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ORIGINAL PAPER

The role of pigeon consumption in the population dynamics and breeding performance of a peregrine falcon (*Falco peregrinus*) population: conservation implications

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Abstract In this paper, we describe and analyze the diet of peregrine falcons during a long-term period (1982–2002). A combination of direct observations of prey brought to nests, prey remains, and regurgitated pellets were used to calculate diet diversity and dietary overlap between peregrine pairs. We also examined diet diversity in relation to breeding performance. All peregrine pairs fed mainly on birds, with pigeons the most common prey. An increase in pigeon availability has been associated with both an increase in population size and an increase in breeding performance (measured as the average productivity of pairs per year) of a small peregrine falcon population in eastern Spain. Average productivity was lower when dietary breadth was higher. We speculate that our results were the synergistic effect of declining persecution and increased pigeon availability through increased popularity of keeping racing pigeons. There is a conflict of interests between pigeon fanciers and peregrine conservation. As a consequence, this could result to an increased risk of mortality by direct persecution. In accordance with this, conservation measures aimed at preventing direct persecution are encouraged.

Keywords Diet · Castellón · Homing · Pigeon fancying · Raptors · Spain

Introduction

The peregrine falcon *Falco peregrinus* is the most widely distributed raptor. In the Mediterranean region, the subspecies occurring is *F.p. brookei* (Cramp and Simmons 1980; Del Hoyo et al. 1994). With a preferentially avian-based diet (Ratcliffe 1993; Monneret 2000), there are several reported cases of hunting on mammals, insects, and even fishes (Zuberogoitia et al. 2002). Actually, its capacity to prey on species of human interest has caused a traditional rejection by some sectors of the society, especially those related with human economic interest. In the Spanish Mediterranean region, similar to other regions of Southern Europe, pigeon fancying has become a traditional activity which is very deep-routed, with its origins going back to the Muslim occupation of Spain in the eight century (Mínguez et al. 2005). As peregrines can prey on racing pigeons, it gives rise to a clear conflict of interest among pigeon fanciers and peregrine conservation, especially accentuated with those pairs located closer to human populated areas (Ratcliffe 1993; Dixon et al. 2003). Then, it is interesting to clearly describe and analyze the diet of peregrines in such areas and to implement reliable conservation measures aimed at preventing a potential conflict.

In this paper, we describe and analyze the diet of a small population of peregrine falcons located at the East of Spain combining the use of three methods: (1) direct observations of prey brought to nests, (2) collection of prey remains, and (3) collection of pellets during a long-term period. We examine the effect of changes in the diet in relation to the observed duplication of the population size. Furthermore,

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some descriptive parameters of dietary composition like prey diversity, dietary breadth, and dietary overlap among pairs are calculated. Additionally, we also examine diet diversity in relation to breeding performance.

Materials and methods

Study area

The study area was located in eastern Spain, in the southwest of Castellón province, including the Alto Palancia and half of the Alto Mijares districts (40°08′ N, 39°43′ S, 0°26′ E, 0°50′ W; Fig. 1). This area encompasses 1,500 km^2 and ranges from 300 to 1,400 m a.s.l. and is characterized as Mediterranean climate. For a complete description of the study area, see Verdejo (1991, 1994) and Verdejo and López-López (2008). The study was conducted between 1982 and 2002 during each breeding season (from early February to the end of July).

Numerous papers have tested different methods to assess the diet in raptors (Martí 1987; Simmons et al. 1991) and particularly in peregrine falcons (Oro and Tella 1995). These methods include (1) direct observation of prey hunting, (2) observation of prey contribution to the nest, (3) collection of prey remains, and (4) collection of pellets (the regurgitated, indigestible body parts of preys; Dekker 1980; Bird and Aubry 1982; Thiollay 1982). For this study, we have employed the last three methods, given that the combination of them has been suggested as a good estimate of peregrine's diet (Oro and Tella 1995).

