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Dynamics of Woodpecker – Common Starling interactions: a comparison of Old World and New World species and populations

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Abstract Woodpecker species whose cavities are most usurped by Common Starlings *(Sturnus vulgaris)* are widespread and generalists in their use of habitats. These include primarily woodpeckers that are similar in size to or slightly larger than the starling – such as the Great-spotted Woodpecker *(Dendrocopos major)* of Eurasia and the Northern Flicker *(Colaptes auratus)* and Red-bellied *(Melanerpes carolinus)* and Red-headed *(M. erythrocephalus)* Woodpeckers of North America. Usurpation occurs primarily in human-dominated urban, suburban and exurban habitats with pastures, sports fields and other open areas that serve as prime feeding habitats for starlings. Starlings prefer high, more exposed cavities with a minimal entrance diameter relative to their body size. Usurpation success depends on timing – optimally just as a cavity is completed and before egg-laying by the woodpeckers. Starlings likely reduce woodpecker populations in more open, human-dominated habitats. Woodpecker habitat losses and fragmentation are more serious problems that enhance habitat quality for starlings and reduce habitat quality for most woodpeckers. The only woodpeckers that might become in danger of extinction as a primary result of starling cavity usurpation are likely island species with small populations. Conservation of rare species limited to islands, such as Fernandina's Flicker *(Colaptes fernandinae)* of Cuba, may depend on our ability to prevent the establishment of the Common Starling or other aggressive cavity competitors on their island.

Understanding and interpreting impacts of woodpecker cavity usurpation must include consideration of past woodpecker and Common Starling population fluctuations, breadth of habitats used by woodpecker species, and habitat limitations of Common Starlings. Conservation efforts for woodpeckers and other primary and secondary cavity-nesting species must focus on changes in tree, forest and ecosystem management to encourage maintenance of dead wood, large contiguous tracts that include diverse tree species and old growth, and forested linkages among such areas.

Keywords: woodpecker, *Sturnus vulgaris*, nest-site competition, habitat

Összefoglalás Azon harkályfajok, amelyek odúit gyakran elfoglalják a seregélyek *(Sturnus vulgaris)*, széleskörűen elterjedtek, és élőhelyhasználat szempontjából generalisták. Ilyen például a hasonló vagy a seregélynél alig nagyobb testmérettel rendelkező nagy fakopáncs *(Dendrocopos major)* Európában, az aranyküllő *(Colaptes auratus)*, a karolinai *(Melanerpes carolinus)* és a vörösfejű küllő *(M. erythrocephalus)* Észak-Amerikában. Az odúk elfoglalása nagyrészt emberlakta/alakította élőhelyeken jellemző, ahol legelők, sportpályák és olyan nyílt területek találhatóak, melyek táplálkozási lehetőséget biztosítanak a seregélyek számára. A seregélyek elsősorban a magasabban, szabadon elhelyezkedő, és testméretükhöz mérve relatíve kisebb átmérőjű bejárattal rendelkező odúkat részesítik előnyben. Az odúk elfoglalása nagyban függ az időzítéstől: akkor a legeredményesebb, amikor az odú már kész van, de a harkályok még nem kezdtek tojást rakni. Úgy tűnik, hogy a seregélyek hozzájárulnak a harkályok ember uralta területeken bekövetkező populációinak csökkenéséhez. Azonban a harkályok élőhelyeinek megszűnése és feldarabolódása ennél komolyabb problémát jelent, hiszen a seregélyek számára kedvezőbb élőhelyi feltételek a harkályok számára csökkenő élőhelyminőséget jelentenek. Az egyetlen harkályfaj, amely a kihalás szélére került a seregélyek odúelfoglalásának köszönhetően, kis populációval rendelkező, szigetlakó faj. A ritka, szigetlakó fajok védelme, mint például a Fernandina-küllő *(Colaptes fernandinae)* Kubában, nagyban függ attól, hogy mennyire vagyunk képesek megakadályozni a seregély vagy más agresszív fajok odúfoglalási tevékenységét.

Az odúfoglalások megértéséhez figyelembe kell venni mind a harkályok, mind a seregélyek populációinak múltbeli ingadozását, valamint a harkályok és seregélyek élőhelyhasználatát. A harkályokra és más odúlakó fajokra irányuló természetvédelmi törekvésekben – a fa-, erdő- és ökoszisztéma-gazdálkodáson keresztül – ösztönözni kell a holt faanyag mindenkori jelenlétét, a hosszú, egybefüggő sávok biztosítását, melyekben különböző fafajok és öreg növényzet is megtalálható, úgy, hogy a területek közötti erdőkapcsolatok biztosítva legyenek.

Kulcsszavak: harkály, seregély, fészkelőhely, kompetíció, élőhely

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Introduction

As primary cavity nesters, woodpeckers are "keystone species" – they excavate nest and roost cavities that become prime real estate for a host of secondary cavity nesters. Secondary cavity nesters compete for abandoned woodpecker cavities and those formed by natural decay or other processes, or they may usurp an active nest or roost cavity from a primary or another secondary cavity nester. The Common (or European) Starling *(Sturnus vulgaris)* is a secondary cavity nester, well known to usurp active woodpecker cavities. This species will be the primary cavity competitor focused on in our assessment of the relationship between starlings and woodpeckers.

Native to Eurasia, the Common Starling has been introduced elsewhere and is now found on every continent except Antarctica and on many islands. Woodpeckers in Eurasia have coexisted with multiple species of starlings (Sturninae) for millennia. But even in Eurasia, starlings sometimes usurp cavities occupied by woodpeckers. There is little discussion of usurpation of active roost or nest cavities by starlings in Eurasia (but see Löhrl 1956, Mazgajski 2000, Smith 2005, 2006 for focus on the issue).

In contrast to Eurasia, the impacts of starling competition on woodpeckers have been more extensively studied in North America (e.g. see references in Ingold 1989, 1994, 1996, 1997, 1998, Ingold & Densmore 1992, Koenig 2003). North American woodpeckers have been challenged by competition from the Common Starling for their nest and roost cavities for a little over a century. The frequency, timing and impacts of such usurpation need further quantification, but vary among woodpecker species and habitats.

Wherever they are found, Common Starlings fill a broad niche and seem intimately adapted for living in human-altered landscapes (Kalmbach 1921, Feare 1984, 1989, Feare & Craig 1999, Jackson 2003a). They are omnivorous and feed in mowed grass, open agricultural fields, along roadsides and in other open areas. They often take advantage of the refuse of human patrons near fast-food restaurants, open dumps and open garbage receptacles. Starlings usually search for food in groups and often nest in niches and cavities in buildings and other structures, roost in our parks, wooded residential areas, woodland edges, and on utility towers and lines. Common Starlings are gregarious and outnumber other species in most human-dominated ecosystems. As this starling's numbers grew and populations spread naturally and through human introduction, they initially drew favorable attention to

themselves as consumers of harmful insects (leading to many more introductions), but once established, they soon were considered serious agricultural pests and their massive winter roosts considered health hazards (Feare & Douville de Franssu 1992, Pimentel *et al.* 2000). Perhaps it is no wonder that, in a review of the phenomenon of nest usurpation in birds, Lindell (1996) found that a disproportionately high percentage of reports dealt with Common Starlings and cavity nests.

Successfully introduced to North America in 1890-91, the Common Starling was soon reported aggressively usurping cavity nest sites of many native birds. Between 1901 and 1903, ornithologist Harold H. Bailey observed the introduced Common Starlings in the New York area. He was one of the first to describe how starlings were competing for cavities and causing other damage. The government response, to paraphrase Bailey, was: "We'll study them before taking action" (Bailey 1925).

Forbush (1915) referred to the starling's ability to usurp cavity nests as "combativeness personified". Kalmbach and Gabrielson (1921) reported that "flicker nests were said to be usurped by the wholesale". Moore (1937) assessed the situation in Missouri just after the starling arrived there. He also saw problems for native birds, but, with a more sanguine view, suggested that there would be a "slight decrease, over a long period of time, in the number of nesting bluebirds and woodpeckers." Others have not been so optimistic. Martin *et al.* (2004) characterized the Common Starling in North America as our "most aggressive secondary cavity nester". Today the starling may be the most abundant bird in North America. Its exotic status and success in usurping the cavities of native birds garnered much attention as it spanned the continent in a little over half a century (Cooke 1925, Kessel 1953, 1957, Cabe 1993).

During the 19th century as global human populations grew, forests were opened up or cleared for agriculture and cities and towns, climate changed and populations of Common Starlings grew, expanding the species' range through natural dispersal and introductions by humans (Berthold 1968, Fear 1984). During the last half of the 20th century Common Starling populations began a decline in many areas, perhaps a result of changes in agriculture. There are now fewer pastures that were once the prime foraging habitats for starlings (Smith & Bruun 2002, Bruun & Smith 2003). Though still abundant in many areas, the starling declines in northern Europe have been consistent among many countries (Svensson 2004, Robinson *et al*. 2005, Vysotsky 2005, Freeman *et al*. 2007, Szép *et al.* 2012).

Common Starlings reached much of western North America only by the mid-20th century and since then their populations have continued to grow. They seem to have begun a decline in eastern North America, although that decline is less evident than in Europe (Johnston & Garrett 1994).

In this review we explore the interrelationships between woodpeckers and starlings relative to cavity use, and how they might differ between Eurasia and North America. Examples of specific cases – where past history, current forest management and niche complexity play roles in fostering cavity competition between and among species – will be used to focus on how ignoring these factors might lead to misunderstanding of both woodpecker and starling population dynamics. Major emphases will be on species of woodpeckers that have been reported as having suffered cavity usurpation attempts by starlings *(Table 1),* conditions under which the competition occurs, impacts and potential impacts of competition, and roles

Table 1. Woodpecker species reported to have suffered cavity usurpation efforts by Common Starlings
1. táblázat Azon harkályfajok, amelyeknél megfigyelték a seregélyek odúfoglalását

Woodpecker species that have suffered Common Starling cavity usurpation attempts	Reported location (References for usurpation efforts)	Notes
Lewis's Woodpecker *(Melanerpes lewis)*	California (Bock 1970)	
	Colorado (Hadow 1973, Tashiro-Vierling 1994, Vierling 1998)	
	British Columbia (Cooper *et al.* 1998)	
Red-headed Woodpecker *(Melanerpes erythrocephalus)*	Florida (J. Jackson personal observation)	
	Iowa (Polder 1963)	
	Mississippi (Ingold 1989, J. Jackson personal observation)	
	Ohio (Ingold 1994)	
	Ontario (Frei *et al.* 2015)	
Acorn Woodpecker *(Melanerpes formicivorus)*	California (Troetschler 1970, 1976, Riensche & Cogswell 1993)	
Jamaican Woodpecker *(Melanerpes radiolatus)*	Jamaica, St. Ann Parish (Jeffrey-Smith 1972)	
Gila Woodpecker *(Melanerpes uropygialis)*	Arizona (Brush 1983, Kerpez & Smith 1990)	
	New Mexico (Brenowitz 1978)	
Golden-fronted Woodpecker *(Melanerpes aurifrons)*	Texas (Husak & Maxwell 1998)	
Red-bellied Woodpecker *(Melanerpes carolinus)*	Florida (Breitwisch 1977, J. Jackson personal observation)	
	Illinois (Stickel 1963)	
	Kansas (J. Jackson personal observation)	
	Mississippi (Ingold 1989, J. Jackson personal observation)	
	Ohio (Ingold 1994)	
	Oklahoma (Sutton 1984)	
West Indian Woodpecker *(Melanerpes superciliaris)*	Bahamas (Willimont 1990)	
Yellow-bellied Sapsucker *(Sphyrapicus varius)*	Ontario (Lawrence 1967)	unsuccessful effort
Middle-spotted Woodpecker *(Dendrocopos medius)*	Poland (Kosinski & Ksit 2006)	
Syrian Woodpecker *(Dendrocopos syriacus)*	Poland (Michalczuk & Michalczuk 2016)	
	Serbia (Szlivka 1957)	
Great-spotted Woodpecker *(Dendrocopos major)*	Britain (Glue & Boswell 1994, Smith 2005, 2006)	
	Germany (Lohrl 1956)	
	Poland (Kosinski & Ksit 2006)	
Nuttall's Woodpecker *(Picoides nuttalli)*	California (Riensche & Cogswell 1993)	"increased observed competition" no details
Downy Woodpecker *(Picoides pubescens)*	California (Riensche & Cogswell 1993)	"increased observed competition" no details

Woodpecker species that have suffered Common Starling cavity usurpation attempts	Reported location (References for usurpation efforts)	Notes
Black-backed Woodpecker (*Picoides arcticus*)	Ontario (Ferguson 1938)	
Hairy Woodpecker (*Leuconotopicus villosus*)	New Hampshire (Shelley 1933, Kilham 1968, 1969, 1971)	
	Ontario (Lawrence 1967)	
Red-cockaded Woodpecker (*Leuconotopicus borealis*)	Georgia (J. and B. Jackson personal observations)	
	North Carolina (J. Jackson personal observation)	
	South Carolina (Dennis 1971, J. and B. Jackson personal observations)	
White-headed Woodpecker (*Leuconotopicus albolarvatus*)	Oregon (Garrett *et al.* 1996)	
Northern Flicker (*Colaptes auratus*)	Arizona (Kerpez & Smith 1990)	
	California (Troetschler 1970, 1976)	
	Florida (J. and B. Jackson personal observations)	
	New Hampshire (Shelley 1935, Kilham 1973)	
Gilded Flicker (*Colaptes chrysoides*)	New Mexico (Brenowitz 1978)	
Golden-breasted Woodpecker (*Colaptes melanolaimus*)	Argentina (Ifran & Fiorini 2010)	
Pileated Woodpecker (*Dryocopus pileatus*)	New York (Hoyt 1948, 1957)	starling egg laid in active Pileated nest
	Georgia (Kilham 1979)	chased starling that approached nest
Eurasian Green Woodpecker (*Picus viridis*)	Great Britain (Turner 1908, Glue & Boswell 1994, Short 1982)	
Grey-headed Woodpecker (*Picus canus*)	Germany (Lohrl 1956)	probable, no details

of habitat and habitat changes on the dynamics of woodpecker-starling competitive interactions. We will also focus on a wider scale – woodpeckers, starlings, humans and habitats – how they have changed over the past century and how that history has influenced the ecosystems of starlings and woodpeckers.

Characteristics of woodpecker cavities and their use by woodpeckers

Woodpeckers excavate their own cavities, although a few species sometimes use nest boxes, natural cavities, or usurp the cavities of other woodpeckers. Woodpeckers not only nest in tree cavities, but also routinely roost in them. The result is likely a reduction in nocturnal mortality or at least a reduction in energy expenditure due to weather. For most woodpeckers, each adult usually roosts in a separate cavity and the nest site is typically the male's roost cavity. Woodpeckers add no nest material to the cavity, but chip wood from the cavity's interior to leave a bed of clean chips on the bottom of an active nest. Many woodpeckers

excavate a new cavity each year and abandon the old one as decay progresses. Using a new cavity may also thwart a predator that has had hunting success at a previously used cavity – a risk for all secondary cavity-nesters. This intimate, year-round link to a cavity is characteristic of woodpeckers, but not of most Common Starlings. Some non-migratory Common Starlings show a similar year-round link to a cavity (Lombardo *et al.* 1989), but others join wintering migrant starlings favoring large communal roosts that shift as availability of food resources changes (Morrison & Caccamise 1985).

A cavity excavated by a woodpecker generally has an entrance that is no larger in diameter than is necessary for the woodpecker to enter. The assumption is that a smaller cavity entrance provides greater protection from predators and weather (Short 1979). Available data for woodpecker cavity entrance size is scant, often without indication of how the entrance diameter was measured, and rarely with measurements for both horizontal and vertical diameter. It is also confounded by other irregularities such as enlargement of cavities by wear from continued use, and enlargement by other woodpeckers or squirrels.

Measurement of cavity entrance parameters is fraught with problems that do not allow analysis that requires precision data. In one case cavity entrance parameters were estimated from the ground by using a bird at the cavity as a "tool" for making the estimate to the nearest centimeter. In another case a metric ruler was taped to a long pole, held in front of the cavity, and the diameter read through binoculars from the ground. In both cases the mean entrance diameter for the species was presented to the nearest millimeter. Such data have limited use. Even more problematic, authors often do not describe how cavity measurements were taken. Thus data we gleaned from the literature and included in *Table 2* should be viewed with an understanding of its potential limitations and used with caution. We use the data in *Table 2* only to suggest potential cavity usefulness to Common Starlings and to demonstrate potential cavity-entrance variability within and among species. Examples of useful cavity dimensions often measured are shown in diagrams in Kerpez and Smith (1990) and Remm *et al.* (2006).

Widespread species, such as the non-migratory Hairy Woodpecker of North America and the Great-spotted Woodpecker of Eurasia, vary geographically, often showing clinal variation in body size consistent with Bergman's Rule as it relates to warm-blooded vertebrates. Here we use body mass (g) to suggest relative body size within and among species *(Table 3)*. In colder climates body size is larger (reducing surface area per mass) and appendages relatively smaller – adaptations that reduce heat loss. In the Hairy Woodpecker, for example, mean body mass at the northern limits of this sedentary species can exceed 95 g, while at its southern limits can be about 44 g (Jackson *et al.* 2002). It also seems likely that cavity entrance size varies geographically and that potentially a species' nest cavities might be suitable for starling use in some regions, but not in others.

