

Breeding biology of the Lilford Woodpecker *Dendrocopos leucotos lilfordi* in the Western Pyrenees (SW France)

Jean-Louis GRANGÉ

Abstract: Studies of the reproductive biology of the Lilford Woodpecker *Dendrocopos leucotos lilfordi* were conducted, based on a total of 126 nest-trees and 50 breeding events, and led to the definition of reproductive parameters for the species. In 97% of cases the nest was situated in a beech *Fagus sylvatica* at an average height of 20 m and a BHD of 45.5 cm. The nest cavity was at 14.4 m from the ground, often at a point where a branch joins the trunk. Cavity and egg dimensions are provided for the first time for the Pyrenean population. Breeding is remarkably precocious with on average eggs being laid around the April 20, and the young leaving the nest May 28. These dates should be placed in the context of the food availability, principally wood-boring invertebrate larvae. The total reproductive cycle takes 38-40 days. The young are fed at a rate that varies according to their age, with an average of 4.5 times per hour over the entire cycle. Some interesting characteristics are mentioned: long absences of the parents during the feeding period, foraging near to the nest site, variation in the feeding rate with a reduction in mid-morning and increase in mid-afternoon. Breeding failure was 16%. Most losses occurred during incubation and in the first nestling stage. A comparison with information from populations outside the Pyrenees, in particular the Abruzzo, Balkans (*lilfordi*), Poland and Scandinavia (*leucotos*) and Japan (*subcirris*), provided the opportunity to underline the convergence of the parameters that were studied (deciduous trees predominant, early breeding linked with a specialised food source that necessitate a high percentage of dead or dying trees). Differences related to environmental constraints such as state of the forest, (height and the species of tree used for the nestcavity), available food sources, varying feeding rates and breeding failures. However, it appears that some differences were related to the habitat preferred. *Lilfordi* lives exclusively in mountain, predominantly beech, forests with extreme sedentariness that reduces the chances of expansion into new territories, low population dynamics and low productivity. Nominant *leucotos* shows greater ecological flexibility in its choice of habitat and expansion tendencies (especially north of the Alps), with erratic habits in some populations.

Key words: Lilford Woodpecker, western French Pyrenees, nest-trees, nest-cavities, breeding biology.

Introduction

The Western Pyrenees are home to an isolated population of Lilford Woodpecker *Dendrocopos leucotos lilfordi* currently included in the “*leucotos* complex” which comprises 9 to 12 different taxa depending on the authors (VAURIE 1959, SHORT 1982, WINKLER et al. 1995, WINKLER & CHRISTIE 2002, GORMAN 2014, DEL HOYO & COLLAR 2014). The Lilford Woodpecker inhabits the mountains of southern Europe (Pyrenees, Abruzzo, Balkan Peninsula) and the centre and west of the Caucasus with a total population estimated to range from 6500 to 9860 pairs and around 400-500 pairs for the French-Spanish Pyrenees (GRANGÉ 2001, 2013, FERNANDEZ & ESCOBAL 1997, CARCAMO et al. unpublished). In recent decades, several studies have clarified the habitat preferences (GRANGÉ 1991, FERNANDEZ et al. 1994, FERNANDEZ & AZKONA 1996, CARCAMO-BRAVO 2006) and the distribution of the species in its

stronghold in the Pyrenees between France and Spain (SENOSIAIN 1985, FERNANDEZ & ESCOBAL 1997, LORENTE et al. 2000, GRANGÉ 2001, GARMENDIA et al. 2006, SCHWENDTNER et al. unpublished) as well as in the Balkans (ČIKOVIĆ et al. 2008, DENAC et al. 2013, DENAC 2014). However, its reproductive biology in the Pyrenees has not been adequately studied. Only some anecdotal observations (BROSSE & JACQUEMARD-BROSSE 1964, PURROY 1972, SENOSIAIN 1977) and a preliminary study which monitored five breeding attempts (GRANGÉ 1993) have been published.

Elsewhere, regarding the *D. lilfordi* taxon, only BERNONI (1994b) and MELLETTI & PENTERIANI (2003) provide significant results on reproduction in Abruzzo (Italy).

The other stronghold of *Dendrocopos leucotos lilfordi*, the Balkan Peninsula, has been the subject of only a few publication papers on reproductive biology

Table 1: summarizes the meteorological characteristics of the study area: the two selected stations are located at its core with an average altitude corresponding to that harbouring the pairs monitored. The climate is oceanic (1630-1723 mm annual rainfall during the period 1961-1990), mountainous (average minimum 3.6 to 4.9 °C temperatures during the period 1980-1990 with a presence of snow 20-45 days per year).

Lescun	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
T° Min. (°C)	-0.5	0	1.8	3.2	5.7	8.7	10.7	11.3	9.4	5.9	2.8	0.3	4.9
T° Max. (°C)	7.9	9.6	11	11.8	14.7	18.9	22	21.9	20.8	16.5	11.8	8.3	14.6
P (mm.)	178.9	155.9	152.5	162.2	157.1	96.8	83.4	95.9	103.1	156.4	175	206	1723.2
Freezing (days)	16.9	14.4	11.7	5.1	0.9	0	0	0	0	0.5	7	16.8	73.3
Snow (days)	4.2	4.2	3.6	1.9	0.6	0	0	0	0	0.5	2.6	3.3	20.9
Laruns/Artouste													
T° Min. (°C)	-2	-2	-0.9	1.3	4.5	7.5	10	10	8.5	5.3	1.3	-1.1	3.6
T° Max. (°C)	3.6	4.3	7	9.6	13.7	17.4	20.8	20.2	18.1	12.5	6.8	4.3	11.6
P (mm.)	163.6	139.7	138.7	147.1	155.9	94.3	75.8	91.9	106.1	154.5	184.4	180.6	1632.6
Freezing (days)	23.1	20.6	19.8	12.5	3.3	0.2	0	0	0	2.4	11.5	20.9	113.8
Snow (days)	7.5	8.6	8.7	5.9	1.5	0	0	0	0.1	1.5	5	7.1	45.9

(PERUSEK 1991, GAŠIĆ 2007, DOMOKOS & CRISTEA 2014), based on a very small number of monitored pairs. This is in contrast to Scandinavia and Central Europe, inhabited by nominate *leucotos*, where several extensive studies have been carried out (e. g. RUGE & WEBER 1974, AULÉN 1988, STENBERG 1990, WESOŁOWSKI 1995, BÜHLER 2008).