For the detection of breeding pairs, direct searches for nesting places were conducted, and all known breeding places and potential ones were visited (Ratcliffe 1993). Observations were made ≈300 m from cliff nest sites with a 20–60× spotting scope during clear days to avoid disturbance to falcons. A territory was considered occupied if we observed nests with hollows, typical pair behavior, courtship, brood rearing activity, or young (Newton 1979; Steenhof and Kochert 1982). We considered as the same pair those that occupied the same breeding place during all years or at least one part of the study period, although presumably, some individuals conforming breeding pairs could have changed. Dietary data of at least 5 years for each pair was obtained, except for one new pair settled in 2002 which only data for this year were available, excluding them from the analysis. Data on number of prey items recorded per pair, monitored years, breeding performance (measured as average productivity per pair per year), distance to nearest neighbor, and distance to nearest village were recorded for all the pairs in the study area.

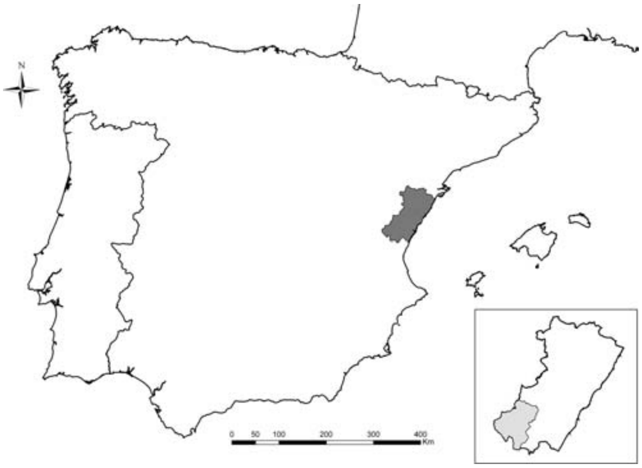

Fig. 1 Iberian Peninsula with the Castellón province *shaded*. *In box*: Castellón province. The study area is shaded in *gray*

All nest sites and frequently used roosting places were visited to collect pellets and abandoned prey remains during the breeding season. In addition, in order to minimize the bias of pellets and prey remains in the composition of the peregrine diet, we also conducted direct observations of prey contribution to the nests (Dekker 1980; Bird and Aubry 1982; Thiollay 1982; Oro and Tella 1995). Data from the three sources were pooled together for the analyses. It might be possible that some minor duplication could have occurred because the same prey item may have been recorded by each of the three methods. At least three visits were made to each pair during the breeding period, with an average duration of 240 min per visit. Prey items were identified to species level by comparison to field guides and a private collection of bones and feathers owned by the second author. In several cases, principally in pellet analysis, prey identification to species level was impossible, and data were grouped as a single category named "unidentified passerines". This group was deducted in the sum of species richness for each pair. Prey biomass was estimated according to Cramp et al. (1977–1985) and Jutglar and Masó (1999).

Prey diversity

We calculated the Gini index of diversity (Gotelli and Ellison 2004) instead of other commonly used indexes of diversity (e.g., the Shannon–Weiner index) because it does not confound species richness and evenness and especially because of its lack of dependence on sample size (Gotelli and Graves 1996; review in Magurran 2003). This index is used taxonomically at species level, and similarly to other indexes, the higher the index value, the higher the diversity measure (Gotelli and Graves 1996).

The index was calculated as:

$$G = 1 - \sum_{i=1}^{n} p_i^2$$

where p_i^2 is the square of the proportion of each prey item i in the sample.

Dietary breadth

Dietary breadth allows measuring how diverse the peregrines' diet is. This is similar to the Gini prey diversity index, but in this case, prey items are grouped by taxa higher than the species level (family, order, etc.). Dietary breadth was calculated following Steenhof and Kochert (1985) on the basis of the formula proposed by Levins (1968). According to them, dietary breadth was calculated as:

$$B = 1\Big/\sum p_i^2$$

where p_i^2 represents in this case the square of the proportion of the diet contributed by the ith taxon. Values for this index range from 1 to ∞. For consistency, prey taxa were grouped by family for birds and mammals and for order for reptiles, allowing comparisons among pairs (Watson 1997). In both prey diversity and dietary breadth indexes, unidentified passerines were treated as a single category.