Body mass varies not only geographically, but seasonally, with time of day, sex, age and health. When body mass is taken, it should be recorded in the context of all of these parameters. Usually it is not, thus such data out of context are useful primarily as a general indication of body size. In this review we were interested in body mass as an indication of a woodpecker's cavity potentially being suitable as a Common Starling's nest site and as a potential factor in both woodpecker and Common Starling potential for success in cavity usurpation.

Table 2. Cavity entrance dimensions reported for woodpecker species reported to have suffered cavity usurpation attempts by Common Starlings

2. táblázat A seregélyek által elfoglalt odúk röpnyílásainak átmérői (a röpnyílás vízszintes, függőleges és nem ismert irányú átmérőjének terjedelme)

Species	Cavity Entrance Diameter (cm)[1]			Location	References for Cavity Dimensions
	Horizontal Range (Mean)	Vertical Range (Mean)	Unknown Range (Mean)		
Lewis's Woodpecker (*Melanerpes lewis*)			(6.2)	NA[2]	Tobalske 1997
			6.3–7.5 (6.7)	California	Bock 1970
Red-headed Woodpecker (*Melanerpes erythrocephalus*)			(5.87)	Wyoming	Gutzwiller & Anderson 1987
			(5.6)	Colorado	Sedgwick & Knopf 1990
	5.4–7.6 (6.2)	6.4–7.4 (6.9)		Kansas	Jackson 1976
Acorn Woodpecker (*Melanerpes formicivorus*)				California	Troetschler 1976
Jamaican Woodpecker (*Melanerpes radiolatus*)			4.7–7.7 (6.5)	Jamaica	Cruz 1977
Gila Woodpecker (*Melanerpes uropygialis*)	(6.3)	(5.7)		Arizona	Kerpez & Smith 1990
	(5.5)	(5.1)		Arizona	McAuliffe & Hendricks 1988
Golden-fronted Woodpecker (*Melanerpes aurifrons*)	(4.9)	(5.5)		Texas	Husak & Maxwell 1998
Red-bellied Woodpecker (*Melanerpes carolinus*)	5.7–6.4 (5.9)	5.1–6.2 (5.7)		Kansas	Jackson 1976
West Indian Woodpecker (*Melanerpes superciliaris*)					No data
Williamson's Sapsucker (*Sphyrapicus thyroideus*)			(4.0)	Colorado	Dobbs *et al.* 1997
Yellow-bellied Sapsucker (*Sphyrapicus varius*)			3.2–4.1	Maine	Brewster 1876
			4.1–5.6 (4.6)	Colorado	Ingold & Ingold 1984
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	(3.8)	(4.1)		British Columbia, Caribou Parklands	Erskine & McLaren 1972
	3.2–4.7 (3.8)	3.3–5.7 (4.2)		British Columbia, Hat Creek	Walters *et al.* 2002b
	(4.0)	(4.6)		Oregon	Dobkin *et al.* 1995
Red-breasted Sapsucker (*Sphyrapicus ruber*)	3.9–5.7 (4.6)	4.3–5.4 (4.7)		British Columbia	Joy 2000
			(3.8)	California	Raphael & White 1984
Lesser-spotted Woodpecker (*Dryobates minor*)			3.5–5.1 (3.9)	Great Britain	Glue & Boswell 1994

[1] All data in this table are rounded to the nearest 0.1 cm, although level of accuracy is likely much less for reasons discussed in the text.
[2] NA = Data not available.

Species	Cavity Entrance Diameter (cm)[1]			Location	References for Cavity Dimensions
	Horizontal Range (Mean)	Vertical Range (Mean)	Unknown Range (Mean)		
Syrian Woodpecker (*Dendrocopos syriacus*)			(3.5)	NA	Snow *et al*. 1998
	(4.5)			Yugoslavia	Szlivka 1957
Middle-spotted Woodpecker (*Dendrocopos medius*)			(5)	NA	Snow *et al*. 1998
Great-spotted Woodpecker (*Dendrocopos major*)			3.9–5.0 (4.3)	Estonia	Remm *et al*. 2006
			4.8–7.6 (5.8)	Great Britain	Glue & Boswell 1994
Nuttall's Woodpecker (*Picoides nuttalli*)			4–8 (5.0)	California	Miller & Bock 1972
Downy Woodpecker (*Picoides pubescens*)			2.5–2.9	British Columbia	Campbell *et al*. 1990
			2.8–3.8	Illinois	Calef 1953
			(3.2)	Ohio	Oberholser 1896
Black-backed Woodpecker (*Picoides arcticus*)			(4.4)	California	Dixon & Saab 2000
			3.3–4.1	Wisconsin	Eckstein 1983
Hairy Woodpecker (*Leuconotopicus villosus*)	(3.8)	(4.8)		Massachu-setts	Bent 1939
			(4.8)	Colorado	Ingold & Ingold 1984
Red-cockaded Woodpecker (*Leuconotopicus borealis*)	(4.1)	(4.1)		North Carolina	Price 1971
	(3.8)	(3.5)		South Carolina	Cely 1985
White-headed Woodpecker (*Leuconotopicus albolarvatus*)			(4.6)	California	Garrett *et al*. 1996
	(4.5)	(4.8)		Oregon	Garrett *et al*. 1996
	(4.8)	(5.0)		central Oregon	Garrett *et al*. 1996
Northern Flicker (*Colaptes auratus*)			5.6–12.7 (8.3)	eastern North America	Burns 1900
	(8.3)	(7.0)		Arizona	Kerpez & Smith 1990
			7.1–9.4 (8.4)	Colorado	Ingold & Ingold 1984
			(6.6)	Colorado	Sedgwick & Knopf 1990
			(6.6)	Wyoming	Gutzwiller & Anderson 1987
			4.2–9.6 (6.4)	British Columbia	Wiebe 2001
Gilded Flicker (*C. chrysoides*)	(7.0)	(8.3)		Arizona	Kerpez & Smith 1990
	(8.6)	(6.8)		Arizona	McAuliffe & Hendricks 1988
	(4.6)			Colorado	Ingold & Ingold 1984
Pileated Woodpecker (*Dryocopus pileatus*)[3]	(7.6)			California	Carriger & Wells 1919
	(8.3)	(10.8)		New York	Hoyt 1957
	(9)	(12)		Oregon	Bull 1987
	(8.9)	(11.4)		Tennessee	Humphrey 1946

[3] All of the data shown here for Pileated Woodpecker appears in Bull and Jackson (1995), but there is rounded to the nearest 0.5 cm.

Species	Cavity Entrance Diameter (cm)[1]			Location	References for Cavity Dimensions
	Horizontal Range (Mean)	Vertical Range (Mean)	Unknown Range (Mean)		
Black Woodpecker *(Dryocopus martius)*			7.5–8.6 (7.9)	Estonia	Remm *et al.* 2006
Eurasian Green Woodpecker *(Picus viridis)*			4.4–5.7 (5.3)	Great Britain	Glue & Boswell 1994
Common Starling *(Sturnus vulgaris)*	(6.6)	(5.7)		Arizona	Kerpez & Smith 1990
			4.1–7.9 (5.3)	Colorado	Ingold & Ingold 1984
			(6.5)	Colorado	Sedgwick & Knopf 1990
			(6.2)	Wyoming	Gutzwiller & Anderson 1987

Starlings also show geographic variation in body size (Blem 1981), but more data and more evaluation of it are needed. Since northern populations of starlings are migratory and leave colder regions, geographic size variation may not be as dramatic as in resident woodpecker species. *Table 3* also includes data for Common Starling body mass for comparison with the woodpecker data. Much of the literature on starling body mass is based on experimental manipulation of birds in captivity and such data are not included in *Table 3*.

The Starling has been described as a "compact, stocky" bird (Cabe 1993) – short, but not slender, thus one that might need a larger cavity entrance than a more slender bird of the same mass. In addition it has been shown that both male and female Common Starlings reach their peak mass just prior to nesting (Hicks 1934), thus might require a larger cavity entrance at that time.

Woodpecker cavities vary in many other ways including the depth of the cavity, variation in the diameter of the entrance tunnel, size of the nesting chamber, thickness of the walls, direction of opening and height above ground. These may vary among woodpecker species, among individual cavities within a species, among tree species and size, and by the extent of fungal decay. Other factors such as wear and enlargement by another species may alter the characteristics of a cavity after excavation by its original owner.

Red-cockaded Woodpecker cavities are often used for years, and by multiple generations, and cavity entrances are enlarged by wear over time and often by other potential cavity usurpers. In addition, those species that excavate a cavity in a living tree, such as Red-cockaded Woodpeckers, often begin their cavity at or just below a fungal-decayed branch stub that is surrounded by sound wood (Jackson & Jackson 2004). They then follow the decay through a tunnel of rotted wood and down through rotted hardwood, creating an entrance tunnel three or more inches long before turning downward. This can result in the narrowest part of the cavity entrance being inward from the surface of the tree and difficult to measure.

Clearly, more precise and more consistently collected data are needed before we can fully understand the significance of variation in both woodpecker body size and cavity-dimension parameters.

Table 3. Body mass (g) of Common Starlings and woodpeckers that suffer from or potentially could suffer from cavity usurpation by starlings

3. táblázat A seregélyek által elfoglalt odúkat készítő harkályfajok, illetve a seregélyek testtömege (hímek, tojók, illetve az ivarra nem határozott egyedek esetében). A helyszíneknél az „NA" nem elérhető adatot jelent

Species	Body Mass (g)[1]			References for Mass
	Range (Mean)			
	Male	Female	Sex unknown	
Lewis's Woodpecker (*Melanerpes lewis*)			85–138	NA[2] (Short 1982)
			108–138 (116)	California (Dunning 1993)
	105–122 (113)	88.3–106 (99)		Montana (Tobalske 1996)
Red-headed Woodpecker (*Melanerpes erythrocephalus*)			61–97	NA (Short 1982)
			56.1–90.5 (71.6)	Ontario (Dunning 1993)
Acorn Woodpecker (*Melanerpes formicivorus*)			62–90	NA (Short 1982)
	(82.9)	(78.1)		California (Dunning 1993)
	(81.8)	(77.5)		California (Dunning 2008)
Jamaican Woodpecker (*Melanerpes radiolatus*)			92–131	Jamaica (Short 1982)
			(108)	Jamaica (Dunning 1993)
	97.3–130.5 (114.8)	91.6–118.5 (102)		Jamaica (Cruz 1977)
Gila Woodpecker (*Melanerpes uropygialis*)			51–79	NA (Short 1982)
	54.6–80.6 (69.7)	53.8–67 (60)		Arizona (Dunning 2008)
Golden-fronted Woodpecker (*Melanerpes aurifrons*)			67–100	NA (Short 1982)
	73–99 (85.4)	66–90 (76.4)		San Luis Potosi, Mexico (Selander 1966, Dunning 1993)
Red-bellied Woodpecker (*Melanerpes carolinus*)			67–91	NA (Short 1982)
	(67.2)	(56.2)		Florida (Dunning 1993)
West Indian Woodpecker (*Melanerpes superciliaris*)			70–126	NA (Short 1982)
	71.3–99.3 (84.2)	67.3–73.5 (71.0)		Cayman Islands (Dunning 1993)
Williamson's Sapsucker (*Sphyrapicus thyroideus*)			44–64	NA (Short 1982)
			44.4–55.3 (47.6)	Nevada (Dunning 2008)
Yellow-bellied Sapsucker (*Sphyrapicus varius*)			43–45	NA (Short 1982)

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[1] Weights for woodpecker species provided as given in Short (1982) are presumably from specimen labels; Short gives no indication for source or sample size of weight data or, in most cases, for weight differences between sexes. Frugis *et al.* (1988) include the weight data provided in Short (1982). We provide additional weight data from sources that identify location, sex, and additional information. These additional data may provide indication of some of the extent of species' geographic and sex specific variation – and perhaps limitations of available data. Weights from Dunning (1993, 2008) are often from banding (ringing) efforts and often include large sample sizes (rarely 100+) but seasonality and time of day data are not provided – two factors that greatly influence variation in weights. Note that Dunning 1993 and 2008 each includes data not in the other publication

[2] NA = Locality data not available

Species	Body Mass (g)[1]			References for Mass
	Range (Mean)			
	Male	Female	Sex unknown	
Red-naped Sapsucker *(Sphyrapicus nuchalis)*			37–61	NA (Short 1982)
			36–54.9 (45.9)	Arizona (Dunning 2008)
	(50.5)	(49.2)		British Columbia (Dunning 2008)
			(47.4)	California (Tobalske 1996)
Red-breasted Sapsucker *(Sphyrapicus ruber)*			39–60	NA (Short 1982)
	(58.3)	(57.7)		British Columbia (Dunning 2008)
			40.1–54.7 (48.9)	California (Dunning 2008)
Middle-spotted Woodpecker *(Dendrocopos medius)*			50–85	NA (Short 1982)
			50–80 (59)	Central Europe (Dunning 2008)
Syrian Woodpecker *(Dendrocopos syriacus)*			70–82	NA (Short 1982)
	76.0–82.0 (79.5)			SE Europe (Dunning 1993)
			70–83	NA (Snow *et al.* 1998)
Great-spotted Woodpecker *(Dendrocopos major)*			58–110	NA (Short 1982)
			50–80	NA (Snow *et al.* 1998)
			71–83 (81.6)	Britain (Dunning 2008)
	65–98 (76)	58–77 (69)		China (Dunning 2008)
	70–87 (76)	68–79 (72.7)		Netherlands (Dunning 2008)
Nuttall's Woodpecker *(Picoides nuttalli)*			32.8–43.1 (38.3)	Lowther 2000
Downy Woodpecker *(Picoides pubescens)*	(27.8)	(28.6)		Hoover 1972
			(21.6)	Georgia (Dunning 2008)
	26–29.1 (27.5)	22.2–28.5 (25.9)		Pennsylvania (Dunning 2008)
Black-backed Woodpecker *(Picoides arcticus)*			61–88	NA (Short 1982)
Hairy Woodpecker *(Leuconotopicus villosus)*			38–94	NA (Short 1982)
			(51.7)	Bahamas (Dunning 2008)
	(60)	(52.4)		Baja California, Mexico (Dunning 2008)
	60.8–79.6 (70)	59.3–65.9 (62.5)		Pennsylvania (Dunning 1993)
			(70.5)	Montana (Tobalske 1996)
	(79)	(67.5)		Montana (Dunning 2008)

Species	Body Mass (g)[1]			References for Mass
	Range (Mean)			
	Male	Female	Sex unknown	
Red-cockaded Woodpecker *(Leuconotopicus borealis)*			40–55	NA (Short 1982)
			(43,6)	Florida (Dunning 1993)
	(48.6)	(47.4)		North Carolina (Dunning 2008)
White-headed Woodpecker *(Leuconotopicus albolarvatus)*			50–79	NA (Short 1982)
	55.6–68 (63.0)	52.6–66.4 (59.2)		Oregon (Dunning 1993)
Northern Flicker *(Colaptes auratus)*			92–193	NA (Short 1982)
			(148.1)	Montana (Tobalske 1996)
			121–167 (142)	Oregon (Dunning 1993)
	106–143 (128)	104–137 (125)		Pennsylvania (Dunning 2008)
Gilded Flicker *(Colaptes chrysoides)*			92.2–129.0 (111)	Arizona (Dunning 1993)
Golden-breasted Woodpecker *(Colaptes melanolaimus)*	(129)	104–120		Paraguay (Dunning 2008)
Pileated Woodpecker *(Dryocopus pileatus)*			240–341	NA (Short 1982)
	308–309 (308)	250–284 (266)		Pennsylvania (Dunning 1993)
			(262.5)	Montana (Tobalske 1996)
Eurasian Green Woodpecker *(Picus viridis)*			160–250	NA (Short 1982)
			138–190 (176)	France (Dunning 1993)
Grey-headed Woodpecker *(Picus canus)*			125–165 (137)	Switzerland (Dunning 2008)
Common Starling *(Sturnus vulgaris)*	79–100 (87.6)	76.3–92 (84.4)		New York (Dunning 2008)
	(84.7)	(79.9)		Ohio (Dunning 1993)
			55–72 (62.1)	India and Pakistan (Ali & Ripley 1983)

Common Starling preferences in cavity selection

Many authors have suggested characteristics of nest sites that might be "preferred" by Common Starlings; others have suggested characteristics that might deter starlings. Our list, derived from the published literature and our own experience, is likely incomplete and no doubt the extent to which a characteristic is favored varies with local conditions. We feel that all are worthy of further investigation. Demonstrated and suggested starling preferences include the following:

(1) *Woodpecker cavity over a natural cavity.* – Howell (1943) and Ingold (1994) suggested that Common Starlings in North America prefer woodpecker cavities over natural cavities. Perhaps the volume and internal contours of a woodpecker cavity are more

consistently favorable. While starling-preferred and starling-deterrent characteristics might be found in both natural and woodpecker-excavated cavities, under the primeval conditions of Poland's Bialowieza forest where there is an abundance of both natural and woodpecker-excavated cavities, 60% of Common Starling nests were in woodpecker cavities (Wesolowski 2007). Some of these were ones abandoned by woodpeckers, others were likely usurped from woodpeckers that were occupying them.