This lack of information on an important aspect of the ecology of the species, motivated the development of a monitoring program of breeding pairs in, mainly, Béarn (département of Pyrenees-Atlantiques), to obtain meaningful data on some aspects of the reproductive biology of the species (site characterization, nest tree, phenology, feeding rate, reproductive success). The results of this work are based on 126 nests of which 50 were monitored extensively until fledging (or premature failure) in a population of fifteen different pairs, subsequent to a first publication in 2002 (GRANGÉ et al. 2002).

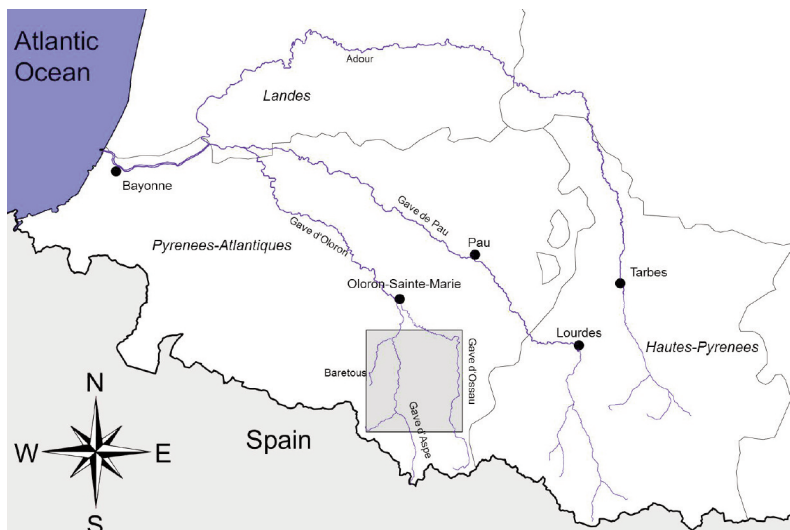


Fig. 1: Location of the study area (grey rectangle) in the western French Pyrenees.

Study Area

The study was conducted in the western part of the French Pyrenees (Pyrenees-Atlantiques) in montane forests between 700 m and 1700 m (Fig. 1). The main valleys here are oriented in a north-south direction. Three Béarn valleys were monitored:

Barétous Valley: Valley with mountainous character which includes nearly 7,000 ha of managed forest: pure beech stands are the most common (43%) but mature mixed forest of beech *Fagus sylvatica* and fir *Abies alba* is almost as extensive (41%). There are few pure fir stands, and this is the only valley where *Pinus uncinata* is well represented.

Aspe Valley: includes more than 14,000 ha of managed forests: pure beech forest also predominates here (42%). Mixed beech and fir forest accounts only for 31%, and pure fir forest covers nearly one tenth of the wooded area; a few small pinewoods are found here as well.

Ossau Valley: this area comprises 13,000 ha of managed forest, 41% beech and fir, 18% pure fir and only 20% pure beech forests.

Method

The monitoring of the reproduction of a species requires the discovery of occupied nests: For this purpose the areas selected were surveyed regularly from early March on to establish where the territories of the pairs were (based on calls and drumming) and using our previous knowledge of sites. After the discovery of a cavity, regular visits allowed us to study the characteristics of the different stages of reproduction: egg laying, incubation, nestling feeding, fledging. A minimum presence of 150 minutes was devoted to each visit to ensure that breeding was actually in progress. Potential neigh-

Table 2: Characteristics of the nest-trees of the Lilford Woodpecker in the Western French Pyrénées.

Height nest-tree (m)	Diameter nest-tree (cm)	Height of cavity (m)	Diameter at cavity (cm)	H. cavity/ Nest-tree	Location of cavity	Tree condition
20 ± 5.21	45.5 ± 11,86	14.46 ± 4.25	27.52 ± 6.83	0.73	71 % trunk	67.5 % alive
N= 112	N= 113	N= 123	N= 92	N= 115	N= 91	N= 120
8-33	25-85	5-27	18-55			

bouring pairs were sought in order to measure inter-pair distances. The beginning of incubation was determined by visits close to the supposed time of laying, when the birds exhibit typical behaviour such as extended stays inside the cavity, deposition of the first egg and defence of the cavity by the male. The end was determined by the observation of the first feeding of the young. We increased observations during the nestling period to identify and characterize the various stages (I to III, see "Results"). We also carried out detailed observations during the first part of the fledging stage.

We repeatedly measured nest tree height, diameter and health status, and cavity variables such as location, height, diameter to the cavity and orientation, to account for measurement errors. At no time was there any intervention at the nest or capturing of birds for ringing purposes. The observations were carried out at a discreet distance and with the observer partly concealed. In addition, knowledge of flight routes used by the pairs monitored allowed us to position ourselves out of sight.

Results

Characteristics of the nest site (Table 2)

We present here, although in a less detailed manner, the results of a recent publication (GRANGÉ 2009), with the addition of the results of the last five years.

Altitude and site exposure

The average elevation of breeding sites for the pairs monitored was 1077 m (range 700 m to 1750 m). Most of the sites (92.8%) faced north. South facing slopes had no significant wooded areas and thus they and those with a westerly exposure were seldom used.

Nest tree

Beech *Fagus sylvatica* was the main tree used for nesting sites 97.4% (N= 121). There were only three exceptions (one fir *Abies alba*, one oak *Quercus sp.* and one mountain Elm *Ulmus montana*), despite the habitats having a predominance of conifers. The average height of trees used was 20 m ± 5.21 (minimum = 8 m; maximum = 33 m, N = 112) with an average diameter (at breast height) of 45.5 ± 11.86 cm (min = 25 cm; max = 85 cm, N = 113). In 67% of cases, the overall health of the trees housing a cavity was good, although the cavity

itself was often excavated in a decaying part of the tree. Some cavities used by the woodpeckers were used for 12-15 years ~~before being used~~ by secondary cavity nesters (European Nuthatch, Tits sp.) One beech tree had been used as a nest site for a record 26 years, since 1989.



Cavity

The average height of the 126 nests cavities recorded was 14.4 m ± 4.25 (min = 5 m, max = 27 m), with a trunk diameter (at the height of the cavity) of 27.5 cm ± 6.83 (min = 18 cm, max = 55 cm, N = 92). Orientation was predominantly to the north (34%) and to the south (22%). In a few cases (10 to 15%), several nest cavities were excavated on the same tree in successive years. Fig. 2 shows the dimensions of a nest-cavity recovered during the logging of a parcel occupied by the species.