Dietary overlap

The dietary overlap among breeding pairs was calculated by means of the Pianka's overlap index (Pianka 1973). A null model of dietary overlap was performed using the "niche overlap" module of the freely available EcoSim v7.0 software (Gotelli and Graves 1996; Gotelli and Entsminger 2001, www.garyentsminger.com). It allowed us to test if the observed dietary overlaps differ from that expected by chance (Sale 1974; Schoener 1974; Inger and Colwell 1977). A randomization algorithm was performed retaining the dietary breadth of each pair, but randomizing which particular resource states was utilized. Following Lawlor (1980), it would correspond to a randomization algorithm of type 3, and it is especially recommended to study dietary niche overlap when all resources are all potentially available (in our case, it means that there is no biological constraints preventing peregrines consumption from any class of prey; Gotelli and Graves 1996). This index was used taxonomically at species level. A complete review of the advantages and potential applications of this method are available in Haefner (1988) and Winemiller and Pianka (1990).

Pigeon availability

Pigeon availability was estimated by interviewing pigeon fanciers of the municipalities included in study area. We also obtained data from the Spanish National Institute of Statistics (www.ine.es). Pigeons were classified as wild birds (including *Columba livia*, *C. oenas*, *C. palumbus*, *Streptopelia decaocto*, *S. turtur*), racing birds, strays (birds that have been lost and not returned to lofts), and ferals (birds that have been incorporated into the wild population). We gathered information about number of pigeon fanciers' clubs, year of creation, initial and current number of pigeon fancying licenses, and presence of "pigeon barriers" (pigeon lofts built to prevent falcons and eagles from attacking racing pigeons) in the vicinity of the nesting areas. The number of flying days per week, number of flying pigeons per day, and number of racing pigeons per competition were also obtained.

Statistical analysis

Differences in diet composition among pairs were tested by means of chi-square tests on contingency tables. Non-parametric correlations were performed to examine the effect of changes in the proportion of pigeon consumption by year in relation to changes in the peregrine population size and between the average productivity (calculated as fledged chicks/ number of years of occupied territory) of peregrine's pairs and the percentage of pigeons in the diet. In addition, to test how the diversity of their diet affects peregrines' breeding performance, a non-parametric correlation was performed between the average productivity and the dietary breadth of each pair. All computations were performed using STATISTICA version 7.0 for Windows (StatSoft 2004). Statistical significance was set at $P<0.05$.

Results

Population size of peregrines almost doubled during the study period, starting with five pairs until a maximum of nine pairs in 2002. In relation to dietary analysis, 42% of data came from pellet collection, 22% from direct observations, and 36% from prey remains collected in nests and roosting places ($N=820$; Table 1). Overall the diet was

Table 1 Descriptive parameters recorded for the nine pairs of peregrine falcon in the study area

Pair no.	Prey items	Monitored years	Average productivity (chicks/year)	Distance to nearest neighbor (m)	Distance to village (m)
1	132	21	2.29	5,800	3,800
2	93	20	2.35	6,160	3,600
3	91	19	2.63	8,450	7,300
4	136	16	2.17	8,450	3,500
5	112	21	2.55	3,650	3,000
6	68	6	2.40	6,160	2,000
7	84	6	2.00	3,650	2,000
8	54	5	2.60	1,300	1,500
9	50	5	2.60	9,150	3,000

essentially composed by birds, accounting for 99.15% of the prey items from at least 35 different species (Table 2). Six mammals were detected as a prey, including four rabbits, *Oryctolagus cuniculus*, and two undetermined bats (probably *Myotis* or *Rinholophus* spp.). We also could observe the contribution to the nest of one ladder snake (*Rinechis scalaris*) 50 cm in length approximately. Average prey mass weighted according to its frequency in the diet was 204.79 g (range=9–1,200, $N=820$). The Gini index of diversity ranged from 0.73 to 0.88 (mean=0.83, SD=0.05). Niche breadth ranged from 2.32 to 5.00 (mean=3.81, SD=0.95). Average dietary overlap was 0.93 (range=0.84–0.97), higher than that expected by chance (expected dietary overlap=0.17, $P<0.0001$).