(2) *Woodpecker cavity over a nest box.* – There are many factors that might be involved in this dichotomy – among the more important are likely the cavity entrance diameter, internal dimensions and location of the nest box. Most woodpecker cavities have an oval bowl at the bottom; perhaps this suggests another aspect of a starling preference for woodpecker cavities over other types of cavities. Carlson *et al.* (1998) found that Common Starlings showed a preference for thicker-walled cavities – such as found in many woodpecker nest cavities and usually not found in nest boxes. Ingold (1998) found that Common Starlings usually preferred using a Northern Flicker cavity over a nest box and suggested that providing nest boxes near a flicker nest might reduce flicker fecundity and ultimately increase the likelihood of starling usurpation of flicker cavities by increasing the local starling population.

(3) *Natural cavities with cavity dimensions similar to those of woodpecker-excavated cavities.* – Although Common Starlings seem to prefer woodpecker-excavated cavities, Aitkin and Martin (2007) found that starlings alternatively prefer natural cavities with dimensions similar to those of woodpecker cavities, except that in their study woodpecker-excavated cavities had significantly larger entrance openings – perhaps because flickers, which have relatively large cavity entrances *(Table 2)*, were the most abundant woodpeckers present.

(4) *Cavity in an isolated tree rather than near forest edge or in a forest interior.* – Forest fragmentation increases the potential for cavity competition between woodpeckers and starlings in that it creates more open habitat that might provide prime foraging for starlings (Kilham 1971, van Balen *et al.* 1982, Bai 2005, Bai *et al.* 2005, Mazgajski & Rejt 2006, Aitken & Martin 2008). In a study using nest boxes placed in different habitats in Ontario, Canada, Gibo *et al*. (1976) found the greatest starling nest success was in boxes placed in the middle of an old field (46.83% egg to fledgling success). The poorest success (0%) was in boxes placed within wooded areas (an arboretum, a pine stand and an oak-maple stand). Other sites included an orchard (16% success) and boxes placed at the edge of an old field (1.96% success). There were some confounding factors – some boxes were attached to poles, others to trees, but box design was uniform and box height was similar. Similar nest-box studies in Poland (Gromadzki 1980) produced similar results: The boxes most used by Common Starlings were ones placed in the middle of an open area – away from forest or forest edge. Such results support a starling preference for openness that may reflect greater predation at starling nests along edges and/or greater access to optimal starling foraging areas. Such preferences also support the idea that cavities of ground-foraging flickers (*Colaptes* spp.) and Red-headed Woodpeckers – species that favor excavating their cavities in isolated snags in open habitats – would be especially favored by starlings.

(5) *Cavity with little vegetation around it.* – Kilham (1971) and Fisher and Wiebe (2006) suggested this as a possible preference, noting that close vegetation surrounding a cavity could hide a potential predator or facilitate access by a predator. On the other hand, we, and several authors have noticed that a branch stub (barren of leaves) near a cavity is often a favored starling display perch.

(6) *High cavity, rather than a low one.* – One of the strongest, best documented of Common Starling nest-site preferences is that for higher cavities (e.g. Verheijen 1969, Coleman 1974, Ingold & Ingold 1984, Nilsson 1984, Carlson *et al.* 1998, J. and B. Jackson personal observations). Even in experimental situations with nest boxes placed at different heights, starlings have favored higher cavities. This could be more a function of the locations of most natural and woodpecker cavities – a result of the ecology and dynamics of heart-rot fungi (Jackson & Jackson 2004) – but it has also often been attributed to a reduced potential for predation at a higher cavity (e.g. Nilsson 1984).

(7) *Cavity in a living tree to one in a dead snag.* – Aitken and Martin (2004) presented evidence that Common Starlings prefer to nest in a cavity in a living tree infected with a heart-rot fungus. Live trees are more likely to have stronger cavity walls (Wesolowski 2007), thus perhaps making them less vulnerable to some predators and/or to wind or fire.

(8) *Cavity that opens to the east-southeast.* – Verheijen (1969) reported this preference in Belgium. In the Netherlands van Balen *et al.* (1982) noted what amounts to the same tendency from the opposite perspective – starlings tended to avoid cavities that opened to the west or north-northwest. This could be a thermoregulatory choice. It is also a choice that may vary geographically, topographically, and with the woodpecker species in a particular area.

(9) *Cavity on a vertical trunk rather than one on the under side of a more horizontal limb.* – Kilham (1971) suggested that starlings prefer Hairy Woodpecker cavities that open on a vertical tree trunk over those that open on the under side of a limb. Gaining entrance to a more downward-facing cavity would be more difficult for a starling.

(10) *Cavity with a larger bottom area and volume.* – The inside dimensions of a woodpecker cavity can vary among woodpecker species and individuals for many reasons discussed above. Moeed and Dawson (1979), van Balen *et al.* (1982) and Carlson *et al.* (1998) considered the bottom area and volume of nest boxes used by Common Starlings and found some evidence that larger cavities were favored over the smallest ones in their studies, although their results were inconclusive.

(11) *Deeper cavity rather than a shallow one.* – Deeper cavities were preferred by Common Starlings in studies by Carlson *et al.* (1998) and Mazgajski (2003). A shallow cavity might allow easy access to the arm of a mammalian predator; a deeper cavity might better conceal eggs and young in darkness.

(12) *Cavity entrance that is minimal.* – Cavity entrance diameter is important in that a smaller entrance may exclude more competitors or predators. It may also influence the microclimate inside the cavity (Wiebe 2001). Cavity-nesting birds sometimes create or select a cavity that they literally have to squeeze into (van Balen *et al.* 1982, Martin *et al.* 2004). In choice tests of nest holes with different-sized cavity entrances, starlings preferred smaller openings even when the smallest entrance was bigger than optimum for starlings (e.g. Lumsden 1976).

(13) *Circular entrance opening as opposed to a square-shaped entrance.* – In a nest-box study in New Zealand, Coleman (1974) found that starlings preferred a circular opening to a square one. This suggests the possibility that the irregular-shaped entrance of some woodpecker cavities might make them less inviting to a starling. However, starlings do use the cavities of Red-headed Woodpeckers, and these are often flat on one or more sides due to their excavations beginning at a crack (Jackson 1976).

In North America a Common Starling-excluder that results in an irregular-shaped entrance has been patented for use on Purple Martin *(Progne subis)* houses (Snyder 2003). Also with reference to Purple Martins, Day (2012) suggests that starlings can be controlled at nest boxes by the use of rectangular or crescent-shaped box entrances. Metal plates around cavity entrances are also used to protect Red-cockaded Woodpecker cavities from cavity enlargement and/or usurpation by larger cavity competitors (Carter *et al.* 1989, Jackson 1994) and might be a useful tool in protecting some other small woodpeckers from Common Starlings.

(14) *A nest-box entrance that is to the side (off-center), rather than centered on the box.* – This preference was discovered in a nest-box study in New Zealand (Flux & Flux 1981) and seemed to show that starlings were confused by having two corners to look at as they looked in. Some built two separate nest bowls, one in each of the back corners. With the entrance off-center, there would be only one corner prominently seen from the entrance and apparently less confusion. A natural cavity could conceivably present a similar dilemma for starlings.

(15) *Dark cavity interior.* – In an experimental study Lumsden (1976) found that starlings preferred nest boxes with black interiors to those with natural wood interiors. Jackson and Tate (1974) also found some indication of a starling preference for a darker cavity interior in a continent-wide survey of Purple Martin and cavity competitor use of nest boxes. Most freshly cut heartwood of a tree is lighter in color and, over time, various species of heart-rot fungi and other processes stain the wood darker.

(16) *Clean cavity.* – A preference for a clean cavity – as opposed to one containing an old nest – might possibly be influenced by (a) the cavity being too shallow with a new nest built atop an old one, hence more vulnerable to predators, (b) the old nest containing parasites that might reduce nest success, and/or (c) the energetic expense needed to clean it out.

(17) *Newer or older cavity?* – This may be related to a preference for a clean cavity over one that contains old nesting material or perhaps to a greater potential for predation in an older cavity (Nilsson 1991, Sorace *et al.* 2004, Mazgajski 2007b), although in an earlier experimental study of the role of cavity depth in site selection, the presence of old nest material seemed to not influence cavity selection (Mazgajski 2003). It might also be related to the preference for a cavity with a darker interior. Wiebe *et al.* (2007) found that old Northern Flicker nest cavities that were reused by flickers were more likely to be usurped by Common Starlings. They also noted that old cavities were more likely to be used by male flickers that were in poorer condition – thus perhaps less able to excavate a new cavity and less able to defend a cavity. Clearly starlings will usurp old or new cavities, but this may depend on the cavities available, the species of woodpecker, predation, the health of the occupant, and other factors.

The nature of interactions between woodpeckers and starlings

We know the basics of why woodpeckers must defend their nest and roost cavities against starlings – and why starlings must aggressively seek those cavities. But what do we know about when and how starlings select a cavity to usurp and how they go about securing it for their own use? What do we know about how woodpeckers defend their cavities successfully, why they sometimes fail, how starlings are successful in usurping them, and when they fail? We have assembled here a compilation of observations, suggestions and results of experimental studies that may guide further studies that might provide more definitive answers to these questions.

Starlings are opportunistic and readily take advantage of any appropriate-sized cavity for nesting if nothing better is available at a lesser "cost". "Cost" here refers to the energy expenditure, threat of harm associated with trying to usurp a cavity, and the threat of harm associated with cavity location (e.g. ease of access by a predator, exposure to rain or more negative weather events).

Starlings are very persistent, often waiting by a cavity day-after-day until the opportunity arrives for them to enter the cavity to take possession (Marples 1936, Lawrence 1967, Ingold 1994, J. Jackson personal observations). At the appropriate time they are also very aggressive towards owners of a cavity they are trying to usurp, towards woodpeckers that try to usurp a cavity the starlings are in possession of, and towards others of their own species that try to usurp their cavity or steal their mate. Common Starlings use their feet and sharp, curved claws to grab onto opponents and are reluctant to let go as they use their bill to strike repeatedly at their adversary.

With both woodpeckers and starlings, defense of a territory or mate against a conspecific is generally male against male and female against female, but the level and the duration of aggression seems much greater on the part of starlings and can vary greatly among woodpecker species. For example, neither Red-bellied Woodpeckers (Ingold 1989, J. A. Jackson personal observations) nor Yellow-bellied Sapsuckers *(Sphyrapicus varius)* (Lawrence 1967) seem to aggressively defend their nest against Common Starlings. Red-headed Woodpeckers, in contrast, vigorously defend against starlings (Ingold 1989). During a cavity usurpation effort, however, there often seems to be a high level of apparent cooperation between members of a starling pair (Howell 1943, Mathis 1975, J. A. Jackson personal observation). We suspect that because male and female starlings are not as distinctively marked as most woodpeckers and because both lack any hint of red, a male sexually dichromic woodpecker might sometimes treat all starlings as "females" and let his mate take care of the intruders. Nichols and Jackson (1987) suggested a similar scenario allows the sexually monochromic Red-headed Woodpeckers to almost always succeed in usurping cavities of Red-bellied Woodpeckers; only the male Red-bellied goes after the intruders while the female watches, apparently accepting both extensively Red-headed adults as males. This is certainly not always the case in all woodpecker species. Lawrence (1967) and Kilham (1968) describe cooperative defense against starlings by Hairy Woodpecker pairs.

Timing is very important in Common Starling selection of a potential woodpecker nest cavity and success at usurping (Ingold & Densmore 1992, Paclic *et al*. 2009, J. A. and B. J. S.

Jackson personal observations). Usurpation usually takes place early in the woodpecker reproductive cycle, often just as a cavity is being completed and before eggs are laid (Ingold 1989). The activity of excavation might alert starlings to the presence of the cavity and there are typically intervals with neither woodpecker at the cavity during a lull in excavation. Starlings tend to move in at such times and one member of the pair may remain in the cavity and strongly defend it (e.g. Howell 1943, J. A. Jackson personal observation).

The next best timing is after woodpecker egg-laying has begun, but before incubation has begun. Again, the starlings move in while the woodpeckers are away and then vigorously defend the cavity, usually with one starling inside. In such cases the eggs are removed and discarded or eaten by the starlings (Howell 1943, J. A. Jackson personal observation). The key is that a woodpecker cavity is most easily usurped if no woodpeckers are present when the starlings move in. Defending the cavity from the inside seems optimal. Once woodpecker incubation has begun, an adult woodpecker is much more likely to be present and therefore successful in defending the cavity. Woodpecker cavities are sometimes, but rarely, usurped when there are young in the nest. This may be due to a combination of timing relative to the starling's breeding cycle, the greater presence of the woodpeckers at the nest, and perhaps more intense nest defense by the woodpeckers as a result of their greater parental investment.

Lack of availability of suitable cavities is often mentioned as a stimulus for cavity usurpation efforts. Mazgajski (2000) conducted an experimental study in which he built up a nesting Common Starling population by providing nest boxes. After starling numbers had increased, Mazgajski reduced cavity availability by closing the nest boxes. Woodpeckers generally retained possession of their nest cavities – in spite of the increased starling population and decreased availability of cavities. He concluded (p. 105) "the starling, although a powerful competitor, is probably not able to influence the cavity nesting community to a great extent." Most of the woodpecker nests under study, however, already had nestlings, and that late stage of the nesting cycle of woodpeckers in the area might have influenced starling inability to usurp woodpecker cavities. This is a topic and an approach worthy of further study.

To follow, here are several facets of the process of Common Starling usurpation of a woodpecker cavity pieced together from our own observations and multiple studies by other authors of multiple woodpecker species across a broad range of habitats. Many of these facets are generalizations based on few observations. Only some are supported by experimental data.

(1) *Location and assessment of a potential nest cavity and somewhat benignly watching it.* – It seems likely that a woodpecker cavity is targeted for usurpation by Common Starlings as a result of (a) lack of other suitable cavities, (b) starling observations of the woodpecker excavation process, and (c) acceptability of the site to the starlings. It is critical for the starlings not to be aggressive towards the woodpecker until the cavity is completed. To be aggressive earlier might result in abandonment of cavity excavation. The starlings often perch nearby, merely watching as the excavation proceeds (Wood 1924, J. A. Jackson personal observations). Thus targeted, the initiation of more intense interactions with the woodpeckers usually begins after the cavity is completed.

(2) *Occupation of a cavity and construction of a nest*. – Once a cavity is completed, starlings visit it during a woodpecker absence. If encountered by the woodpeckers, a woodpecker usually will give chase. During a woodpecker absence, the starlings begin taking nest material into the cavity. One starling may remain within the cavity for long periods while the other gathers nest material. The starlings often retain possession from the advantage gained by being within the cavity. If the starlings leave and a woodpecker returns, the first order of business is for the woodpeckers to clean the cavity, dropping the starling nest material to the ground. During woodpecker absence, the starlings may begin the process of nest-building anew. This can be repeated multiple times, with neither starlings nor woodpeckers giving in. Although anthropomorphic, Kalmbach (1928) describes well how a human might perceive the starlings' behavior: "Unrelenting perseverance dominates the starlings activities… more battles won by dogged persistence… actuated more by the morbid pleasure of annoying its neighbors than by any necessity arising from a scarcity of nesting sites."

(3) *Outnumbering woodpeckers*. – Starling populations are much larger than woodpecker populations and interactions between starlings and woodpeckers at a cavity can attract additional starlings that may join in the effort for the same cavity and seem as if they are all working together to evict the woodpeckers (Turner 1908, Mathis 1975). Sutton (1967) killed 17 Starlings at a Red-bellied Woodpecker nest and 37 (including 22 males with enlarged testes) within 15 m of a flicker nest in Oklahoma; J. A. Jackson (personal observation) saw at least six starlings involved in usurping a Red-bellied Woodpecker cavity in Kansas.

(4) *Offensive and defensive physical aggression*. – Physical aggression during an effort by starlings to usurp a cavity can involve both members of a starling pair. Early efforts by starlings often involve chases and physical attack of a woodpecker at or near a nest (e.g. Allard 1940). If one of the starlings is within a cavity and the owner returns and enters, a noisy fight can take place within the cavity. Usually the intruder quickly emerges with the starling hanging onto it or in pursuit (e.g. Howell 1943, Ingold 1994). In such attacks Common Starlings have killed an adult flicker with a blow to the head (Shelley 1935, McAtee 1940, Sutton 1967).

(5) *Removal of eggs and young*. – If a cavity usurpation effort starts after woodpecker eggs have been laid, the starlings will enter the cavity during woodpecker absence and remove the eggs one at a time. If there are already woodpecker nestlings in the cavity, the starlings will remove them one at a time, sometimes killing them, sometimes merely dropping them out of the cavity (e.g. Shelley 1935, flickers; J. A. Jackson personal observation, Red-bellied Woodpeckers). Such efforts may extend to young in cavities that are too small to be entered by Common Starlings – such as those of Downy Woodpeckers with young that are old enough to come to the cavity entrance to beg (Howell 1943, J. A. Jackson personal observation).