In the Pyrenees, the Lilford Woodpecker on average excavates its nest-hole at a significantly higher position on trees than other species: mean of 14.4 m versus 11.6 m for the Lesser Spotted Woodpecker *Dryobates minor* (N = 101), 10.5 m for the Black Woodpecker *Dryocopus martius* (N = 416) and Iberian/Green Woodpecker *Picus viridis sharpie/ P. v. viridis* (N = 190), 9 m for the Middle-spotted Woodpecker *Leiopicus medius* (N = 74) and 8.8 m for the Great spotted Woodpecker *Dendrocopos major* (N = 376) (GRANGÉ in prep.). The mean nest height difference between the two sympatric *Dendrocopos* species amounted to 5.6 m.

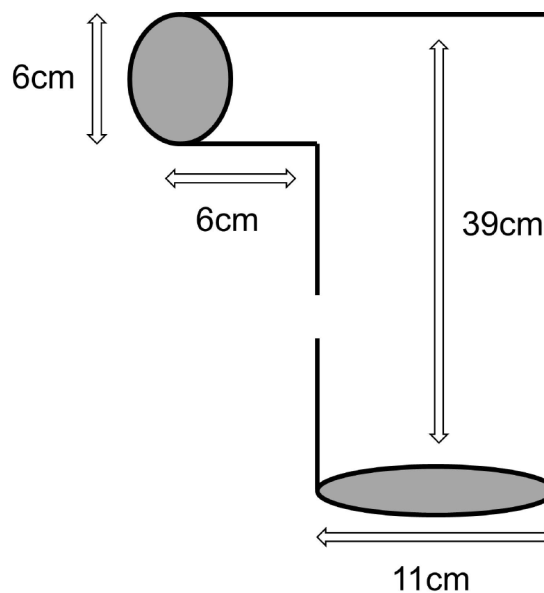


Fig. 2: Dimensions of a nest cavity of the Lilford Woodpecker in the western French Pyrenees.

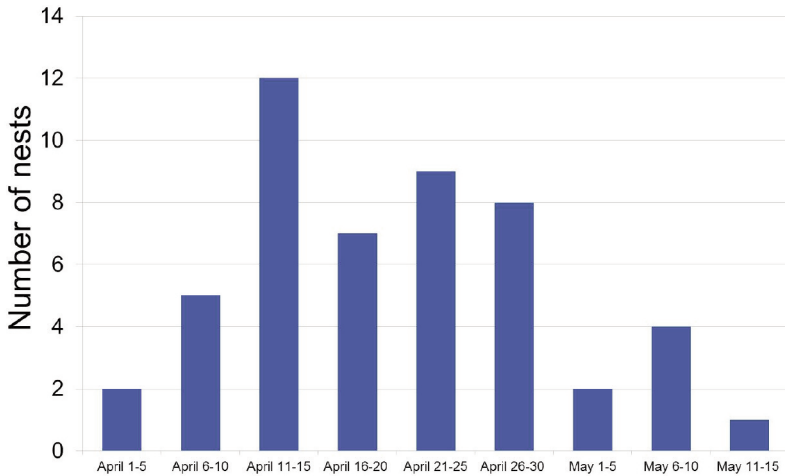


Fig. 3: Laying dates of the Lilford Woodpecker in the western French Pyrenees (N=48 nests).

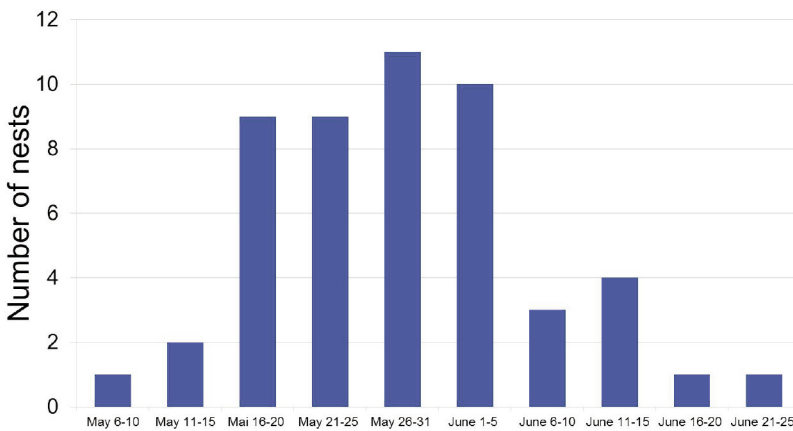
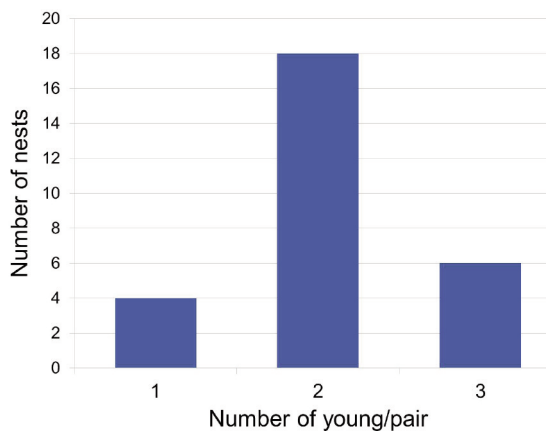


Fig. 4: Fledging dates of the Lilford Woodpecker in the western French Pyrenees (N=50 nests).

Fig. 5: Fledgling numbers per pair of the Lilford Woodpecker in the western French Pyrenees (N=28 broods).



Nest location on the tree

The ratio “height of the cavity / tree height“, was 0.73 (n = 118), showing that the cavity was placed in the upper part of the tree, usually on the trunk (71%) or at the joint with a branch (25%). The tree crown was home to 42.8% of cavities against 32% below (n = 91), indicating, too, the remarkable height of the nesting cavity.

Distance of nesting cavities from each other

A new cavity was excavated each year by all the pairs monitored. The distance between two cavities occupied in successive years by the same pair, varied from 0 (same tree used) to 350 m maximum for an average of 50.4 ± 19.35 m (50 nests of 8 different pairs). To date, the same area of the home range was used by the various pairs monitored, although it extended over 100 hectares (excluding two cases where changes occurred due to logging).