Among bird preys, the family Columbidae accounts for 43.78% of the diet by number of individuals and 68.69% by mass. Within Columbidae, 69.70% of the biomass corresponds to rock pigeon, *Columba livia* ($N=268$ items), with the rest corresponding to common wood pigeon, *Columba palumbus* (19.90%) and stock dove, *Columba oenas* (10.40%). There were no differences in the proportion of pigeon consumption among pairs ($\chi^2=0.089$, $df=8$, $P>0.05$), showing that all peregrine pairs prey mainly on this family. More interestingly, the proportion of pigeons in the diet was positively associated with peregrine numbers (Spearman $r=0.79$, $P<0.001$, $N=21$; Fig. 2) and average productivity (Spearman $r=0.66$, $P=0.052$, $N=9$), this in the threshold of significance. Conversely, average productivity

Table 2 Summary of the diet of peregrine falcons in eastern Spain (1982–2002), as estimated by direct observations, pellets, and prey remains

Prey type	Number of items	% number of preys	% prey mass
Rock pigeon, *Columba livia*	268	32.68	47.88
Common wood pigeon, *Columba palumbus*	51	6.22	13.67
Magpie, *Pica pica*	64	7.80	8.19
Stock dove, *Columba oenas*	40	4.88	7.15
Partridge, *Alectoris rufa*	19	2.32	5.43
Spotless starling, *Sturnus unicolor*	47	5.73	2.38
Unidentified passerines[a]	125	15.24	2.23
Rabbit, *Oryctolagus cuniculus*[b]	4	0.49	2.14
Eurasian turtle dove, *Streptopelia turtur*	24	2.93	2.00
Hoopoe, *Upupa epops*	44	5.37	1.76
Blackbird, *Turdus merula*	22	2.68	1.05
Eurasian jackdaw, *Corvus monedula*	7	0.85	1.00
Collared dove, *Streptopelia decaocto*	6	0.73	0.71
Common pheasant, *Phasianus colchicus*	1	0.12	0.71
Little owl, *Athene noctua*	6	0.73	0.63
Green woodpecker, *Picus viridis*	5	0.61	0.54
Common krestel, *Falco tinnunculus*	3	0.37	0.37
Sky lark, *Alauda arvensis*	12	1.46	0.29
Common swift, *Apus apus*	12	1.46	0.29
Rock sparrow, *Petronia petronia*	14	1.71	0.25
Song thrush, *Turdus philomelos*	5	0.61	0.21
Moorhen, *Gallinula chloropus*	1	0.12	0.19
Great spotted cuckoo, *Clamator glandarius*	2	0.24	0.18
Crested lark, *Galerida cristata*	6	0.73	0.16
Common quail, *Coturnix coturnix*	2	0.24	0.12
Greenfinch, *Carduelis chloris*	5	0.61	0.08
Blue rock thrush, *Monticola solitarius*	2	0.24	0.07
Mistle thrush, *Turdus viscivorus*	1	0.12	0.07
House sparrow, *Passer domesticus*	4	0.49	0.07
Goldfinch, *Carduelis carduelis*	6	0.73	0.05
Black redstart, *Phoenicurus ochruros*	5	0.61	0.05
Eurasian crag martin, *Ptyonoprogne rupestris*	3	0.37	0.04
Black wheatear, *Oenanthe leucura*	1	0.12	0.02
Ladder snake, *Rinechis scalaris*[c]	1	0.12	0.01
Bat spp.[b]	2	0.24	0.01
Total	820	100	100

Rows are organized in descending percentage of prey by mass

[a] An average of 30 g/item was used to obtain the % of prey mass (Cramp et al. 1977–1985)

[b] Mammals

[c] Reptile

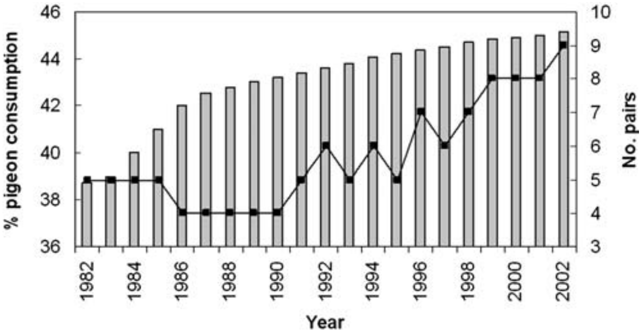

Fig. 2 Relationship between pigeon consumption and the observed duplication of population size between 1982 and 2002

was lower when dietary breadth was higher (Spearman $r=-0.90$, $P=0.002$, $N=9$).