(6) *Cavity entrance enlargement*. – While Common Starlings are not known for their ability to excavate, they will sometimes enlarge or attempt to enlarge a cavity entrance to make a small cavity accessible (Lawrence 1967).

(7) *Woodpecker usurpation of Common Starling nests*. – Woodpeckers also are sometimes successful in usurping an active Common Starling nest. A pair of Red-bellied

Woodpeckers approached a starling nest in Florida and the male entered and removed three naked nestlings, striking the head of each against the tree trunk before dropping it to the ground. He then began excavating inside the cavity (Baker & Payne 1993). In this instance, the original owners of the cavity were unknown (but might have been the same pair of Red-bellied Woodpeckers); no interaction was observed between the woodpeckers and the adult starlings.

Which woodpeckers are most-commonly targeted by Starlings?

The question posed by the heading of this section will be looked at from two different perspectives. (1) Which individual woodpeckers are most often targeted for cavity usurpation? And (2) which woodpecker species are most often targeted? We will look at both perspectives, because both have relevance to the future of species.

Woodpecker species that are most vulnerable to competition from woodpeckers are ones that excavate an appropriate-sized cavity in an appropriate site within foraging habitat that supports starlings, at a time that coincides with the beginning of the Common Starling nesting season. Woodpecker species for which active nest or roost cavities have been reported usurped by Common Starlings are those that nest within or near good foraging habitat frequented by starlings and that have a cavity entrance greater than about 4-cm diameter (see data in *Table 2*). Forbush (1915) suggested Common Starlings need an entrance diameter of 1.5 to 1.75 inches (3.81–4.45 cm); Zeleny (1969) suggested 1.5 inches (3.81 cm) – although both estimates were based on limited trials using birdhouses. Holes drilled in the boxes would be circular, with vertical and horizontal diameter equal. Many woodpecker cavity entrances are not circular, but have a larger vertical or horizontal diameter that might admit a starling in spite of a more limiting opposite diameter. Other factors that would or might increase their vulnerability include (1) low availability of potential starling nest sites, (2) a high starling population in the area, (3) woodpecker choice of a specific site for cavity excavation, (4) woodpeckers that had never before experienced starling competition, and (5) perhaps especially woodpeckers attempting to breed for the first time.

After more than a century of coexistence with starlings in North America, most reports of cavity usurpation involve the Northern Flicker and woodpeckers of the Genus *Melanerpes* (Red-bellied, Red-headed, Gila, Golden-fronted, Acorn, Lewis's Woodpeckers). The Northern Flicker was the first woodpecker reported to suffer from cavity usurpation by Common Starlings (e.g. Stone 1908, Kohler 1912, Taber 1921). Flickers forage extensively on ants in habitats that are bare to covered with very short vegetation – mostly less than 5–7 cm tall (Moore 1995, J. A. Jackson personal observation). Northern Flickers are much larger (ca 130 g) than starlings (ca 82 g), yet starlings often succeed in usurping flicker cavities. *Melanerpes* woodpeckers are similar in size (ca. 63–115 g) to the Common Starling, omnivorous, and live in somewhat open environments, often in habitats greatly altered and landscaped by humans.

To these we must add woodpecker species whose nest sites are only occasionally close to humans and starlings, and some whose cavity entrances are enlarged by other species, yet

remain in use by the original owner. For example, many Red-cockaded Woodpecker cavities are enlarged slightly by Red-bellied, Red-headed, or Hairy Woodpeckers or Northern Flickers. Since these cavities are in living trees, they may be used by Red-cockaded Woodpeckers or other species, including starlings, for many years.

Woodpecker species that are unlikely to have cavities successfully usurped by starlings are those with cavities that are usually too small for starlings to gain entrance. However, woodpeckers that excavate cavities with entrances normally too small for Common Starlings to enter (e.g. Downy and Nuttall's Woodpeckers, *Table 3*) sometimes suffer starling cavity usurpation attempts by starlings. Often they fail because the potential usurper can't get in (Lawrence 1967), but sometimes they succeed, such as after other woodpeckers enlarge their cavities.

The Yellow-bellied Sapsucker is a species whose decline has perhaps been mistakenly attributed to starlings. This species makes an exceptionally small entrance to its nest cavity *(Table 2)* – so small that it often has to forcibly squeeze through, sometimes losing feathers in the process (Lawrence 1967, Kilham 1977). It also typically nests in wooded areas – less open than areas usually frequented by Common Starlings. The mass of a Yellow-bellied Sapsucker is, at best, a little over half that of a Common Starling *(Table 3)*. Thus we believe that Yellow-bellied Sapsucker cavities are unsuitable for use by Common Starlings unless enlarged by a larger woodpecker, and we have found no documentation of successful usurpation of Yellow-bellied Sapsucker cavity by starlings. Lawrence (1967) did observe interference competition by starlings at a sapsucker nest cavity, but noted "What finally stopped the starlings was the size of the hole. It would yield neither to the starlings' energetic attempts at excavation nor to their efforts to squeeze their plump bodies through the aperture." Kilham (1971) considered the Common Starling "not a competitor" of Yellow-bellied Sapsuckers in New Hampshire. Walters *et al.* (2002a) do not mention Common Starlings as a cavity competitor of Yellow-bellied Sapsuckers.

Considering the normal nesting habitat of Yellow-bellied Sapsuckers and their small cavity entrances, we find it unlikely that they might be a species that is declining due to competition with Common Starlings. An alternative view was suggested as a result of an analysis of Christmas Bird Count data showing a decline in sapsucker numbers over the years (Koenig 2003). At the same time, North American Breeding Bird Survey data showed no significant decline.

Koenig (2003) lumped data for two western species, the Red-naped Sapsucker *(Sphyrapicus nuchalis)* and Red-breasted Sapsucker *(Sphyrapicus ruber)*, with data for the much more widespread Yellow-bellied Sapsucker – a closely related trio once treated as a single species. The two western forms may make slightly larger cavity entrances *(Table 2)* and may weigh slightly more than the Yellow-bellied Sapsucker – still about two-thirds the mass of a European Starling. Both western species also favor more wooded areas (Walters *et al.* 2002b). We have found no references to cavity competition with starlings for any of these species (see discussion of cavity competitors of these three species in Walters *et al.* 2002a, 2002b).

We suspect that the CBC data might reflect habitat losses on wintering grounds and differential migration of sexes associated with climate changes. In sum, analysis of these data sets is worthwhile, but interpretation of results of such analyses could better reflect the

nature of the data, the behavioral ecology of the sapsuckers, and changes that have taken place and are taking place in both nesting and wintering areas of the sapsuckers.

Impacts of Starling usurpation of woodpecker nests

The impacts of starling usurpation of a woodpecker nest cavity are probably not serious at the species level if adequate alternative cavities are available or if time remains and sites exist for woodpeckers to excavate another cavity (Brush 1983, Ingold & Densmore 1992). Even over the short term, however, we suspect that local population-level impacts occur. Certain and suggested impacts of woodpecker cavity usurpation or usurpation attempts by Common Starlings include the following:

(1) If a cavity is usurped, the woodpeckers' reproductive energy expenditure to that point is lost.

(2) Cavity usurpation may mean that the pair cannot reproduce that year.

(3) If the woodpeckers are able to excavate or acquire a new cavity and begin anew, it would require more energy expenditure and might reduce fecundity as a result of energy already lost.

(4) As the reproductive season progresses, available food often changes and may be less appropriate and or less abundant for feeding later nestlings.

(5) As the reproductive season progresses, weather patterns change. In some areas (e.g. south Florida) daily rain may increase stress and decrease feedings for nestlings. Alternatively, warmer temperatures later in the season may stress nestlings (Ingold 1989).

(6) During late season rains mosquito populations likely increase and the potential for transmission of mosquito-borne pathogens and parasites to bare-skinned nestlings is increased.

(7) Reduced nestling or fledgling survival – even if the renesting effort is successful – over the long term, could mean increased isolation of populations and less dispersal among populations. With continuation of such a trajectory, there could be an increased risk of species extinction.

(8) On the positive side, excavation of a new cavity after successful cavity usurpation adds an additional cavity to the cavity resource pool for future reproduction of the woodpeckers and other cavity nesters.

Coincidence of starling and woodpecker breeding cycles is very important and influences which species of woodpeckers might be more vulnerable to cavity usurpation. Ingold and Densmore (1992) demonstrated that in Ohio, the coincidence in timing of Common Starling and Red-bellied Woodpecker nesting cycles, along with weaker cavity defense by Red-bellied Woodpeckers, results in a high incidence of Red-bellied Woodpecker cavity usurpation in suburban habitats. The high incidence of Red-bellied Woodpecker cavity usurpation by starlings may in time drive Red-bellied Woodpeckers to become more aggressive in cavity defense, to nest later, or to limit their nesting to more closed-canopy forest. Among the impacts of nesting later, however, might be a reduced food supply for nestlings and increased competition with Red-headed Woodpeckers (Jackson 1976).

Later nesting of Northern Flickers and Red-headed Woodpeckers and stronger cavity defense result in a lesser incidence of cavity usurpation in those woodpeckers, but cavity usurpation and energy expended in cavity defense might also, over the long term, result in a shift in their nesting phenology and habitat parameters. Giese and Cuthbert (2003) found a high incidence of Red-headed Woodpecker nests in closed-canopy oak forest in Minnesota and suggested that a combination of loss of snags in more open areas and competition from starlings may have "forced" them into a habitat where they would have to compete with more woodpecker species and with Southern Flying Squirrels *(Glaucomys volans)*. Clearly cavity nesters of many taxa are as pawns on a very dynamic chessboard of habitats – each move impacts the status of all of the other cavity nesters and the game may not be over for many lifetimes of competition.

We concur with Koenig (2003) that most woodpecker species are "holding their own" against cavity competition with Common Starlings. The level of impact on woodpeckers is less than sometimes perceived only because most woodpeckers are intimately linked with forest habitats and Common Starlings favor open habitats where humans are more likely to observe the competition. There are, however some woodpecker species that could be vulnerable to extinction as a result of cavity usurpation by starlings.

The woodpecker species most vulnerable to extinction associated with competition from Common Starlings have: (1) small populations, (2) a geographically limited range with no place to which their species can escape environmental change, (3) little time to adapt as a result of population and geographic limitations, (4) a narrow foraging niche and (4) narrow habitat preferences that favor habitats that economically-motivated humans consider "less desirable". Even among species already in danger of extinction, there are some species more vulnerable to starling competition than others: those species that share favored habitats with starlings, are similar in size to a starling, and excavate cavities with an entrance large enough to admit a starling, but small enough to exclude most predators and buffer the occupant from inclement weather.

Among the most starling-vulnerable endangered woodpeckers are island species such as the Fernandina's Flicker of Cuba – a species that does not yet encounter competition from starlings, but one that is endangered and has a very small and fragmented population of perhaps 600–800 individuals (BirdLife International 2016a). The history of starling usurpation of flicker cavities in North America suggests that the addition of competition from starlings to the Fernandina's Flicker's tenuous existence could be disastrous.

The Common Starling is a vagrant in Cuba with three reports at two locations along Cuba's north coast, suggesting that they might have come from North America. One report was from Havana, 171 km from Key West, and the other from Gibara in Holguin Province, 662 km from Miami (Garrido & Kirkconnell 2000). There are two small populations of Fernandina's Flickers in Holguin Province (Mitchell *et al.* 2000). While the starling has nested in north Florida since the 1920s, its breeding range did not extend south to central Florida until the 1950s. It has since expanded its breeding range south to Miami and the Florida Keys, where it now nests all the way to Key West (Stevenson & Anderson 1994). Starling populations continue to grow in south Florida.

Starlings might also have come to Cuba from the south, from Jamaica (766 km to Havana, 355 km to Gibara), where starlings were introduced about 1904 (Graves 2014). Considering the propensity for starlings to move in flocks, the frequency of hurricanes in the region, and the potential for them to be carried by hurricane winds (Jeffrey-Smith 1972, Wiley & Wunderle 1993), it seems inevitable that a breeding population of Common Starlings will eventually be established in Cuba. Such could be very bad for Fernandina's Flicker whose palm savanna/pasture habitats seem perfect for starlings. With renewed socio-economic ties between the United States and Cuba we could see further degradation of the habitats of Fernandina's Flicker as a result of the introduction of more mechanized agricultural practices. This could further stress this species' populations while creating more favorable conditions for starlings.

We considered the vulnerability of other endemic West Indian woodpeckers to potential cavity competition from Common Starlings, but no other woodpecker species in the West Indies appears likely to be threatened with extinction as a result of starling competition – under current conditions. South of the Bahamas, in the West Indies starlings have an established breeding population only on Jamaica, and it has now co-existed with the Jamaican Woodpecker for a little over a hundred years. Cruz (1977) described these woodpeckers as competing with starlings, but apparently not to a serious extent. He had one instance in which starlings and woodpeckers simultaneously nested in different holes in the same limb. Gosse (1847) described the Jamaican Woodpecker more than 50 years before the starling was introduced as "among the commonest of Jamaican birds, being abundant in all situations, from the shores to the summits of the mountains." Haynes *et al.* (1989), in a review of conservation trends and threats to Jamaica's endemic birds, noted that the Jamaican Woodpecker seemed to be holding its populations at constant levels, although they noted competition between these woodpeckers and Common Starlings. They also noted that the biggest problem their endemic birds faced was loss of habitat. Raffaele *et al.* (1998), nearly a hundred years after the introduction of the starling to Jamaica, noted that the Jamaican Woodpecker remains "widespread and common at all elevations… from coastal coconut groves to forested mountain summits."

Why have Jamaican Woodpeckers been so successful in the face of starling competition? We believe their success in coexisting with starlings (thus far) is because they are the only resident woodpecker on the island and as a result, are consummate generalists with very broad foraging and nesting habitat niches, having had no need to narrow their niches in response to competition from other woodpeckers. The Jamaican Woodpecker has a more diverse foraging niche than any of the seven woodpecker species occurring in Florida and defends small territories, thus allowing a high population density (Cruz 1977). Following their introduction near Annotto Bay, starlings established a population in St. Ann Parish, about 40–48 km inland in an area with extensive pasture land. Starlings do compete with the Jamaican Woodpecker for cavities and Jeffrey-Smith (1972) ominously noted that they "oust original owners from their homes. The woodpeckers at Huntley, St. Ann, have been well-nigh exterminated by the starlings."

By the early 1950s they seemed to have moved only another 48 km (Taylor 1953, Jeffrey-Smith 1972). Such a lag time between the introduction of a species and build-up and

expansion of the range of its new population is typical. It may be many more decades before we begin to see the full impacts of starlings on the Jamaican Woodpecker and the rest of the local avifauna – by which time it may be too late.

Two other West Indian endemic woodpeckers, the Puerto Rican Woodpecker *(Melanerpes portoricensis)* and the Hispaniolan Woodpecker *(Melanerpes striatus)* are also very social with very broad foraging and nesting habitat niches. The Puerto Rican Woodpecker is also the only resident woodpecker on the islands of Puerto Rico and Vieques (Raffaele *et al.* 1998); the Hispaniolan Woodpecker coexists on Hispaniola with the tiny Antillean Piculet *(Nesoctites micromegas)*, thus neither has "real" woodpecker competition for resources (Short 1974, Raffaele *et al.* 1998). Starlings have recently been reported from Puerto Rico, and may be getting established there. We suspect, in view of our knowledge of the Jamaican Woodpecker and the broad niches and social behavior of the Hispaniolan and Puerto Rican Woodpeckers, coupled with the size of their islands, that these species will probably compete effectively with starlings although the long-term impacts of starling competition are more difficult to assess.

The Guadeloupe Woodpecker *(Melanerpes herminieri)*, endemic on Guadeloupe is a common species that is omnivorous, shy and not social (Villard 1999). It occurs from sea level to high elevations and in all forest types on the island, thus seems to have broad foraging and nesting habitat niches. These apparently broad niches could help at least some populations to evade competition were starlings to be introduced or immigrate to the island. However, Villard (1999) suggests that competition for nest sites with other species could negatively impact the Guadeloupe Woodpecker's population dynamics. Guadeloupe is 1596 km from the starling population on Jamaica, but only 578 km from Puerto Rico. Guadeloupe is a much smaller island (1,510 km^2) compared to Hispaniola (76,192 km^2) or Puerto Rico (9,104 km^2), thus the total population of the species is very limited and any threat to the Guadeloupe Woodpecker could be serious.

Woodpeckers, starlings, humans, and a chaotic web of interactions and impacts

Starlings, woodpeckers and humans have a long and complex history with one another as well with physical and other biotic components within and among their ecosystems. To follow are four case histories that relate in different ways to competition or potential competition between woodpeckers and Common Starlings. Some of these woodpeckers are endangered or declining, others are expanding their range. The role of starlings in each case may be more complicated than thus far suggested, resulting in an interpretation that may be flawed as a result of lack of consideration of past history and/or additional factors.