Breeding phenology

Mating

Few observations have been made to date. Typically, mating takes place from early March to early May, but may occur later when replacement clutches are needed. The duration of three copulations observed was five seconds each. The male joins the female resting on a branch, mates and then leaves; the female, lying down along the branch, takes off a few seconds later, after ruffling her feathers. Pairings can be preceded by flight pursuits, with characteristic calls, that can only be heard in this context.

Excavation of the cavity

Both sexes are involved in nest construction, although the majority of work is done by the male. The excavation duration varied from 10 to 13 days, with an average completion date of April 13 (n = 22). The first pairs commenced work around March 10. Some pairs often excavate two adjacent cavities, the reason for which is unclear. However, the cavity excavated last was always used for breeding.

Laying and incubation

The mean laying date was $April\ 20 \pm 9.76$ (n = 50), with a range of 41 days (April 1-May 11). This long period includes replacement clutches: in fact, 52% of clutches are deposited before April 21 and 86% before May 1 (Fig. 3). The dimensions of the elliptical and white egg obtained, were 29×21 mm (D. VINCENT, in litt.).

The incubation period spans 11 to 12 days (n = 15). Both sexes share incubation equally. The change-overs mostly took place without calls and single incubation turns lasted 2-3 hours. The late laying dates of three nesting pairs (6, 7 May and 13 May) suggested that these were replacement clutches. However, in 2001, one of the pairs monitored allowed us to confirm the existence of such clutches for this species: after an early clutch was laid in April, the nest was abandoned in early May after the death of the young (at the latest on

May 4). On May 9, the pair excavated a new cavity about 100m away from the previous one, but subsequently did not occupy it. On May 16, D. VINCENT found the remains of two eggs and a third perforated one below the first cavity, evidence that the birds had laid again but lost the clutch. Predation by a conspecific male was strongly suspected, as disputes were repeatedly observed at this site.

Fledging

The average fledging date was 28 ± 9.89 May ($n = 51$) within the period May 6 to June 21. However, 20% of the fledging occurred before May 20 and only 11.7% after June 10 (Fig. 4). The average number of young fledged was 2.07 (Figure 5; min = 1. max = 3; $N = 28$), minimum value without intervention at the nest (unlike Scandinavian studies): hence, we may have overlooked some additional juveniles. The accurate calculation of the number of young using only feeding observations is almost impossible: usually only one young at a time appears at the entrance. However, the sexual dimorphism of the juveniles facilitates the task. The male has a red cap, the female a completely black cap. Failures caused by the weather in April-May (snow, cold), were common in the study area and affected 16% of the broods. In 50 monitored broods, 8 failures occurred, including six before stage I ended (young aged less than 6-7 days, see below). The young fledge according to the order of hatching, usually over a period of two days. Fledging occurred mainly in the morning.

The young spend the first two days near the nest tree, being fed by adults. They are usually noisy, but well concealed in foliage. Over the following days they gradually move away from the fledging site. The age at which young in the Pyrenees become totally independent of their parents is not known.

Feeding rate

The nestling period (26 to 29 days) was divided into three stages, corresponding to the development of distinct characteristics:

Stage I: an adult remains permanently in the nest to brood the young (for the first six to eight days).

Stage II: both adults are engaged in feeding, and enter the cavity at each food delivery (days 8 to 12).

Stage III: adults remain at the nest entrance, first entering it halfway (phase 1: 4 to 5 days) and, later, nestlings come for the food at the cavity entrance (phase 2: 3 to 5 days).

Consequently, it follows that during stage I feeding rates are low (average 3.01 /h; min = 1.2; max. = 8.2) due to the fact that only one adult a time can deliver

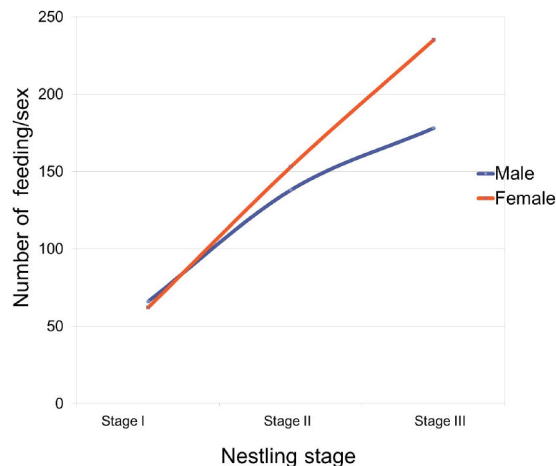


Fig. 6: Feeding rates of the Lilford Woodpecker in the western French Pyrenees.

food, but the rhythm increases in stage II (mean: 5.9 / h; min = 2.5; max. = 10.1) to an average of 6.04 feedings/h (min. = 2.9, max. = 12.8) in stage III ($n = 1155$ food deliveries, all stages, in 80 observation sessions). The respective contributions of the sexes was roughly equal in the population studied, although some pairs showed a preponderance of one or the other member of the pair: 53% for the female and 47% for the male ($N = 1155$). On average, in the nestling period, the contribution of the male tended to decrease, being greater than that of the female in stage I, and then was reduced further to 43% of the total contributions in stage III ($N = 832$; Fig 6). However, these findings are preliminary and need confirmation with a larger sample size.

Feeding rates were highest early in the day (as the young were not fed overnight), decreased in the late morning and recovered in the afternoon. Weather conditions also affected feeding rates. For example, only one food delivery every 46 min in cold weather and rain in stage II, while the average rate at this time was one intake /11 min. The absence of one member of the pair between two feedings could mean as much as a 134 minute pause, with an average of 55 min ($n = 35$), but this did not seem to effect reproductive success and was not related to weather conditions. Conversely, several successive contributions over a short time period were sometimes made by one of the adults, which was probably due to a food source having been found nearby and which thus was fully exploited. At the very end of stage III, phase 2, feeding did not significantly decrease. This is at variance with what has been suggested in the literature. We observed an average of five feedings/h in seven pairs monitored one to two days before fledgling (average feeding rate was 6.04/h over the full length of stage III).

When possible, the nature of the prey species brought to the young was noted. Two categories were distinguished: 1) wood-boring insect larvae and 2) fly-

Table 3: Characteristics of nest-trees in the White-backed Woodpecker *Dendrocopos leucotos* sensu lato.