Discussion

Direct observation of prey hunting and observation of prey contribution to the nest has been suggested as the best method to determine the diet of peregrine falcons (Dekker 1980; Bird and Aubry 1982; Thiollay 1982). However, these methods require a great deal of time, and studies based only on them are scarce (Marti 1987). Usually, diet studies on peregrine falcon have been based on the collection of prey remains and pellets, but they are blamed for bias in the analysis of diet (Mearns 1983). Whereas pellet analysis tend to overestimate consumption of small to medium-sized preys, studies based on prey remains tend to overestimate the consumption of large-size preys (Mearns 1983; Oro and Tella 1995; Zuberogoitia et al. 2002). In this study, we have combined the use of all methods aforementioned in order to minimize the possible bias, as demonstrated by several authors (Collopy 1983; Simmons et al. 1991; Mersmann et al. 1992; Mañosa 1994; Oro and Tella 1995; Zuberogoitia et al. 2002). However, other methods like video recording directly at nest sites could also be used (Margalida et al. 2006; review in Reif and Tornberg 2006; López-López and Urios, submitted).

Peregrines can prey on preys lower than 10 g up to preys larger than them and over 1,200–1,500 g (Ratcliffe 1993). This author estimated the optimal prey mass around 100–150 g depending on factors like sex, temperature, health status, experience, etc. (Ratcliffe 1993; Jenkins and Avery 1999). Other authors estimate 188 g of prey mass per day necessary for an adult and calculated a prey delivery rate of 222 g per nestling (and dependent fledgling) per day (Redpath and Thirgood 1997). In any case, pigeons with an average mass of 300–450 g are above the optimal prey mass. Our results show that peregrines prey mainly on pigeons without differences among pairs in the proportion of this type of prey in the diet. Similar results have been found in other studies of this species, showing the key role of pigeons in the peregrine's diet (review in Valkama et al. 2005). For example, pigeons represent nearly 50% in the diet by number in UK (Ratcliffe 1993) and Scotland (Mearns 1983; Redpath and Thirgood 1997) and even 57.8% in France (Bayle 1981). It has been suggested that peregrines would tend to a generalization in prey consumption as the climate becomes more extreme (e.g., tundra, deserts), whereas they would tend to specialization in regions with a temperate climate (Jenckins and Avery 1999). Our results might support this prediction, taking into account the high proportion of pigeon in the diet (in some cases representing more than 50% of prey items detected). However, another explanation is that peregrine falcons prey according to prey availability (Ratcliffe 1993; Zuberogoitia et al. 2002), or even that some pairs could have a preference for a certain class of prey (Thiollay 1988; Rosenfield et al. 1995).

In our study area, pigeon availability has notably increased from the eighties. This increase is related with the increase in pigeon fancying licenses and the creation of new pigeon fanciers' clubs (Mínguez et al. 2005). Unfortunately, even though we could not tag racing pigeons to conduct a specific study on the impact of peregrines on this type of prey, the general increase of the number of pigeon fancying licenses and pigeon fanciers' clubs can be taken as a

Table 3 Summary of the pigeon fancying activity in six municipalities of the study area

Municipality	Population [a]	Pigeon societies	Year of creation	Initial licenses	Licenses in 2005	Pigeon barriers	Flying days/ week	Pigeons/ day	Pigeons/ competition
Segorbe	8,023	1	1965	3	47	1	7	150	200
Jérica	1,561	1	1990	4	11	3	3	60/80	90
Altura	3,140	1	1975	5	40	2	4	100	100
Soneja	1,383	1	1980	1	5	2	4	60	90
Castellnovo	1,026	1	1980	2	23	2	4	90	90
Sot de Ferrer	407	1	1980	No data	No data	No data	3	70	90

Data were obtained by interviewing pigeon fanciers directly and kindly provided by Mínguez et al. (2005)

[a] Data taken from the Spanish National Institute of Statistics (www.ine.es)

proper surrogate on the increase of pigeon availability in our study area (Table 3). Currently, there are 953 pigeon fancying licenses and 40 clubs in the whole Castellón province. More specifically, for example, in the municipalities included in the study area, there are flying nearly 100–150 pigeons per training day, and nearly 2% of these pigeons are lost every day, becoming available for falcons (data provided directly by the pigeon fanciers; Table 3).