(1) *The endangered Red-cockaded Woodpecker.* – Some woodpeckers have suffered serious losses as a result of modern industrial forestry practices that eliminate tree species and tree age diversity, old growth trees in general, and the fertile milieu of standing and fallen dead wood. These forestry practices, the need for frequent fire in its natural ecosystem, and the conversion of forest habitats to non-forest habitats are clearly the

greatest problems facing the Red-cockaded Woodpecker, an old-growth southern pine forest species. Yet some Red-cockaded Woodpeckers have survived in pine areas within and adjacent to towns, cities and suburban areas at Southern Pines, North Carolina; Aiken and Myrtle Beach, South Carolina; and at Columbus and Fort Benning, Georgia (Dennis 1971, Carter & Kocher 1995, J. A. and B. J. S. Jackson personal observations). These habitats provide diversity and essential old growth for the woodpeckers, although in relatively small patches and generally with little accumulation of dead wood due to human "manicuring" of the landscape. The openness, mowed lawns, and largess of human-supplied foods also make these areas favored habitats of Common Starlings. In each area starlings have usurped Red-cockaded Woodpecker cavities that have been enlarged by Red-bellied or Red-headed Woodpeckers and can be expected to similarly affect other woodpeckers in suburban and exurban settings elsewhere. As a result of Common Starling populations, without intensive management – and perhaps with it – such areas may become ecological sinks for the Red-cockaded Woodpecker rather than the haven that is sometimes suggested (Carter & Kocher 1995).

(2) *The endangered White-backed Woodpecker.* – The White-backed Woodpecker *(Dendrocopos leucotos)* is an example of a species not known to be impacted by starlings, but anthropogenic factors could change that. This woodpecker is resident over a broad range of latitude extending north into the taiga from Great Britain on the west to Japan and Kamchatka in Russia on the east and has been considered an umbrella species for boreal and hemiboreal forests (Roberge *et al.* 2008). It has suffered recent declines through much of its range, especially in the north, and is considered endangered in several areas (Czeszczewik & Walankiewicz 2006). As with the Red-cockaded Woodpecker, the proximate causes of these declines are clearly loss and fragmentation of its old-growth forest habitat (Aulen 1986), and conversion of forest habitat to agricultural and other uses. As its habitats are diminished, the White-backed Woodpecker might well face yet another problem – usurpation of its cavities by Common Starlings. In Russia, the Purple-backed Starling *(Sturnia sturnina)* is known to use the cavities of White-backed Woodpeckers (Feare & Craig 1999), although cavity usurpation of active White-backed Woodpecker cavities apparently has not been documented.

With a body mass slightly larger than that of a Common Starling (Aulen 1986), the White-backed Woodpecker, an old-growth deciduous forest species, produces an appropriate-sized cavity for the starling. We found no mention of Common Starling use of White-backed Woodpecker cavities, likely a consequence of their favoring extensive forested areas. However, marginal habitats, such as forests that are fragmented and opened up, could create open areas with good foraging for starlings – sites more vulnerable to nest-site competition.

The White-backed Woodpecker's larger size may facilitate its cavity defense, but that is not certain. Common Starlings often succeed in usurping cavities of the Northern Flicker, a species that can be double the mass of a starling *(Table 3)*. Even if the White-backed Woodpecker were successful in competition with Common Starlings, the energy expenditure associated with defense would be a negative contributing to the impacts of habitat and food-base losses.

Mikusinski *et al.* (2003) and Stighäll (2015) note that in Sweden, where deciduous forests have been replaced by conifer monocultures, deciduous trees that come back in old fields or that are used in landscaping near and within villages might provide small refuges for deciduous forest species. Such areas may be too small for the White-backed Woodpecker to survive in, and the mowed lawns and human-provided food resources of nearby villages would be favored by starlings. Perhaps such areas could provide a splinter of hope for the White-backed Woodpecker if linked to well-planned and executed species and ecosystem monitoring programs, efforts to minimize cavity competitors such as the starling, much broader corridors of mixed species, and mixed age forests that are allowed to restore old growth and the elixir of dead wood to the ecosystem.

(3) *Range expansion of Syrian and Red-bellied Woodpeckers.* – Both the Syrian Woodpecker *(Dendrocopos syriacus)* in the Middle East and the Red-bellied Woodpecker in eastern North America are frequent targets of cavity usurpation by Common Starlings. Each of these woodpecker species is a generalist compatible with living in association with humans, and each has been expanding its range – potentially for the same reasons. Both have been expanding into suburban and urban areas with well-established concentrations of trees. Ciach and Fröhlich (2013) found high pollution emissions where Syrian Woodpecker numbers were greatest, and our examination of range expansion records for the Red-bellied Woodpecker (e.g. Jackson & Davis 1998) suggests they also moved into polluted urban areas. Ciach and Fröhlich hypothesize that the higher pollution levels weaken trees, making them more subject to insect and fungal attack, thus increasing woodpecker food supplies and the potential for woodpecker cavity excavation. While pollution levels could be involved, we feel a more likely factor for the expansion of both woodpecker species might be maturation of trees planted as new areas were developed in the early- to mid-20th century combined with increased development of greenbelts and parks.

Range expansion is often viewed as an indicator of a successful species whose populations are growing. Changing habitats as a result of growth of human populations, irrigation, landscaping changes, increasingly connected corridors of suitable habitats and food supplies along highways are also likely involved as facilitators of range expansion of both some woodpeckers and starlings. Generalist species are best able to adapt to these types of evolving habitats.

(4) *The causes of declines of the Red-headed Woodpecker and Northern Flicker.* – The Red-headed Woodpecker and Northern Flicker have both experienced declines in recent decades and studies have suggested that both are suffering from loss of habitat and from cavity usurpation by starlings. We agree with this assessment, but feel that the roles of the Common Starling in these cases are over-stated and misunderstood as a result of lack of consideration of past history and other factors.

The Red-headed Woodpecker is about the same size as the Common Starling *(Table 2)* and excavates nest and roost cavities with an entrance diameter that is well suited for starlings. Starlings usurp active Red-headed Woodpecker nest and roost cavities, but these woodpeckers typically begin nesting later than starlings and vigorously – and usually successfully – defend their cavities against starlings.

In recent decades, Red-headed Woodpecker populations have declined over much of their range. Frei *et al.* (2013) refer to this woodpecker's nesting habitat as a "maladaptive choice" and attribute the decline in its populations to competition for nest sites with Common Starlings, cutting of snags potentially useful for cavity excavation, and potential poisoning from pesticides. We agree that each of these problems likely influences Red-headed Woodpecker population dynamics. However, before introduced Common Starlings had colonized areas outside of the metropolitan New York area, Butler (1897) described dramatic population fluctuations of Red-headed Woodpeckers in Indiana, noting great increases in their numbers when flooding, insect pests, or other calamities killed many trees, opening up habitats and providing both nest and feeding sites. These population surges were followed by great decreases when the dead trees were surrounded by regrowth of vegetation and then rotted and fell. The current decline of Red-headed Woodpeckers may be the result of such a widespread calamity that created an abundance of suitable nest sites and a substantially increased woodpecker population, now followed by woodpecker declines as the largesse of the calamity disappeared.

A massive die-off of American elms *(Ulmus americana)* occurred throughout eastern North America following the introduction in 1930 of Dutch elm disease *(Ophiostoma ulmi)* and the European Bark Beetle *(Scolytus multistriatus)* that greatly facilitated its spread (Kilham 1973, Karnosky 1979). Death of elms created nesting habitat for woodpeckers and stimulated increases in woodpecker populations as the disease spread (Kilham 1973, Graber *et al.* 1977). By 1959, it was estimated that Illinois had lost 95% of its elms (George 1979). In the late 1960s Jackson (1976) found that nearly 50% of the nests of Red-headed and Red-bellied Woodpeckers he studied in eastern Kansas were in dead American elms. Thus, the populations of Red-headed Woodpeckers in the mid-20th century were likely "temporarily" high and the resulting increase in abundance of cavities likely also facilitated growth in Common Starling populations. A decline in woodpecker numbers could have been expected as the course of the disease passed and the dead trees fell. A similar Dutch elm disease catastrophe occurred in Britain and Europe (e.g. Osborne 1982) in the early to mid-20th century and may also have resulted in woodpecker and starling range expansions and population increases similarly followed by range contractions and population declines.

Other factors that came into play in both North America and Europe were the proliferation of automobiles along with subsequent increases in speed at which they travel, and a great increase in numbers of roads. It is likely that there would have been concomitant increases in mortality of Red-headed Woodpeckers because they had adapted to perch on fence posts, utility poles and trees along roads and fly to the road to take insects blown from roadside weeds or hit by cars or to consume bits of food tossed from cars (Stoner 1925, Linsdale 1929, Jackson 2003b). The more open habitat associated with roads was also favorable for an increase in Common Starling populations – and yes, with the advent of the automobile early in the history of starlings in North America, they became frequent road casualties (Bishop & Brogan 2013).

Northern Flickers also commonly used dead American elms as nest and roost sites in open areas of eastern North America. Breeding bird surveys suggest that Northern Flicker populations (in eastern North America) decreased by 52% between 1966 and 1991 and Moore

(1995) suggests the declines are a result of habitat loss and competition with Common Starlings for nest cavities. We believe the causes of the decline, again, include those factors, but that the authors ignored an artificially high flicker population during the Dutch elm disease die-off and the impact from loss of those nest sites as the trees decayed or were cut.

While Northern Flicker cavities may be the most readily available cavities within prime Common Starling habitat, they may not be the optimum cavities because a flicker's cavity entrance is much larger than needed by a starling. Indeed, in the open desert southwest where both the Gila Woodpecker *(Melanerpes uropygialis)* and Northern Flicker are frequent, Common Starlings readily use the smaller Gila Woodpecker cavities, but rarely the flicker cavities, supporting the notion that the starlings prefer a smaller entrance (Kerpez & Smith 1990). As with the Red-headed Woodpecker and the Common Starling, Northern Flickers also suffer from road mortality (e.g. Stoner 1925, Bishop & Brogan 2013).

Interactions with humans, starlings and woodpeckers can sometimes result in maladaptive behavior, especially when there is limited cavity availability. For example, Jackson (2000) observed a starling repeatedly deposit recently cut grass stems into an opening in the tail of a commercial aircraft after it had been taxied into position to load passengers. Flickers sometimes show resourcefulness in the face of treeless habitats, such as excavating cavities in wood or foam siding on buildings. It was a Northern Flicker (captured on video) that excavated over 200 holes in the rust-colored, foam-like insulation on the external fuel tank of the Space Shuttle Discovery in 1995. None of the cavities could be completed because at a certain depth, the woodpecker encountered metal – so it had to back out and start over. Hundreds of Common Starlings were also present in the area with flocks of up to about 80 perching on the gantry with the space shuttle being prepared for launch. We also found a flicker cavity that had been excavated into foil-covered insulation around a large diameter pipe that was perhaps two-feet above the ground that apparently carried fuel to the Space Shuttle. A starling investigating that hole drew our attention to it. We assisted with developing a way to prevent future damage to shuttles. The answer was simple. NASA had cleared all trees from the area and was maintaining grass trimmed to less than about 5 cm tall in order to prevent a wildfire during a launch. Activity in the area assured that there were many bare areas. NASA had created and was maintaining perfect foraging habitat for both the starlings and the flickers. Our recommendation was to let the grass grow to a height that would deter ground feeding by the birds (Jackson 1997, 2002). Solving a problem with a species – whether one caused by the species or one that is causing a species to be on the path to extinction – first requires an understanding of the species role in its ecosystem, its relationship to the physical environment and the species with which it lives.

Other cavity-nesting Starlings that may threaten woodpecker populations

Other cavity-nesting starling species are also on the move, expanding into human-dominated habitats in several areas – and providing new competition for woodpeckers and other cavity-nesting species in those areas.

The Crested Myna *(Acridotheres cristatellus)* has been breeding in La Plata, Argentina, since the 1980s and its population is growing. It has been reported using abandoned cavities of the Green-barred Woodpecker *(Colaptes melanochoros)* (Navas 2002). The Crested Myna was also introduced to the Vancouver, British Columbia area of Canada sometime in the late 1890s (Brooks & Swarth 1925). Its populations began growing and most of its nest sites were in the cavities of Northern Flickers or other woodpeckers (Scheffer & Cottam 1935). Some cavities had likely been abandoned by the woodpeckers, but others were actively usurped. The populations grew and spread, but only in the Vancouver area – and then they began to decline (Johnson & Campbell 1995). The last two Crested Mynas in Vancouver died in about 2003 (Self 2003, Simberloff & Gibbons 2004) and the species was removed from the American Ornithologists' Union Checklist of North American Birds (Banks *et al.* 2005).

The manner of woodpecker cavity usurpation by Crested Mynas was clearly described by Scheffer and Cottam (1935) and seems to also reflect the approach taken by Common Starlings:

> "In conflict with the flicker, the myna shows tact and persistence. If a new home of the former is under construction in a tree stub, the mynas …wait patiently for its completion…. When … ready for use, several pairs of the intruders may contest for its possession…. The result is … eviction of the woodpecker tenants."

The Common Myna *(Acridotheres tristis)* is today spreading through the Middle East and aggression between it and Syrian Woodpeckers has been observed at nest cavities (Holzapfel *et al*. 2006); however, in Israel the Common Myna also evicts Vinous-breasted Starlings *(Sturnus burmannicus)*, which compete directly for Syrian Woodpecker cavities (Orchan *et al*. 2013). The Common Myna was also introduced (probably through the pet trade) in southern California and Florida. It has nested in California (Willet 1930), but Choi *et al*. (2011) found no recent evidence of them. The Common Myna did become established in south Florida where its populations are growing, but interactions with woodpeckers have not yet been reported (Pranty 2007). All Common Myna nests we have thus far observed in Florida (around 15) have been in or behind large signs on or near buildings in urban and suburban areas. Common Mynas are using sites more commonly occupied here by introduced House Sparrows *(Passer domesticus)* and Common Starlings.

Common Myna, Bank Myna *(A. ginginianus)*, Jungle Myna *(A. fuscus)*, Crested Myna and the introduced Pied Starling *(Sturnus contra)* are now breeding in Japan (Eguchi & Amano 2004). The Pied Starling and the first three species of Mynas still have limited and primarily urban populations. The Crested Myna is widespread and locally common. Eguchi and Amano (2004) had observed no instances of cavity usurpation by any of the Myna species, noting however, that at the time, the Mynas remained primarily in urban areas. If habitats continue to be altered by forest fragmentation or change in land use in the region of the critically endangered (fewer than 600 individuals) Okinawa Woodpecker *(Dendrocopos noguchii)* (BirdLife International 2016b), there is potential that one or more myna or starling species could become established and become a serious additional threat to that woodpecker. Kotaka and Matsuoka (2002) have observed active nest cavities of Great-spotted Woodpecker usurped by the Chestnut-cheeked Starling *(Sturnus philippensis)*.

Discussion

As primary cavity nesters, woodpeckers face many challenges in the modern world – mostly at the hands of humans. These include the introduction of exotic species that are competitors or predators such as the Common Starling. While a significant problem, far more important to most woodpecker species is clearing and fragmentation of forests, conversion of natural forests to monocultures of economically important tree species, short-rotation forestry that harvests trees at their prime economic value, restriction of fire where fire is essential, the use of prescribed burns at times other than when natural fires would have occurred, and removal of dead wood from parks, fence rows and residential areas.

As these habitat changes have progressed, the Common Starling has prospered – both in its native land and where it has been introduced because it is a generalist that favors the open, low-grass areas associated with human disturbances associated with the clearing of forest lands, growth of our crops, grazing of livestock, and construction of our towns and cities. As we have expanded our range and numbers, so has this starling.

As a secondary cavity nester, Common Starlings are known for their aggressiveness and success in usurping cavities from woodpeckers and other species. Observations of their aggression and persistence have led some to predict endangerment or extinction of species as a consequence of cavity usurpation. The impact of Common Starlings on most woodpecker species seems not so dire. The Common Starling may be successful within the parameters of its favored habitat, but it is also very selective of nest sites, favoring high cavities near good foraging habitat, with a favored narrow range of other cavity and cavity-site parameters and a relatively narrow window of time in which it is most successful. These limitations, while evolutionarily malleable, are countered in many cases by ecological plasticity that allows other species to adapt to the starling invasion of altered ecosystems (Aitken & Martin 2008).

Each woodpecker species has its own adaptive range for habitats and nest sites. Some such as the White-backed Woodpecker and the Red-cockaded Woodpecker have little or no overlap with the Common Starling – at the present. Other, more generalist woodpeckers such as the Great-spotted Woodpecker and the Red-bellied Woodpecker overlap the habitat niche and the nesting phenology of the Common Starling – especially in urban, suburban and exurban areas. In those areas the woodpeckers suffer frequent cavity usurpation. However, these woodpeckers also have broad areas of habitat non-overlap, thus limiting starling impacts on the species. Species such as the Eurasian Green Woodpecker, Northern Flicker and Red-headed and Lewis's Woodpeckers *(Melanerpes lewis)* are ground- or aerial-feeding, open habitat specialists whose habitat niches broadly overlap that of the Common Starling. These might be considered the most vulnerable of species, yet within this group we find the strongest cavity-defense behavior among the woodpeckers and some evidence of changes in nesting phenology that perhaps reduce cavity usurpation.