Country	Tree species	Tree Height (m)	DBH at 1.3 M (cm)	Tree condition	Cavity Height (m)
Japan Hokkaido	broad leaved trees only	16.3	56.5	75 to 100% healthy	13.3
Scandinavia, Latvia	57 % <i>Populus tremula</i> 22 % <i>Betula</i> , 19 % <i>Alnus</i>	12.05	33.7	63,2 % dead (N= 262)	7.44
Centr. Europe Switzerland, Germany, Poland, Slovakia	Beech 100 % <i>Alnus-Carpinus</i> 64 %	15.7	47.9	100 % dead 48 % dead	12.2
Balkans Bosnia, Slovenia, Romania	Beech	24.5	51.2	Romania: 100 % healthy	13.75
Italy (Abruzzo)	Beech (97 to 100%)	20.4	49.8	68 % healthy (N= 40)	10.1
Spain (Pyrenees)	Beech 100%	22 24.4	41 52.2	50 % healthy Mostly healthy	11 11.3
France (Pyrenees)	Beech 97.4 % (N= 126)	20	45.5	67.5 % healthy (N= 120)	14.4

ing insect larvae and other items. 35% of prey items (390 in total) comprised wood-boring insect larvae. The transport modalities (longitudinally or transversely in the beak) have not been subject to a rigorous study, but it appeared that the mode of transport used is related to the size of the prey, longitudinal being preferred for larger prey.

For some pairs, we were able to record the preferential use of specific areas in the surroundings of the nests. This data confirmed our previous observations (GRANGÉ 1993). Birds evidently departed to individually preferred sectors. It remains open to what extent the particular location of the nest site forced the birds to take a specific path.

Discussion

The two taxa of White-backed Woodpeckers inhabiting Western Europe almost certainly have a different history (VOOUS 1947, GRANGÉ & VUILLEUMIER 2009):

- *lilfordi*, of more ancient origin (plumage pattern similarity to certain isolated forms in southern China, in the extreme east of the distribution area of the species and presence of Pleistocene fossils only in the south of Europe) and confined from the beginning to forested mountainous ranges of southern Europe (Pyrenees, Corsica, Abruzzo, Balkans, Caucasus).
- *leucotos*, a more recent arrival (settlement dating from the post-glacial) and populating Central and Northern Europe (Northern Alps, Scandinavia, Poland and part of Western Russia) and exhibiting an absence of genetic differentiation (ELLEGREN et al. 1999).

This pattern of settlement allows us to suppose that there has been no contact other than very marginal (north of the Balkan Peninsula) between these taxa, hence the need to compare their respective reproduc-

tive biology to identify any differences resulting from different evolutionary histories. To this end, a literature review of studies devoted to the description of nesting sites and breeding phenology was conducted and summarized in Tables 3 and 4.

Nest tree (Table 3)

The tree chosen to host the nest was a broadleaved species in the vast majority of cases, for both taxa, regardless of the region. However, in Scandinavia, it was often birch *Betula sp.* and Aspen *Populus tremula*. (SARKANEN 1974, AULÉN 1988, STENBERG 1990, HÅGVAR et al. 1990). In Poland, several tree species were used in equal frequencies: birch, alder *Alnus sp.*, *Quercus sp.* oak, hornbeam *Carpinus betulus* (WESOŁOWSKI & TOMIAŁOJ 1986, WESOŁOWSKI 1995) reflecting the high tree species richness of the forest studied (Białowieża National Park).

Further south, beech is used exclusively (BÜHLER 2008, PAVLÍK 1999, SCHERZINGER 1990). The taxon *lilfordi* is very closely linked to beech (97% of nest trees in Abruzzo; BERNONI 1994b; MELETTI & PENTERANI 2003) and the Pyrenees (118 of 121 nests in beech trees in the French Pyrenees and 100 % of nest-trees in Spanish Pyrenees- CAMPRODON 2007, CARCAMO & SENOSIAIN unpublished). The predilection for broadleaved trees of the taxon *D. l. subcirris* in Hokkaido (MATSUOKA 1979) shows that the "leucotos complex" is very dependent on deciduous forests.

Height of the trees and cavities

The mean nest tree heights used by the White-backed Woodpecker sensu lato range from 12 m in Scandinavia to 24 m in the Balkans, the average values for *D. leucotos lilfordi* being very similar in the various populations: 20 to 24 m.

Regarding the mean diameter at breast height of the nest trees, a large difference exists between Scandinavia with 33.7 cm (AULÉN 1988, HOGSTAD & STENBERG

D. at cavity (cm)	Nest orientation	Taxon	Author
23.3		<i>subcirris</i>	Matsuoka (1979)
24.62	no pref.	<i>leucotos</i>	Aulén (1988), Stenberg (1996), Hogstad & Stenberg (1994), Hågvar et al. (1990), Sarkanen (1974), Krams (1998)
24.2	N : 36.2%, S : 36.2 % E : 27.5%, W : 25.8% (Poland only)	<i>leucotos</i> <i>lilfordi</i>	Wesołowski (1995), Wesołowski & Tomiałojc (1986), Pavlík (1999), Scherzinger (1990), Ruge & Weber (1974), Bühler (2008) Perusek (1991), Gaši (2007), Domokos & Cristea (2014) Bernoni (1994), Melletti & Penteriani (2003)
27.6	NW: 37.5%, SW : 25 % W : 25 %, SE : 21.8 % S :40 %; E : 26.6 %	<i>lilfordi</i> <i>lilfordi</i>	Camprodon (2007), Senosiain (1977), Carcamo & Senosiain (unpubl.)
27.5	N : 33.9 %, S : 22 % W : 11 %, E : 11 %	<i>lilfordi</i>	Grangé (2002, 2013, present study)

1994, STENBERG 1996, KRAMS 1998) and Japan (56.5 cm; MATSUOKA 1979). The Balkans-51.2 cm (GAŠIĆ, 2007, DOMOKOS & CRISTEA 2014), Central Europe-47.9 cm. (WESOŁOWSKI 1996, PAVLÍK, 1999, BÜHLER 2008), the Pyrenees 45.5-52.2 cm (GRANGÉ 2013, CAMPRODON 2007, CARCAMO & SENOSIAIN unpublished) and Abruzzo with 49.8 cm (BERNONI 1994) showing similar values.

The heights of the cavities (Tab. 3) follow an increasing gradient from Scandinavia with 7.44 m to Poland (17.2 m) (WESOŁOWSKI 1995, WESOŁOWSKI & TOMIAŁOJ 1986), the Pyrénées (14.4) being intermediate and very close to the data from Hokkaido, Japan with 13.3 m (MATSUOKA 1979; taxon *D. l. subcirris*) and the Balkan Peninsula (13.75 m) (PERUSEK 1991, GAŠI 2007, DOMOKOS & CRISTEA 2014). They are much higher than those of Abruzzo (10.01 m) (BERNONI 1994a,b, MELLETTI & PENTERIANI 2003) and the Spanish Pyrenees (11 m) (CAMPRODON & PLANA 2007, CARCAMO & SENOSIAIN unpublished).

