reveal its effect on parental behavior. Furthermore, for birds in general, and flycatcher in particular, the three dimensions structure of the vegetation is probably more important than the relative surface of the canopy (i.e., woods with equal canopy surface may have strongly different vegetation structure in term of tree height, density of shrubs, etc.).

The distance from the river is an interesting parameter, because birds are very attracted by water availability, in particular in Mediterranean habitats. Water bodies can be an ecological trap, hiding high level of parasitism behind a higher quantity of prey, reducing their fitness (Krams et al., 2022). The map itself is coherent, because it has been made by a person tracking the river shape and direction. However, the availability of water in these small rivers was not measured, and some of them may have suffer from drought resulting in a lack of water during the breeding season. It is therefore possible that in this study, the effect of rivers or stream of water on breeding populations is actually underestimated.

The distance from the secondary roads was used to investigate the reaction to the human presence (on foot, by bike, riding horses). This parameter was estimated from a satellite map and it surely would have been more precise if the map was made directly on the field by a person using a tracking GPS. There are different types of secondary roads, in a closed or open environment, of different width, and surely other differences can be spotted making the map directly. Making the map based on the satellite doesn't allow to recognize the entire path, and also, the roads under the canopy are not observable. Whether roads under the canopy affect habitat quality for flycatcher, however, is not known and may even be favorable for a predator that adopt a sit-and-wait strategy, like flycatchers often do.

The rainfall on the same day was not correlated with any of the investigated estimates of parental effort. The rainfall value used was the mean value of the day. Since recordings were done in the morning, it is likely that most rainfall actually occurred after recordings have been made and hance have limited effect on parenting behavior.

5. Conclusions

The aim of this study was to check whether the environmental factors affect the parental strategy in a bird population.

My results evidenced that several different environmental parameters were positively or negatively associated with the parental behavior of the study species. Differences between the sexes have been highlighted and confirmed results from previous studies. Most studies on parental strategies in birds tend to focus of “internal” parameters, such as bird age, sex and condition. My results demonstrate that differences in the environmental conditions experienced by the parents during the breeding season do play an important role in defining parents’ strategies and, most likely, their breeding success. It is therefore of critical importance to better understand how habitat characteristics influence the behavior of the natural populations, to better predict their response to the challenges of environmental changes.

6. References

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