The evolutionary "apple cart" has been violently and rapidly upset during the last two centuries and many of the "fruits" of natural ecosystems that have developed over millennia have been bruised – some so badly that they might not be salvageable. Others we can "clean-up" – but it doesn't mean they aren't bruised. A species' presence in a severely altered ecosystem doesn't mean it favors the altered ecosystem. It may simply mean that it has

nowhere else to go and in time it will disappear like rotted fruit left behind. The "decay" and loss of species due to ecosystem changes may take decades, even centuries, but may nonetheless be final.

Perhaps the best insight relative to the impacts of competition for cavities between woodpeckers and starlings will come from careful monitoring of both starling and woodpecker species with an understanding of their ecological needs and changes that have occurred and are occurring to their ecosystems. Following recognition of recent declines in some Common Starling populations, Smith (2005) has taken a broad view with data that suggest Great-spotted Woodpecker populations are rebounding as the starling populations decline. He suggests that interference competition at the nest site may have been reducing woodpecker nesting success even if the starlings were unsuccessful in usurping cavities. Another suggested result of declines in starling populations in Europe and Great Britain is the recent establishment of the Great-spotted Woodpecker as a breeding bird in Ireland (McComb *et al.* 2010, Pocock 2015). DNA analyses suggest the Irish woodpeckers had come from Great Britain, where Great-spotted Woodpeckers have been increasing in numbers (McDevitt *et al.* 2011).

Ónodi and Csörgő (2013) were able to capture another essence of change relative to Great-spotted Woodpeckers by using aerial photos and on-site measurements of vegetation to evaluate the habitat in which 1411 Great-spotted Woodpeckers had been captured for banding over 27 years. As the vegetation became increasingly dense, more woodpeckers were captured – thus it seems that as the habitat became less favorable to starlings, it was becoming more favorable to Great-spotted Woodpeckers. As a result of decreased visibility due to increased vegetation density, using only a visual census of the woodpeckers may not have revealed their numbers. The authors identified several other factors that might have influenced the results (e.g. single dead or larger trees, a localized abundant food resource). Mazgajski and Rejt (2006) provide excellent related discussion from a different perspective – that of the potential cascading impacts of habitat fragmentation on Great-spotted Woodpeckers.

In Hungary, in recent years census data suggest that Common Starling populations have remained large and apparently stable and Great-spotted Woodpecker populations have had a moderate increase (Szép *et al.* 2012). There, as well as in North America, starlings are most abundant in open agricultural areas, next most abundant in urban areas, and least abundant in heavily forested areas. How do changes in habitats in Hungary compare to changes in areas where starlings are declining and Great-spotted Woodpeckers are increasing?

Away from urban, suburban and exurban areas, we are negatively impacting many more woodpecker species, but often don't clearly see the changes we have wrought. We have redesigned and redefined "forest" in many ways. We have set new benchmarks for what constitutes a forest, what constitutes old growth, and even what constitutes a "healthy" forest. Our new benchmarks are in part ones defined by human needs and in part a reflection of what we see today. Today a 60-year-old, even-aged, monoculture of longleaf pine *(Pinus palustris)*, a North American species with a natural potential longevity of nearly 500 years, is regularly called "old-growth." We have forgotten the past, ignored interconnections within, between and among species and ecosystems and we focus on short-term economic goals.

It is not merely loss of naturally forested area that has resulted in declines in woodpecker (and other species), but also changes that have been exacerbated by our manipulation of forests. Ultimately, we are to blame for the ecosystem changes that have led to declines of some species, excessive successes of others, and in some cases extinction. We, as a species, introduced Common Starlings to North America and elsewhere. We invented automobiles and chainsaws and fragmented habitats that opened forests and provided avenues for expansion of non-forest species like this starling and barriers to forest species. We can't ship starlings back to their "homeland" or do away with our cultural infrastructure. But we can do a much better job of maintaining biodiversity by fostering an understanding of ecosystem structure and function and the supporting roles that each species plays in the stability of ecosystems.

From a management perspective, the focus of much conservation effort is on target – maintain the various components of diversity within ecosystems, and understand the complexity of interactions among components. Mimic the efficiency of nature, not the efficiency of factory assembly lines. Understanding why some woodpecker species are declining requires that we "see" the whole forest as it once was, not merely the trees and the avifauna as they are today.

The trees in parks, greenbelts and neighborhoods of our cities and towns have grown with the cities and now often provide more old growth than can be found in areas away from them. But humans have a penchant for removing dead trees and dead limbs and for using pesticides to "control" insects, while at the same time creating vast areas of close-mowed grass and landscaping with exotic plants of little ecological value for native birds. Starlings find food in dumpsters and weedy edges, and nest sites in ramshackle structures as well as in natural and woodpecker cavities. They may make these "substitute habitats" ecological sinks for some species in the long term, although over the short term, for some, they may be refugia. If we continue with the current path of forest monoculture and short rotations, only the generalists among woodpeckers can survive, but even for them, such areas can become an ecological sink when highly competitive starlings are added to the mix. Morrison and Chapman (2005) censused woodpeckers during the summer months at six urban "parks" in Connecticut and concluded that they provided for most of the woodpecker species in the region, with increasing woodpecker diversity in larger tracts of woodland. However, they did not look at woodpecker nesting success and their monthly census counts were averaged over the three month period such that some counts would likely have included fledglings, with early nesting species having fledglings potentially counted in all three months, but later nesting birds with fledglings counted in only one or two months. The study was a worthy effort that deserves to be replicated there and elsewhere – but to also consider nesting success, timing of fledging, tallies of adult and juvenile woodpeckers, and also of Common Starlings. Only with a more holistic approach can we truly begin to understand the broader implications of parks as refugia – or as ecological sinks – for woodpeckers and other wildlife.

Angelstam *et al.* (2011) reviewed forest management needs for conservation, and the development and implementation of policies to assure a continued presence of forest biodiversity – including habitats with the presence of starlings and habitats where starlings normally don't venture. They noted that it is difficult to reach consensus on needs. The development of policies that will promote a continued presence of forest biodiversity is a slow process

that must be based on understanding of the complexity and dynamics of ecosystems. Implementation of those polices is even slower. Mandated actions get results; voluntary actions get only some results. How important is it that we maintain biodiversity on this planet?

Much of what we know about the interrelationships of starlings and woodpeckers has come from incidental observations rather than from in-depth study of the birds and the problems. Such observations are important. They provide documentation of interactions that might stimulate in-depth study; they raise the questions and often offer interpretive suggestions that get us interested in the problems. Such casual observations are often made where humans live and work – largely in open habitats that are optimal for Common Starlings and less than optimal for most woodpeckers – thus there is an inherent bias that we must be wary of.

The bottom line that links all of the perceived problems is us: *Homo sapiens*. We introduced Common Starlings around the world at a time when birds were recognized as primary agents of pest control and little thought was given to the concept of problems being caused by invasiveness of species when introduced to new environments. At the same time we became so much more efficient at exploiting natural resources. Cities and towns and connecting transportation systems grew and natural forests disappeared, were fragmented, or converted to even-aged crops of single species that are now harvested when of greatest short-term economic benefit – with little consideration of ecosystem stability or the conservation of biodiversity. Starlings are not so much the aggressive competitors that have conquered populations of other cavity nesters. It is just that humans have altered natural habitats in ways that are more optimal for starlings and less than optimal for many of the species with which they compete.

Many studies are merely "snapshots" in time, with little consideration of events and changes that occurred earlier or of changes that might have been triggered that will become evident only in the future. We tend to think of change on the scale of human lifetimes. Aldo Leopold's (1949) essay "Thinking Like a Mountain" tells us that we should learn to think "like a mountain" – on a much grander time scale – in order to fully understand how the images in our "snapshot" came to be and how they might become.

Acknowledgments

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The Middle-spotted Woodpecker *Leiopicus medius* in the Basque Country, Northern Spain: review of current ecological status

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José María Fernández-García 2016. The Middle-spotted Woodpecker *Leiopicus medius* in the Basque Country, Northern Spain: review of current ecological status. – Ornis Hungarica 24(1): 42–54.

Abstract Despite previous inventories and atlas of the avifauna in the Basque Country, Northern Spain, the dense population of the Middle-spotted Woodpecker *Leiopicus medius* in the Izki forest was not discovered until the 1990's. This population mainly occupies a 3,700 ha *Quercus pyrenaica* forest, showing an average density of 0.89 territories/10 ha. The occurrence and abundance of territories is positively associated to the density of large caducifolious *Quercus* trees (>35 cm diameter). While nesting trees are apparently easily available, large trees for foraging could be a more limiting resource, given the historical exploitation regime of the forest. There are several other massifs in the region with smaller populations, but the functional connectivity, demographic and dispersal dynamics relating the core Izki and the peripheral areas have not been investigated. The conservation relevance of the Izki population in the Spanish context is high and given the need to understand the effects of forest management, future research should include spatial ecology, breeding performance as well as population monitoring.

Keywords: Picidae, *Quercus pyrenaica*, forest, Iberian Peninsula, conservation

Összefoglalás A korábbi madárfaunisztikai felmérések és a Baszkföldről (Észak-Spanyolország) készült madártani atlasz ellenére csupán az 1990-es években írták le az Izki-i erdőben található, népes közép fakopáncs *(Leiopicus medius)* populációt. Ez a populáció egy 3700 hektáros, főleg pireneusi tölgyekből *(Quercus pyrenaica)* álló erdőben található, 0,89 territórium/ha sűrűséggel. A territóriumok megoszlása pozitív összefüggést mutat a vastag törzsű, lombhullató tölgyek (>35 cm átmérő) jelenlétével. Míg a fészkelésre alkalmas fák könnyen elérhetőek, addig a táplálkozásra szolgáló vastagabbak limitáló forrást jelenthetnek a sokéves erdőgazdálkodásnak tulajdoníthatóan. A térségben számos kisebb költőállomány is megtalálható, azonban az Izki-i populációval fennálló kapcsolatukat, demográfiai és terjedési dinamikájukat még nem vizsgálták. Az Izki-i populáció természetvédelmi jelentősége igen magas, és szükségessé teszi az erdőgazdálkodás hatásának feltérképezését. A jövőbeli kutatásoknak egyaránt tartalmaznia kell a faj ökológiájának, költésbiológiájának és populációdinamikájának felmérését.

Kulcsszavak: Picidae, pireneusi tölgy, erdőgazdálkodás, Ibériai-félsziget, természetvédelem

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Introduction

The Middle-spotted Woodpecker *Leiopicus medius* is nearly endemic in the Western Palearctic, from European Russia and the Caucasus, to France and the Iberian Peninsula (Gorman 2014). The nominate race is distributed across continental Europe, as the formerly described Iberian race *lilianae* is not currently recognized (Gorman 2004). This woodpecker is a resident of temperate forests, strongly preferring mature oak woodlands. It also inhabits mixed deciduous and riparian forests, parklands, wooded pastures and even beech stands, provided

the availability of standing large, decaying and rough-barked trees (Pasinelli 2003). The oak volume and the number of suitable trees for foraging (>35 cm girth) and nesting (>20 cm girth) have been related to patch occupancy, colonization and persistence. The overall long-term trend is declining, because the species is sensitive to the general fragmentation of the original lowland oak forests in Europe (Lammertink 2014). More recently, various trends and moderate increases have been reported for core Central European countries, and the conservation status proposed by the IUCN Red List is "least concern", both globally (BirdLife International 2012) and regionally in the European Union (BirdLife International 2015). In spite of this, small, isolated and peripheral populations face an increased risk of extinction (Pasinelli 2003).

Northern Spain holds the westernmost population of the species. It encompasses the main mountain ranges, namely the Cantabrians, the Basque and the Pyrenees. These form an 800 km long, W-E oriented corridor. Although traditionally exploited, degraded and reduced in their original surface, oak (*Quercus pyrenaica*, *Q. faginea*, *Q. robur* and *Q. petraea*) forests remain mainly at altitudes between 700 and 1300 m, with lowland forests showing a much more relict and patchy occurrence. Three separate populations of the Middle-spotted Woodpecker are known in Northern Spain. The Cantabrian is located in the provinces of Asturias, Cantabria, León and Palencia, and its extent of occurrence (*sensu* IUCN 2014) covers
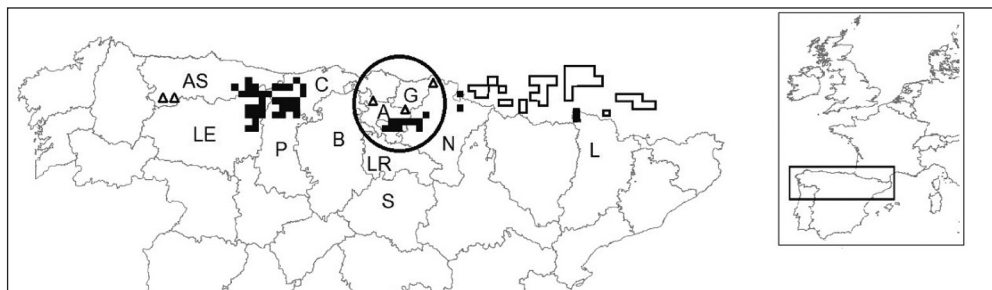
Figure 1. Current distribution of the Middle-spotted Woodpecker *Leiopicus medius* in Spain, during breeding period. Presence recorded in UTM 100 km² squares, updated from Onrubia *et al.* (2003). Black squares indicate confirmed presence; triangles, old, possible or unconfirmed presence. The area of the population in the Basque Country and neighbouring districts is circled. Borders of Spanish provinces are delineated. Those mentioned in the text are signaled: AS – Asturias, LE – León, P – Palencia, C – Cantabria, B – Burgos, A – Álava, G – Gipuzkoa, N – Navarre, LR – La Rioja, S – Soria and L – Lérida. The UTM 100 km² squares in the northern (French) section of the Pyrenees closer to the Spanish border, with confirmed presence during breeding periods 2009–2012 (Issa & Muller 2015), are also shown (empty squares)

1. ábra A közép fakopáncs *(Leiopicus medius)* jelenlegi spanyolországi költési elterjedése. Az előfordulás feltérképezése 100 km²-es UTM négyzetekben készült, Onrubia *et al.* (2003) nyomán. A fekete négyzetek jelentik a megerősített előkerülést, míg a háromszögek a lehetséges régi vagy nem megerősített előkerülést mutatják. A körön belül találhatóak a baszkföldi és az azt körülvevő populációk. A határvonalak a spanyol tartományokat jelölik. A szövegben említett és az ábrán jelölt tartományok a következők: AS – Asturias, LE – León, P – Palencia, C – Cantabria, B – Burgos, A – Álava, G – Gipuzkoa, N – Navarre, LR – La Rioja, S – Soria and L – Lérida. A Pireneusok Franciaország-felőli részére eső UTM négyzetek (közel a spanyol határhoz) a 2009–2012 közötti költési időszaki megkerülések adatait mutatják (üres négyzetek, Issa & Muller 2015)

around 35 squares of 100 km^2. A subpopulation in the western section of the Cantabrians has probably gone extinct in the last decade (Sánchez *et al*. 2009). As for the Pyrenees, two subpopulations are known from the provinces of Lérida and Navarre respectively, with a joint extent of occurrence of just 5 squares of 100 km^2 (Onrubia *et al.* 2003). In fact, these Pyrenean subpopulations are possibly connected to the population of the Northern (French) slope of the range, where the species is more widely distributed (Issa & Muller 2015).

Finally, the Basque population lays at an intermediate geographic position between the above mentioned, c. 125 km distant to the closest limits depicted for the Cantabrian and 60 km for the Pyrenean. It is found in the province of Álava and the adjacent fringes of Nararre and Burgos (González *et al*. 2006), and covers an extent of occurrence of 10 squares of 100 km^2 (Onrubia *et al*. 2003) *(Figure 1)*. This population is highly relevant from a conservation perspective. In the Spanish context, because it contains the densest population thriving in a continuous, unfragmented forest block (the Izki forest) and it holds at least one third of the country's numbers, even though figures available for the Cantabrian are partial and not completely comparable (García-Fernández *et al*. 2002, Robles & Olea 2003, Fernández & Lozano 2009, Fombellida *et al*. 2009); and globally, because populations at the edge of the distribution may represent local adaptations, distinct evolutionary potential and ability to persist under rapidly changing climatic scenarios (Hampe & Petit 2005, Fuller *et al*. 2011, Rehm *et al*. 2015). In this paper, I review and synthesize the discovery, inventory, research and current state of knowledge about this population.