Here again, considerations of different forest dynamics explain these results. Climax forest in Białowieża, as well as in Hokkaido, low canopy height in Scandinavia due to extreme physical constraints, and woodlands lightly exploited in the Balkans and western Pyrenees. The location of the cavity in or above the crown is predominant in Japan (with 64% of nests above the first branches; MATSUOKA 1979), as in the Pyrenees (ratio H. cavity / H. tree important) and contrary to Abruzzo, where 75-80% of nests are below the crown (BERNONI 1994b, MELLETTI & PENTERIANI 2003).

A survey of the health condition of the trees used reveals similar results: mostly dead trunks or dying in Scandinavia – mean: 63% (AULÉN 1988; HÅGVAR et al. 1990) and Northern-Alps –100% – (Switzerland, Germany BÜHLER 2008; SCHERZINGER 1990), 52% of healthy trees in Poland (WESOŁOWSKI 1995, WESOŁOWSKI & TOMIAŁOJ 1986), and 68% for the Pyrenees and Abruzzo (BERNONI 1994, MELLETTI & PEN-

TERIANI 2003, CARCAMO & SENOSIAIN unpublished). In Japan (MATSUOKA 1979), 75-100% of nest trees were healthy. *Lilfordi* is significantly more inclined to excavate its nests in healthy trees than nominate *leucotos leucotos*, confirming the hypothesis proposed by KILHAM (1979), which classifies the White-backed Woodpecker systematically using healthy trees, because of its relatively strong beak, which allows it to have a nestling period of four weeks (more safety in this type of cavity) unlike other species (*Dendrocopos major*, *D. minor* and *L. medius*) than have a strong tendency to excavate dying trees. Nominate *leucotos* varies greatly from that scheme.

The taxa *lilfordi*, *leucotos* of Central Europe and *subcirris* of Southern Hokkaido place their cavities higher than other sympatric Picidae in Poland (WESOŁOWSKI & TOMIAŁOJ 1986), Japan (MATSUOKA 1979) and French Pyrenees. In Norway, *D. leucotos leucotos* comes behind the Black and Green woodpecker (HÅGVAR et al. 1990).

The distances between nests of the same pair in successive years (50.4 m for the Pyrenees) were given only by AULÉN (1988) for Sweden, where the average was 497 m. (17 pairs) and BERNONI (1994b) for Abruzzo – 2 pairs – (25 m, and same nest tree): This illustrates a difference in the habitat of these two taxa. *Lilfordi* inhabits continuous mountain forests, exhibiting a sedentary lifestyle, and *D. leucotos leucotos* of Scandinavia uses fragmented forested areas involving annual changes of its core home range.

Cavity orientation

The examination of nesting cavity orientations shows no clear preference. Local conditions probably play a more important role in this than phylogenetic affinities. The dimensions of the only nest examined in the Pyrenees agree with the Polish (WESOŁOWSKI 1995), Swiss (BÜHLER 2008) and Italian data (BERNONI 1994b). Tree diameter at the cavity is similar in all regions (23.3

to 27.6 cm on average). The systematic use of a new cavity each year is found throughout the European distribution range of the species, and could be explained by the need for a site devoid of parasites as the young will stay in an enclosed space for around four weeks. This hypothesis, proposed by SHORT (1979), also emphasizes the advantage of excavating entrance holes with a diameter as close as possible to the size of the bird, to reduce the risk of parasitism. The White-backed Woodpecker data fully confirm this hypothesis (maximum width of the bird of 7 cm at shoulder level for a cavity diameter of 5.5 to 6.4 cm). Another hypothesis would be that these systematic changes could prevent potential predators (Pine Marten *Martes martes* in particular) to memorize, from one year to another, nest locations.

The relative consistency with which the birds create two cavities successively in one season, but occupying only the second, can be explained by difficulties encountered during the excavation of the first. The wood could be too hard at the centre, or the site not sheltered enough from bad weather. Moreover, this habit can increase the number of cavities available for the nocturnal roost throughout the year, near a site already very favourable for other ecological reasons.

Reproductive phenology (Table 4)

Reproductive phenology of the White-backed Woodpecker is characterized by the early onset of breeding, compared to other Picidae that share its habitat. The mean laying date ranges from early April in Poland (WESOŁOWSKI 1995) to the end of April in Japan (MATSUOKA 1979), in Abruzzo (BERNONI 1994a, b), and Norway (HOGSTAD & STENBERG 1997). With an average date of April 20, the birds of the Pyrenees occupy an intermediate position. Fledging dates follow the same pattern: 70% at the end of May in Poland (WESOŁOWSKI 1995), May 29 on average in the Pyrenees and Slovakia (PAVLÍK 1999), and early June elsewhere. The few data obtained in the Pyrenees on nests of *D. major*, close to *D. leucotos lilfordi*, showed a difference of more than ten days on average for the fledging dates of these species. This difference reaches 15-20 days in Hokkaido (MATSUOKA 1979). As emphasized by MATSUOKA (1979), the early breeding of the White-backed Woodpecker is due to its relative food specialization on wood-boring insect larvae that enable it to meet the needs of its young at a time when beech trees have barely started to bud (early May in the Pyrenees), and therefore cannot sustain caterpillars and other potential prey. The rate of wood-boring larvae varies from 35% (this work and Spanish Pyrenees-J.L. ROMERO, in litteris) to 80% (BERNONI 1994b) in the number of food items. Note, that if the biomass is used for calculating this rate, the importance

of this type of food is much more significant. It comprises 24 to 29% in number and 70 to 79% in biomass in Norway (HOGSTAD & STENBERG 1997). Furthermore, the larger size of this woodpecker may impede foraging on thin limbs as suggested by MATSUOKA (1979). In the Pyrenees, for 131 foraging events, limbs accounted only for 34% of exploited sites, both sexes combined, the male using the trunks in 85% of events (GRANGÉ 1991 and unpublished), and this supports this hypothesis.