Our results suggest that an increase in pigeon availability has been associated with both an increase in population size and an increase in breeding performance of a peregrine falcon population in eastern Spain. From our point of view, this could be explained as the synergistic effect of a decline in direct persecution, consequence of the publication of the Spanish Law of protection of wild Flora and Fauna in 1989 (Law 4/89) and the Valencian Law of Protection of Natural Areas in 1994 (Law 11/94), and a slight but continuous increase of pigeon availability in the study area. As pigeon availability increased, its proportion in the diet also did the same, decreasing the dietary breadth. According to Watson (1997), analyzing golden eagle's (*Aquila chrysaetos*) diet, raptors should be more successful when they can concentrate on hunting few prey species which lie in the bird's optimal size range. This could also explain the higher breeding performance observed in the study area, in contrast to that reported in other parts of the world (J. Verdejo and P. López-López 2008).

Conservation implications

In some European regions, pigeon fanciers perceive raptors as the main cause of losses, demanding political measures to control peregrine numbers actively or even persecuting peregrines to a significant degree. In these areas, estimating the predation on racing pigeons (as opposed to birds which have strayed, birds which have gone feral, or wild pigeons) becomes an important issue. Racing birds, strays, and ferals are usually ringed. However, it is difficult to distinguish among these different types of pigeons in the diet without conducting a specific sampling design, as in our case. Thus, although we collected a high number of rings, we were unfortunately unable to calculate the proportion of the different pigeon types exactly (feral, racing, strays, or wild). Anyway, recent studies have demonstrated the strong limitations of using ring recoveries to evaluate the impact of peregrine kills on racing pigeons (Parrott et al. 2008).

The increase in pigeon fanciers has been focused in large villages within the study area. This phenomenon brings peregrine falcons closer to populated places in their hunting search. This situation becomes worse provided that the majority of competitions take place from December to May, overlapping with the period when peregrines start to breed in the region and have a corresponding higher need of prey intake. This result corresponds with that reported in UK where the increase and decrease in the pigeon component of the diet coincides with the start and end of the racing pigeon season respectively, indicating the importance of racing pigeons (or strays or ferals) as a food supply (Dixon et al. 2003). Taking into account the fact that racing pigeons could reach a value up to 10.000€ , this could cause a conflict of interests between peregrines and pigeon fanciers. As a consequence, this could result to an increased risk of mortality by direct persecution. Furthermore, another threat to falcons (and other raptors such as the endangered Bonelli's eagle *Aquila fasciata*) is the transmission of diseases from pigeons to raptors, such as trichominiasis, caused by the flagellated protozoon *Trichomonas gallinae* (Höfle et al. 2004; Villanúa et al. 2006; Hegemann et al. 2007). In accordance to these, conservation measures aimed at preventing direct persecution and disease transmission are encouraged.

Finally, there are few reported studies aimed at quantifying the effect of raptor predation in racing pigeons (but see Henderson et al. 2004 and Parrot et al. 2008). Although not conclusive, there is no evidence that birds of prey cause large-scale losses of racing pigeons (Henderson et al. 2004). For example, Parrot et al. (2008) estimated that peregrine kills based on "daily food intake" represented 13–40% of total losses of Scottish racing pigeons to all causes. On this subject, it would be interesting to perform a long-term study of the likely impact of peregrines and other raptors on racing pigeons in the Mediterranean region. Here, the unique study made shows that the perception of local pigeon fanciers of raptors as a risk for pigeon losses figures as the fourth of five causes of concern, after collisions with power lines and cables, losses caused by "wild" pigeons, terrestrial predators, and only before natural diseases (Mínguez et al. 2005). An additional study specifically aimed at determining the effectiveness of "pigeon barriers" would also be necessary. To date, this has been the only measure implemented by the local administration, even though the likely counterproductive effects like raptor habituation to have pigeons as an easy-to-capture prey have not been determined. Future research ought to include such long-term specific analysis.

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