Historical background and discovery

Apparently, there is no specifically attributable mention of the Middle-spotted Woodpecker in the classical Spanish literature (Bernis 1995). Popular, vernacular names have not been described either, the species presence being covered by the much more common and abundant Great-spotted Woodpecker *Dendrocopos major* (Bernis 1995, García-Fernández 2008) The scientific inventory of the avifauna in Spain is quite recent in historical terms, if compared to central and northern European countries. The first systematic approaches date back to the late 19th century, when the catalogues by Ventura Reyes and José Arévalo were published. Ornithological contributions at this stage were highly influenced by visiting naturalists and ornithologists, like Alfred Brehm, Howard Saunders and Howard Irby (Tellería 2004).

Reig (2004) and Salas *et al*. (2005) have compiled and reviewed critically the existing historical records on the occurrence of the Middle-spotted Woodpecker in the Iberian Peninsula. The reliable data – detailed observations or descriptions of museum specimens – are referred to the Catalan Pyrenees (1879, 1913) and the Cantabrians (1876, 1921), apart from northern Portugal (1896) and other Spanish regions where the records are considered doubtful (central Spain) or simply erroneous (southern Spain). Among historical authors, Witherby (1922) provided certain information on the Cantabrian population, and captured eight specimens, that based the already mentioned proposal of the subspecies *Dryobates medius lilianae*. The question whether the Middle-spotted Woodpecker had a wider distribution in the 19th century than today remains open, given the evidences from northern Portugal.

Regarding the Basque-Navarre mountain range, the Middle-spotted Woodpecker was not mentioned by foreign ornithologists visiting the region, although this part of the country did not attract as much interest as southern Spain. Saunders (1884), Chapman and Buck (1893), Gadow (1897), Blasius (1907) and Ticehurst and Whistler (1925) explored several forested areas, especially in Navarre, but found no record on this species, unlike other less cryptic woodpeckers (e.g. Black Woodpecker *Dryocopus martius*). The first mention is credited to Aldaz (1918), who just noted the "rare" occurrence of the species. Despite vague, it may be reliable because his catalogue and descriptions are well founded, based on collections (although apparently this was not the case for the Middle-spotted Woodpecker) (Sansinenea 1908). None of the Spanish populations of the species produced new substantial information until the pioneer study by Purroy *et al*. (1984) in the Cantabrians. As for the Basque region, the only worthwhile was Noval (1967) who stated "few observations and not completely reliable". In Navarre, Purroy (1974) knew an only occupied locality, but better ascribed to the Pyrenean range than to the Basque.

During 1975–1977, field efforts to map the distribution of breeding bird populations in the southern third of the Basque Country – and neighboring regions, namely La Rioja, Burgos and Soria – were undertaken by De Juana (1980). He authored a pioneering atlas, but obtained no records for the Middle-spotted Woodpecker.

The first systematic mapping of the breeding bird populations in the Basque Country and Navarre were performed in years 1982–1984, using conventional atlas methodology and the 100 km^2 squares of the Universal Transverse Mercator (UTM) grid as sampling units. The entire region was covered, but the Middle-spotted Woodpecker was recorded in just two locations. Although no specific census was made, regional population size was estimated less than 10 pairs on account of the scarcity of observations, and distance from the known areas for the Cantabrian and the Pyrenean (French) populations suggested isolation and an endangered status (Elósegui 1985, Faus 1985).

In the early 1990's, Arambarri and Rodríguez (1994) communicated the presence of the species in a new location in the province of Álava. In this case, records were regular and suggested a well-established population. After their discovery, in May-June 1994 and 1995, these authors performed a more systematic census, sampling *Q. pyrenaica* and *Q. faginea* forest patches over a total area of 17 UTM 100 km^2 squares, by means of 387 point counts along pre-fixed itineraries, where play-back was used (Arambarri & Rodríguez 1996). Occurrence of the Middle-spotted Woodpecker was demonstrated in five of those squares, concentrated in and around the so-called Izki forest. This is a vast woodland of nearly 7,000 ha, dominated by *Q. pyrenaica* (3,700 ha), *Q. faginea* (900 ha) and beech *Fagus sylvatica* (1,800 ha). Density in the Izki forest was 1.29±0.12 pairs/10 ha, assuming that birds responded to the tape from a maximum distance of 150 m. The population size was estimated 451±42 pairs, including birds from the close Sabando forest, a patch of nearly 450 ha dominated by *Q. pyrenaica*.

The fact that this population had gone previously unnoticed, contrasts sharply with its shown local abundance, the conspicuousness of the birds at occupied sites and the relatively good knowledge about the regional avifauna. The participants in the 1982–1984 atlas probably mistook observations of the unexpected Middle-spotted Woodpecker for the

Great-spotted, which was frequent in all sorts of forest landscapes and also inhabited the Izki forest at that time (Faus 1985). Gainzarain (2006) pointed out that, decades ago, under a more intensified forest exploitation regime, the Middle-spotted Woodpecker density could be lower, thus preventing detection. But this idea is hard to apply, because the systematic approaches to the description of the regional avifauna began in the late 1970's and deepened in the 1980's, as seen above. This period is not that far from the discovery of the population, and encroachment of the forest as a consequence of rural emigration to cities had already begun in the 1950's (Michel & Gil 2013).

Distribution

Since the discovery of the Izki population, two systematic studies on the distribution, covering the whole Basque region, were performed. The first one took place in 1995 and was focused on the Picidae assemblage (Lanius Ornithological Society *et al*. 1995). The Middle-spotted Woodpecker was searched for in 27 UTM 100 km^2 squares that held a significant surface of caducifolious *Quercus* patches. Occurrence was only noted for seven squares, spread over the already known Izki population and the western tip of Gipuzkoa province, bordering Navarre. Nevertheless, in this latter sector, records of the species were not definitely confirmed.

The second systematic survey was performed in the framework of the Spanish atlas of breeding birds during 1998–2001, and again every UTM 100 km^2 square was surveyed using non-specific atlas methodology. Ten squares were found occupied by the Middle-spotted Woodpecker, six of them in Álava – the Izki forest being the core – and four in neighboring areas of Navarre (Onrubia *et al*. 2003). The species went unrecorded from the squares in Gipuzkoa province where the 1982–1984 atlas and the 1995 survey had signaled it.

While the study by Onrubia *et al*. (2003) is the most recent systematic, extensive approach to the breeding distribution of the population, the picture was still not complete. Two additional populations have been reported in the last decade, from locations where the occurrence of the species was previously unknown. The first one (Montes de Vitoria range) was surveyed in detail, by means of 58 point counts over a total surface of 610 ha of oak patches, interspersed among a forest matrix of beech stands and coniferous plantations (Unanue *et al*. 2010). The number of occupied patches was small (14% of positive point counts). The second population (Sierra de Entzia range) has not been investigated yet, but the presence of territorial individuals has been well established over the years 2013–2015 (J. M. Fernández-García, own data). These two populations are not contiguous to the Izki core population, but in fact functional connectivity among them is probable, because despite the fragmentation of the oak patches, the forest matrix is continuous and distances to the closest boundaries are less than 15 km. This length is within reach for a short-distance natal disperser like the Middle-spotted Woodpecker (Pasinelli 2003).

Even with such intensity of sampling at regional scale, there are three distinct forest massifs where the occurrence of the species has been cited in the past, but which lack reliable evidences about the presence of a permanent breeding population. The first one is the

eastern tip of Gipuzkoa province: surveys in 1982–1984 and 1995 communicated few and unconfirmed records (see above); the one in 1998–2001 did not. During March-May 2015, the best oak habitat patches remaining in six wider areas of Gipuzkoa have been sampled by means of point counts. Just one territory (i.e. a locality where individuals were detected on two visits) was assessed, apart from other two unrepeated records. Therefore, current distribution and population size in Gipuzkoa province appears to be certainly small or even anecdotic (Itsas Enara Ornithological Society 2015).

The other two massifs with previous records lay both in Álava. Opportunistic observations (Elguea-Urkilla range, 1994, Gorbea range, 2006 and 2007) by skilled observers were communicated, and more ambitious surveys have taken place thereafter. However, occupied territories or even isolated birds have not been recorded again (J. M. Fernández-García own data, Unanue *et al.* 2014), in spite of the availability of suitable and large patches of oak habitat. Structural connectivity could play a role in explaining the absence, because these forest patches are either too far from the closest known population (40 km) or separated by broad (5–7 km) cultivated areas that could act as barriers, thus preventing dispersal. Temporal occupancy, inter-annual variability as well as local colonization and extinction processes have been documented for the Cantabrian population of the Middle-spotted Woodpecker (Robles & Ciudad 2012), and tentatively could explain out-of-range records.

Post-breeding (wintering) distribution of bird populations in Álava province was assessed in 2002–2005. Linear transects were performed in every UTM 100 km^2 squares during December-January, applying non-specific methodology. As for the Middle-spotted Woodpecker, a map of occurrence and relative abundance was built, which showed a similar range than the breeding period and absence over areas other than the Izki forest and its surroundings (Gainzarain 2006). Therefore, at the mentioned sampling scale, the resident status of the population was evident.

Density and population size

The census by Arambarri and Rodríguez (1996) was the first to quantify the abundance of the Izki population. In 2000, breeding bird assemblages were investigated at Izki, counting individuals along transects totalizing 2.02 km across *Q. pyrenaica* patches and 1.36 km across *Q. faginea* patches (Onrubia *et al*. 2001). The average Middle-spotted Woodpecker densities were estimated at 1.7 birds/10 ha (*Q. pyrenaica* woodland) and 0.3 birds/10 ha (*Q. faginea* woodland). For comparison, this same study measured abundance of sympatric Great-spotted Woodpecker at 0.2–0.3 birds/10 ha. But the Middle-spotted Woodpecker numbers were later criticized by Robles and Olea (2003), based on invalid methodological assumptions, which probably led to overestimate the population density. Authors of previous censuses had used long emissions of tape vocals, considered 150 m as the maximum attracting range, concentrated their fieldwork in May and June during the incubation and chick-rearing periods, did not separate territorial males and females, and did not acknowledge floaters or dispersing birds. These aspects have been highlighted by Berndt (2009) as potential sources of overestimation of local Middle-spotted Woodpecker population size.

No other attempts to census the Izki population have been made until 2012, when Ciudad and Robles (2014) estimated population size by mapping territories in 37 parcels (30 ha each), selected randomly. Surveyed area was around 16% of the forested surface of Izki, and nearly 25% of the oak woodland, therefore meaning a robust sample. Parcels were visited 3–5 times during pre-breeding period (March-April), when birds showed a peak in territorial behavior. Each parcel was sampled in detail by one skilled observer, at a rate of 20 ha/hour. Every 100 m, vocalizations were emitted during 30 seconds. If Middle-spotted Woodpeckers were detected, the position, activity and movement of the birds were mapped. Territories per parcel were delimited based on repeated detections and interactions among birds, rejecting cases of vagrancy and territories with a minor surface inside the parcel. Average woodpecker density in the Pyrenean oak forest was 0.89 territories/10 ha (95% CI: 0.74–1.04), which yielded a global estimation of 338 territories (280–396) for the entire study area. Densities of 0.2–0.6 territories/10 ha have been measured in the Cantabrian range (Robles & Olea 2003, Fombellida *et al*. 2009), and 0.3–0.6 territories/10 ha in the Pyrenees (Camprodon *et al*. 2009). Therefore, densities at Izki forest outnumber those reported for other Spanish populations, and approach those for Central Europe (Pasinelli 2003), but we must take into account that differences in methodology may prevent reliable comparisons.

Habitat use and selection

The breeding habitat of the Izki population was described for the first time by Arambarri and Rodríguez (1997). They parameterized forestry variables (dominance, coverage, number and dimension of trees, regeneration) in four plots of 50 m diameter, centered in trees with known nests. *Q. pyrenaica* was the dominant tree species (80–90%) in three plots, and *F. sylvatica* (62%) in the remaining. Main accompanying shrubs were *Ilex aquifolium, Crataegus monogyna* and *Malus sylvestris*. Average volume of wood was 189 m³/ha (167–207).

A more focused research was performed by Maldonado *et al*. (2009). The forest structure was characterized along nine transects 200 × 8 m, ascribed to patches occupied and unoccupied by Middle-spotted Woodpeckers, where species of trees, diameter, height, sanitary state, age and dead wood were measured. Transects "with" woodpeckers showed less density of trees, higher numbers of trees > 50 cm diameter (12–50/ha vs. none) and snags > 20 cm (6–90 vs. none), higher average diameters (31 cm vs. 21), older age (>130 years vs. < 100), higher diversity of tree sizes tending to irregular structure, and a marginally higher volume of logs and dead wood on the ground. Statistical tests were not applied in this study, and the Middle-spotted Woodpecker presence-absence patch classification was questionable, based on old (year 1994), indirect or non-systematic information. However, the use of mature to intermediate forest structures – or at least harbouring big caducifolious trees – was evident.

Ciudad and Robles (2014) described habitat selection during breeding, searching for correlations between presence and abundance of territories in 37 parcels (30 ha each; see above) and a number of structural variables (number, height, health condition and holes regarding trees > 9,5 cm diameter), parameterized in 330 circular plots (0,04 ha each) regularly distributed inside the parcels. Generalized linear models (GLM) and multiple linear

regressions (LM) were applied. The occurrence and density of Middle-spotted Woodpecker territories were positively associated to density of large caducifolious *Quercus* trees (> 35 cm diameter); on average there were 65 such trees inside occupied parcels vs. 15 in unoccupied ones. But this influence was not detected for potential nesting trees (>17 cm and decaying). Authors suggested that foraging trees acted as a limiting resource for the population, unlike nesting trees which seemed much more available. This feature was possibly a consequence of the history of coppice exploitation of the forest, which originated stands with high competence among regenerating trees.

Apart from the landscape and parcel scales, habitat selection has been investigated at the nesting-tree scale. Arambarri and Rodríguez (1997) described six trees that had been used for breeding. Five of them were *Q. pyrenaica* and just one *F. sylvatica*, but all were damaged or presented dead parts. Holes had been excavated at 1.1–5.4 m height. No orientation preference was observed. Maldonado *et al*. (2009) characterized in detail 26 nesting trees and plots 15 m diameter around each one of them, although the unambiguous attribution of such holes to Middle-spotted Woodpecker was not verified in the field. They found that the density of trees within the plot was lower than the average in the patch, and that frequency of holes excavated on damaged or dead trees was seven times higher than those on apparently healthy trees (χ^2, p<0.01). Also, a clear preference for trees colonized by the fungus *Fomes fomentarius* was reported: nearly half of the trees in the forest with fungi had been excavated (χ^2, p<0.01). Diameter range for nesting trees was 20–50 cm, but the average diameter (33.7 cm) was larger (t test, p<0.01) than the average tree within the patch. Nest height above ground varied between 1 and 14 m. Finally, there was a trend to increase the number of holes with the intensity of damage in the trees, from healthy to decaying and dead.

In turn, Ciudad and Robles (2014) described physical characteristics of 28 trees (all *Q. pyrenaica*) with holes known to have been used by Middle-spotted Woodpeckers for nesting. Mean height of the hole was 4.5 m (range 1.5–10.5), and entrance was biased towards S-SE. Average diameter of the nesting tree was 33.8 cm (range 18.5–53.2). These parameters were compared for each nesting tree with the three closer trees, by means of generalized linear mixed models (GLMM). Best model associated nesting to tree condition (i.e. health), presence of fungus and of previous holes, either natural or excavated.

Post-breeding habitat use has received little attention. But basically, no relevant differences compared to the breeding period have been reported. Domínguez and Onrubia (2004) found a positive selection for patches with high *Q. pyrenaica* coverage and mature stands, also exhibiting a rich substrate of fruiting shrubs (*I. aquifolium* and *C. monogyna*). Gainzarain (2006) confirmed the extensive use of the *Q. pyrenaica* woodland, and much weaker abundance in certain open *Q. faginea* patches.

Breeding biology

Six breeding attempts monitored by Arambarri and Rodríguez (1997) rendered estimated laying dates between April 27–28 and May 10–11. One adult stayed with the chicks inside the hole until they were 12 days old. From day 16, chicks were generally fed at the entrance of the hole.

Ciudad and Robles (2014) calculated laying date for two broods at Izki forest: May 9 and 12. Breeding success (proportion of nests with at least one fledgling) was 70% (N=10), with losses from predation by carnivorous mammals and *D. major*. Mean fledging date was June 9 (range May 31-June 22, N=7) and average number of fledglings per nest was 2.2 (range 1–3, N=5). This parameter does not depart from the Cantabrian population (H. Robles & C. Ciudad, *in litt*.), but is low if compared to the core of the European distribution (4.1±1.4 from four studies) (Pasinelli 2006).

Diet

Information on this topic is rather anecdotic. Only Arambarri and Rodríguez (1997) recorded feeding activities (N=204) from two nests. They observed an increase in feeding frequency with age of chicks (Kruskal-Wallis test, p<0.01). The most important preys were Hymenoptera (32% of feedings) and Coleoptera (22%). A high relevance of common ivy *Hedera helix* berries was noted in one of the nests (42%), with lower in the other (4%). The presence of ivy in Middle-spotted Woodpecker diet has generally been undervalued (Pasinelli 2003, Spülher *et al*. 2015), but could compensate low availability of insects during energetically demanding periods, like brood-rearing (Froehlich-Schmitt 2015).