Eggs measurements given by MAKATSCH (in CRAMP 1985) – 28×21 mm –, STENBERG (1998) – 28.3×20.8 mm – for *D. leucotos leucotos* and A. SENOSIAIN for Navarra (Spanish Pyrenees) – 27.7×20.1 mm – for *lilfordi* are very close to our own measurements – 29×21 mm.

The nestling period of about four weeks in the White-backed Woodpecker (26-28 days) compared to three weeks (18-22 days) in other European woodpeckers of similar size (*Dendrocopos major*, *L. medius*, *D. syriacus* and *D. minor*), could also be explained by this food specialization (slower growth due to lower energy intake than that provided by prey other than xylophagous insects?), in addition to a significant difference of size and lower feeding rates. For example, the feeding rate of *L. medius* was, on average, 10.8/h (7.69 to 13.95/h) for two pairs in Béarn (Pyrénées-Atlantiques-France; J.L. GRANGÉ) and 14/h for two pairs in NE Spain (J.L. ROMERO, in litteris) compared to 4.5/h for *lilfordi*. The modes of transport of prey were only studied by COSTANTINI et al. (1993), but are consistent with our observations. However, this needs to be validated by further research.

Number of fledglings – Food provisioning rates

The mean number of young fledging per pair ranges from 1.5 in Switzerland (BÜHLER 2008) to 3.4 in Poland (WESOŁOWSKI 1995). The average was 2.5 in Sweden (AULÉN 1988), 2.7 in Finland (VIRKKALA et al. 1993), 2.8 to 3.1 in Norway (STENBERG 1990, BRINGELAND & FJÆRE 1981) and 2.0 in Italy (BERNONI 1994b). The productivity of *lilfordi* is therefore low (2.07 in the Pyrenees) being short of the figure found in the Swiss Alps. However, this result must be put in perspective, since the measurements obtained in Scandinavia are often through visits to nests, unlike in the Pyrenees and Abruzzo where only discreet observations are used (which increases the risk of underestimating the number of juveniles present). The low number of young *lilfordi* produced in the Pyrenees may be caused by the very low rate of feeding the young in stage I (3.01/h) compared to Abruzzo (9.2/h) (BERNONI 1994b) and Norway (3.8/h HOGSTAD & STENBERG 1997). It is how-

ever very close to the figure for the Spanish Pyrenees (2.9/h; MORENO J.L., in litteris). Six of eight brood failures recorded were during this stage. Together with the incubation period, these two stages comprise 90% of the failures in the Pyrenees. Similarly, the mean feeding rate is the lowest in the Pyrenees (4.5/h in the French and Spanish Pyrenees) compared to 9.2/h in Abruzzo (BERNONI 1994), 8.7/h in Slovakia (PAVLÍK 1999), 5.1/h in Scandinavia and 5.2/h in Switzerland (BÜHLER 2008). The early hatching date corresponds to the unstable weather until mid-May that makes finding food more difficult for the adults. The prolonged absence of one of a pair may encourage the other adult to abandon the young to sustain itself (observed several times in the study area), exposing the brood to hypothermia (thermoregulation is not acquired at this early stage).

In general, the rate of feeding increases with the age of the young, and this was the case in the Pyrenees. In some studies, a decrease in this rate has been observed in the last days of nestlings in the cavity. This was interpreted as incitement to leave the nest (MATSUOKA 1979) and is possibly related to the increased risk of predation due to the noisy juveniles in the nest. This was not the case in our study. In most of the pairs monitored, means of 5 feeding/ h were recorded one to two days prior to fledging (slightly different from the average at stage III as a whole, with 6.04 feeding/ h). One pair in the Spanish Pyrennes fed the nestlings at a rate of 7.5 feedings/h two days prior to fledging (CARCAMO & SENOSIAIN unpublished).

Regarding the roles of the sexes, BERNONI (1994) noted an increase in the role of the female from stage I

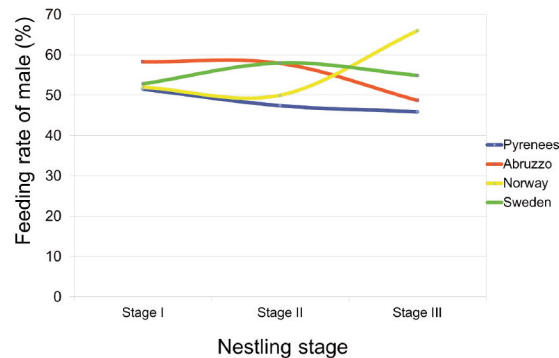


Fig. 7: Feeding rates (%) of male White-backed and Lilford Woodpeckers in different European locations.

to stage III, in Abruzzo, as was the case in the Pyrenees and Sweden (AULÉN 1988), but contrary to Norway (HOGSTAD & STENBERG 1997) where male contributions increased from 52% to 66%. Taking all these studies together, the male feeds the young more frequently than the female, which is contrary to what we found in the Pyrenees (Fig. 7). Greater samples sizes are clearly required for a better evaluation of the roles of the sexes during this phase of reproduction. Regarding the length of non-attendance by one of the parents, BERNONI (1994) in Abruzzo and BÜHLER (2008) in Switzerland noticed long periods, with a maximum of 71 minutes, and a minimum of 102 minutes, respectively.

Developmental stages

The duration of incubation and of the various nestling stages is very similar in the Pyrenees, Japan (I = 12 days, N = 27-28 days; MATSUOKA 1979) and the Abruzzo (N = 26 -28 days; BERNONI 1994b, COSTATINI et al. 1993). Compared to open-nesting species of the same size, woodpeckers generally have a reduced incu-

Table 4: Reproductive parameters (breeding phenology, breeding success) in the White-backed Woodpecker *Dendrocopos leucotos* sensu lato.

Country	Laying date	Fledging date	Number of Fledglings	Feeding rate (n/hour)	Breeding success (%)	Author
Japan Hokkaido	End April	June, 3				Matsuoka (1979)
Scandinavia, Latvia	28 April to 12 May	20 May to 22 June Mean: 14 June	2.4 to 3.1 Mean: 2.7 (N= 129)	5.1 (3.8 to 10.5)	Norway: 52–79 % Mean : 63 % Finland : 72 % (N= 62 broods)	Aulén (1988), Stenberg (1990, 1998), Hogstad & Stenberg (1997), Sarkanen (1974), Virkkala (1993), Bringeland & Fjaere (1981)
Central Europe Poland, Slovakia	First decade of April (20 March Switzerland,	Last decade of May (5 May to to 10 May)	Poland: 3.4 (N= 7) Switzerland: 23 June)	Slovakia: 8.7 (oak forest) Switzerland : 5,2 1.5 (N= 8)	36–83 % (N= 26 broods) Slovakia : 100 % (1 to 13.5)	Wesołowski (1995), Wesołowski & Tomiałojc (1986) Pavlik (1999), Bühler (2008) (N= 7 broods)
Balkans Bosnia, Slovenia	15-20 April	End of May	3 (N= 2)			Gašić (2007)
Italy (Abruzzo)	30 April	6 June 2 (N= 11)		9.2	100 % (N= 11 broods)	Bernoni (1994) Melletti & Penteriani (2003)
Spain (Pyrenees)		End of May		2.9 (stage I) to 6.1 (stage III)		J.L. Romero (in litt.), A. Senosiain (in litt.)
France (Pyrenees)	20 April (1 April to 11 May)	28 May (6 May to 21 June)	2.07 (N= 28)	4.5 (3.1 to 6.4)	84 % (N=28 broods)	Grangé (2002, present study)

bation period and a longer nestling period within a breeding cycle when the total length is equal in these two types of nesting. The N / I is 2.09 for woodpeckers (YOM-TOV & AR 1993) against 1.21 to 1.26 in the species of the same size not using cavities for nesting. According to our data, this ratio reached 2.5 in the Lilford Woodpecker. The explanation proposed by YOM-TOV & AR (1993) for this short incubation period is the difficulty of gas exchange of the embryos through their eggs shells in a cavity with relatively low ventilation, where there is an accumulation of carbon dioxide and oxygen depletion. Thus, as soon as pulmonary respiration is established, the cavity will be better ventilated (also augmented by the movement back and forth of adults, during their visits to the nest). On the other hand, the advanced stage of development of the young requires a longer period of feeding.

Conclusion

This study shows similar adaptations in the taxa with a distinct evolutionary history (*Dendrocopos leucotos leucotos*, *D. l. lilfordi* and *D. l. subcirris*) with respect to the preference of broadleaved forests (beech crucial for *D. l. lilfordi*), early reproduction and certainly due to a specialized diet largely based on wood-boring larvae (at least in biomass). These characteristics oblige this species to inhabit forests with a predominance of dead or dying trees, and with little or no industrial logging. The particular physical and geomorphological constraints of each area explain the differences in the height of nesting cavities, rates of feeding and reproductive output.

Yet, it also appears that great differences with respect to the preferred habitat exist. The subspecies *lilfordi* exclusively inhabits mountainous areas with predominantly moist beech forests, exhibits extreme sedentarieness (which reduces the chances of occupying new territories) and low population dynamics and productivity. The nominate *leucotos* shows greater ecological flexibility in its habitat choice and expansion tendencies (recently especially north of the Alps) with irruptions (especially of Siberian populations) that even see birds arrive in France in some winters (DESJARDINS & MERLE 2006).

In addition to these differences, we can add those in plumage pattern and biometrics. It would be of great interest to assess the genetic distances of these taxa to clarify the degree of divergence achieved to date (subspecies, genuine species, super-species). This may increase the importance of conservation efforts for the Pyrenean population.

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Address of the author:

Jean-Louis GRANGÉ
17bis rue du stade
F-64800 Bénéjacq, France
E-mail: grange.jean-louis@wanadoo.fr

Box 1

Dendrocopos leucotos was described by BECHSTEIN in 1802 under the name of *Picus leucotos* on the basis of an individual female from Silesia (southern Poland today) through an illustration which was provided to him by a certain Sir MICKWITZ (**Picture 1**). The species was thus described without the author of this description having seen the bird! It was not until 1871 that the taxon *lilfordi* made its official appearance, described by SHARPE and DRESSER under the name *Picus lilfordi* from an adult male specimen from Epirus, provided by Lord LILFORD (DRESSER 1871-81). Lord LILFORD (1860) states: "I killed two of these birds in the woods in the winter near Butrinto. It is not uncommon, but very wary, and difficult to shoot. Its voice and general habits are very similar to those of *Picus major*." In a letter to BREE (1875), he adds: "I found this species in the high woods in the Valley of Vrana, near Butrinto, in Epirus, in the winter of 1857." In addition to this specimen, the authors were able to examine eight birds from Macedonia provided by Dr. KRÜPER and one from Turkey sent by Mr. ROBSON as co-types. Distinctive criteria noted were "its crimson crown and rump barred conspicuously. In the northern bird the head is vermilion and the rump pure white." (SHARPE & DRESSER 1871). It should be noted that these authors, at the time, considered *lilfordi* a full species.

The oldest credible testimony of *lilfordi* is from Italy where GERINI in his book *Storia Naturale degli Uccelli* of 1769, published a picture of the species under the name «Picchio vario massimo» (**Picture 2**). The first historical mention of the Lilford Woodpecker in the Pyrenees was in the book of DEGLAND (1840) "Catalogue of birds seen in Europe ..." who stated in 1849: "a subject was killed in France, the Pyrenees, by Ernest DELAHAYE. I saw it in his father's collection, a librarian at Amiens". All we can say is that the specimen collected by DELAHAYE was before 1840. Surprisingly, the species was not found in the Spanish side of the Pyrenees until July 1961 by A. ARAGUES (1969) in Ordesa from where it has since disappeared.

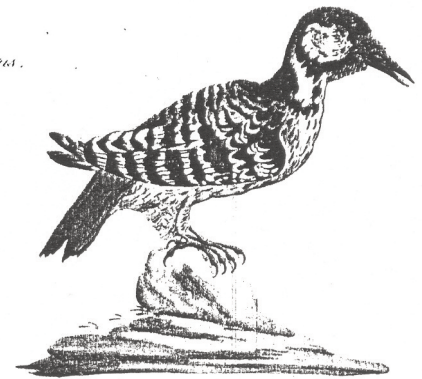
(For more details, see GRANGÉ 2013).



Picture 1: First depiction of a White-backed Woodpecker on the occasion of its first description by Bechstein 1802.

PICUS *leucotos*.

Picture 2: Early depiction of an Italian Lilford Woodpecker in a book by Gerini 1769 on the natural history of birds.



A Sua A D il Serenissimo Infante di Spagna
Carlo Antonio Diego Principe di Asturias etc.



Picture 3: The type specimen of "Picus lilfordi" at the British Museum, Tring. (1) Dorsal view, and (2) ventral view. (With permission by the British Museum, H. Van Grouw).