Concluding remarks

It is surprising that the dense population of Izki was not discovered until the 1990's, given the relatively good knowledge about the regional avifauna. Possibly, ornithologists focused their attention on more attractive or fashionable groups, such as waterbirds, raptors and migrants, which were already subject to monitoring programs. Forest birds in general and woodpeckers in particular could be overlooked, despite the fact that they are a dominant component of most bird assemblages in the Basque Country (Galarza 1996). Again, unknown smaller populations have been described in the 2000's, although in these cases it is not clear whether the reason could be a recent colonization of new forest massifs by the core Izki population. On the contrary, we've witnessed recent and inconclusive efforts to confirm the situation in other areas where the species was recorded in the past.

Interpretation of this picture should take into account spatial ecology, functional connectivity and demography. In the Cantabrian range, persistence of the species on forest patches was related to habitat structure and fragmentation, but also to the size of the local population (Robles & Ciudad 2012). Unluckily, research on Izki has only focused on topics that are essential to estimate the conservation status (census and monitoring) and to design compatible forest exploitation practices (habitat selection). But clearly, understanding the dynamics in the core Izki population and the peripheral forest massifs requires new research priorities. For instance, survival, dispersal and habitat preference of juveniles are important to estimate colonization-extinction rates in suboptimal habitat patches and genetic exchange among subpopulations (Robles *et al*. 2008).

Knowing the reproductive output is key to estimate the impact of forest management on habitat quality and population fitness, because density indicators maybe buffered by demography. Compared to Central European populations, breeding parameters in Spanish Middle-spotted Woodpecker populations show lower values, and that could also apply to the Basque Country (Ciudad & Robles 2014), but sample sizes reported are too small. From a global perspective, the marginal position of the Spanish populations is important to determine genetic conservation units and to decide their relevance for the species conservation in a context of environmental change.

Acknowledgements

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Life history trait differences in isolated populations of the endangered Red-cockaded Woodpecker

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Abstract Changes in life history traits can reveal adaptations to changing environments. Red-cockaded Woodpeckers *(Picoides borealis)* are cooperative breeders that have specific reproductive habitat needs. We examined three separate sites in the southeastern United States to see how life history traits differed among isolated populations of Red-cockaded Woodpeckers from 1980 to 2013. We examined the life history traits group size, partial brood loss, number of fledglings, lay date, clutch size, and lifespan. Traits differed among sites, suggesting that populations were adapted to local conditions and different life history trade-offs were important under different environmental conditions at each site. At the two coastal sites in Florida and North Carolina, the family group sizes, lifespans, and partial brood loss were higher when compared to the inland site in North Carolina. Clutch size and number fledged were higher at the two northernmost sites when compared to the southern site. Identifying the differences in life history traits can allow more specific and effective management practices.

Keywords: clutch size, cooperative breeder, endangered, lay date, life history, Red-cockaded Woodpecker

Összefoglalás Az életmenet jellemzők változásai a környezethez való adaptációt mutathatnak. A kooperatívan költő kokárdás harkály *(Picoides borealis)* élőhely-specialista faj. Az Amerikai Egyesült Államok délkeleti részén, három területen vizsgáltuk, hogy az életmenet bizonyos elemei különböznek-e a vizsgált faj izolált populációi között. Az adatokat 1980–2013-ig gyűjtöttük. Az életmenet következő szegmenseit vizsgáltuk: csoportméret, részleges fészekalj-veszteség, a kirepülő fiatalok száma, a tojásrakás dátuma, fészekalj méret és az élettartam. A felsorolt változók területenként eltéréseket mutattak, sugallva, hogy az egyes populációk adaptálódtak a helyi viszonyokhoz, illetve, hogy az egyes életmenet szegmensek különböző súllyal eshetnek latba az egyes területeken. A két tengerparti területen, Floridában és Észak-Karolinában a csoport mérete, az egyedek élethossza és a részleges fészekalj vesztesége magasabb volt a kontinentális észak-karolinai területhez képest. A fészekalj mérete és a kirepült fiatalok száma ezzel szemben magasabb volt a két északi populáció esetében. Az életmenet jellemzők populációk közötti különbségeinek felderítése lehetővé teszi specifikusabb, effektívebb természetvédelmi kezelések alkalmazását.

Kulcsszavak: fészekaljméret, kooperatív költő, veszélyeztetett, tojásrakási dátum, életmenet, kokárdás harkály

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Introduction

Life history strategies directly affect individual fitness. Examples of key life history traits include clutch size, lifespan, and age at first reproduction (Stearns 1976). Variation in life history traits, such as clutch size, can be determined by factors such as resource availability and environment (Lack 1947). Associations, often negative, between life history traits are referred to as life history trade-offs (Zera & Harshman 2001). Different life history trade-offs and trait values are selected for in different environments (Linden & Møller 1989) even within a single species. For example, life history strategies can vary over elevational gradients within species (Bears *et al.* 2009). The combination of life history trade-offs should result in the highest fitness for individuals under those conditions (Badyaev & Ghalambor 2001), and these individuals will be better represented than their conspecifics in future generations (Stearns 1976). Therefore, examining life history traits is important both because life history theory is a major branch in ecology and because it can assist in conservation and management efforts.

This study investigated life history trait differences among three populations of endangered Red-cockaded Woodpeckers *(Picoides borealis)* for which extensive long-term data were available. In the past decade, the majority of studies on Red-cockaded Woodpeckers focused on habitat requirements and preferences over just a few years. Demographic information obtained from studies conducted over longer periods of time can be beneficial for identifying life history traits that should be targeted for management. Since 1980 (Walters *et al.* 1988), we have monitored three fragmented populations of Red-cockaded Woodpeckers that occur in different locations. These three populations have been managed separately and comparisons among them could reveal differences that can be used to improve site-specific management techniques. Red-cockaded Woodpeckers occur in isolated populations and face different quality habitats, climates, and management regimes. Better management can be achieved by focusing on the different life history strategies and trade-offs utilized at these fragmented sites. Therefore, assessment of life history traits is essential to understanding how different management techniques are affecting populations.

Methods

Study species

Red-cockaded Woodpeckers are cooperative breeders, with 0–4 helpers assisting a single, monogamous breeding pair in defending territories, raising young, and excavating new cavities (Lennartz *et al.* 1987). Most helpers are male offspring from previous breeding seasons, but female offspring and unrelated helpers of both sexes also occur (Walters *et al.* 1988). Red-cockaded Woodpeckers are non-migratory and family groups defend their territories year round. They are a medium-sized woodpecker that eats mostly invertebrates, and clutch sizes vary from 2–5 eggs.

Red-cockaded Woodpeckers inhabit mature, open pine stands throughout the southeastern United States (Schaefer *et al.* 2004). Due to the reduced use of fire and the cutting of

old-growth pine forests in the Southeast, the range and numbers of Red-cockaded Wood-pecker have declined (Schaefer *et al.* 2004). Management of Red-cockaded Woodpeckers has focused on improvement of habitat quality to encourage continued use of territories and addition of new territories. Territories are defended areas that contain a woodpecker family group's activities and its borders may be determined by habitat edges or by other woodpecker groups (Ligon 1970). Each territory contains a set of actively used and defended cavity trees termed the cavity tree cluster (Walters *et al.* 1988, Walters *et al.* 1992). Red-cockaded Woodpeckers are unique in excavating their cavities exclusively in living pine trees. The presence of high quality cavities has been shown to be a critical component of territory quality (Walters *et al.* 1992), presumably due to the difficulty and inordinate length of time required to excavate cavities in living pines (James *et al.* 1997, Harding & Walters 2004). Accordingly, artificial cavities have been used to maintain (i.e. prevent territory abandonment) and improve (i.e. convert unsuitable habitat to suitable habitat) territories (Walters 1991) with great success.

Study Areas

In this study, we used long-term demographic data from three isolated study sites: an inland site in the longleaf pine *(Pinus palustris)* forests of the North Carolina Sandhills (SH), a coastal site of longleaf and loblolly pine *(Pinus tueda)* at Marine Corps Base Camp Lejeune, NC (MCBCL), and a Gulf Coast Florida panhandle site at Eglin Air Force Base, Florida (EAFB) with extensive longleaf pine sandhills habitat *(Map 1)*. Detailed descriptions of the study areas and habitat can be found as follows: North Carolina Sandhills (Carter *et al.* 1983, Walters *et al.* 1988); North Carolina Coastal Plain (Walters *et al.* 1995, Zwicker & Walters 1999) and Eglin Air Force Base (Blanc & Walters 2008).

The inland site (Sandhills, NC) was once dominated by fire-dependent species such as longleaf pines. The other forests are mixed pine and have varying amounts of understory and midstory (Trainor *et al.* 2013). Data were collected during the breeding seasons (April-June) from 1980 to 2013.

Field methods

The demographic data were obtained by monitoring color-marked birds at each site for up to 32 years: coastal Marine Corps Base Camp Lejeune (1986–2011), inland Sandhills (1980–2011), and coastal Eglin Air Force Base (1993–2013). For a detailed description of how data were collected, refer to Walters *et al.* (1988).

Briefly, each year, members of each territory and unaffiliated birds were individually identified by color band combinations and their status (i.e. breeder, helper, floater) was determined (Letcher *et al.* 1998). All active cavities within a cluster were marked and checked repeatedly during the breeding season for signs of nesting, to age nestlings for banding, and to identify fledglings (Walters *et al.* 1988). Reproduction was monitored by identifying and counting banded and fledged young in each territory.
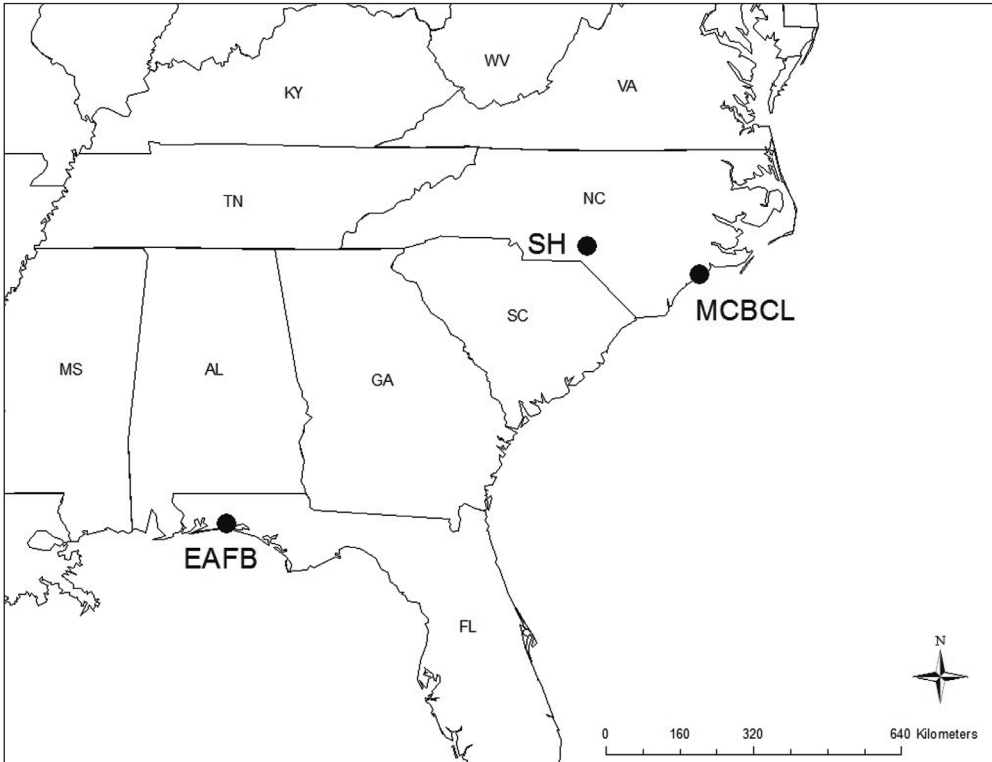
Map 1. Map of the southeastern United States showing the three Red-cockaded Woodpecker study sites: Sandhills (SH), Marine Corps Base Camp Lejeune (MCBCL), Eglin Air Force Base (EAFB)

1. térkép Az Amerikai Egyesült Államok délkeleti részének térképe a vizsgált területekkel: homokdombok (SH), Lejeune haditengerészeti bázis (MCBCL), Eglin légierő bázis (EAFB)

Statistical analyses

We used Generalized Linear Mixed Models (GLMM), Generalized Linear Models (GLM), and Linear Mixed Models (package lme4) (Bates *et al.* 2015) in program R (R Core Team 2014) to compare traits among sites. The life history traits that we examined were group size, lifespan, number of fledglings, clutch size, lay date, and brood loss (eggs laid – eggs hatched). To examine lifespan, we only included birds that survived the first year and hatched before 2001, as only 0.7% (13/1891) of birds hatched before 2001 were still alive in 2013. For lay date, only the first nesting attempt was used. Red-cockaded Woodpeckers typically only re-nest after nest failure. The Eglin Air Force Base data set lacked information on lay date due to differences in monitoring protocols, and was therefore not included in the analysis. Group size included the breeding pair and adult helpers. Except for lifespan, each response variable was treated as a feature of the group, not of the breeders. Therefore, only one observation per territory was included in the analyses. For each dependent variable, we included the variable Site (Sandhills, Marine Corps Base Camp Lejeune, or Eglin Air Forde Base) to examine differences between study sites. We also included other possible predictor variables (covariates) that could explain

variation in life history traits in each model as appropriate. The covariates were group size (but not when group size was the response variable), sex, age, and mate's age. We also included the following random effects: individual identity of the male territory holder, territory and microsite. Microsites were groups of territories that were geographically near each other within each study area. We included different random factors in each analysis depending on how the data were structured and which random factors explained >0 variance. To limit the number of possible models and to avoid problems with model convergence, we did not examine interactions in this analysis (Hoyt & Hannon 2002, Montague-Drake *et al.* 2009). We used a Poisson distribution with a log link for group size, lifespan, number of fledglings, clutch size, and brood loss. We used a Gaussian distribution with an identity link for lay date. We used Akaike's Information Criterion for small sample sizes (AICc) to compare models and to determine if life history traits differed among sites (Burnham & Anderson 2002, Anderson 2008). We used maximum likelihood estimation for the AIC analyses, but estimates were based on restricted maximum likelihood estimation. We tested saturated GLMMs and GLMs for overdispersion by examining the ratio of the deviance to residual degrees of freedom, but the ratios were <1, indicating the data were not overdispersed. All reported estimates and graphs are predicted values for each site from the highest-ranked model and 95% confidence intervals.

Results

Overall, there were 41,396 total observations and 4,514 individual birds. Marine Corps Base Camp Lejeune (coastal site) had the lowest number of birds with 6,754 total observations for 565 individual birds. At Eglin Air Force Base (coastal site), there were 835 individual birds and 2,508 observations. The Sandhills site (inland site) was studied for the most years and had 3,114 individual birds and 32,134 total observations.

Group sizes were larger in the two coastal sites (MCBCL 2.88 adults, 95% CI: 2.79-2.97; EAFB 2.81 adults, 95% CI: 2.66-2.98) than at the inland site (SH 2.64 adults, 95% CI: 2.61-2.68) *(Table 1, Figure 1)*. However, variance at the Eglin site was quite high, with large confidence intervals. Lifespan was longest at Marine Corps Base Camp Lejeune (6.02 years, 95% CI: 5.72-6.33) and was shorter in the inland Sandhills population (4.63 years, 95% CI: 4.52-4.74) *(Table 2, Figure 2)*. The Florida population (Eglin Air Force Base) fell in between with a lifespan of 5.21 (95% CI: 4.30-6.32) years.

Clutch size was significantly larger in the two northern populations (MCBCL 3.41 eggs, 95% CI: 3.29-3.53; SH 3.31, 95% CI: 3.26-3.37) than in the more southern Florida population (EAFB; 2.99, 95% CI: 2.76-3.23) *(Table 3, Figure 3)*. Fledgling production was also significantly higher in the northern populations (SH 1.79 fledglings per breeding male, 95% CI: 1.75-1.83; MCBCL1.66,95% CI: 1.58-1.75), compared to the Florida population at Eglin Air Force Base (1.25, 95% CI: 1.10-1.41) *(Table 4, Figure 4)*. Lay dates were earlier in the inland Sandhills population (Julian date 118, 95% CI: 117-120) than the coastal Marine Corps Base Camp Lejeune population (125, 95% CI: 122-128) *(Table 5, Figure 5)*. The coastal sites experienced more brood loss (MCBCL 1.38 eggs lost, 95% CI: 1.31-1.45; EAFB 1.38 eggs lost, 95% CI: 1.26-1.51) than the inland Sandhills population (1.12 eggs lost, 95% CI: 1.09-1.14) *(Table 6, Figure 6)*.

Model (Group Size)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Territory	4	2390.116	0	-1191.06	0.999999
Territory	2	2418.464	28.347	-1207.23	1

Table 1. Comparison of models examining whether group size differs between study sites in Red-cockaded Woodpeckers (n=9,620). Territory was treated as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

1. táblázat Az egyes vizsgálati területeken rögzített csoportméreteket vizsgáló modellek összehasonlítása a kokárdás harkálynál (n=9620). A territórium random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
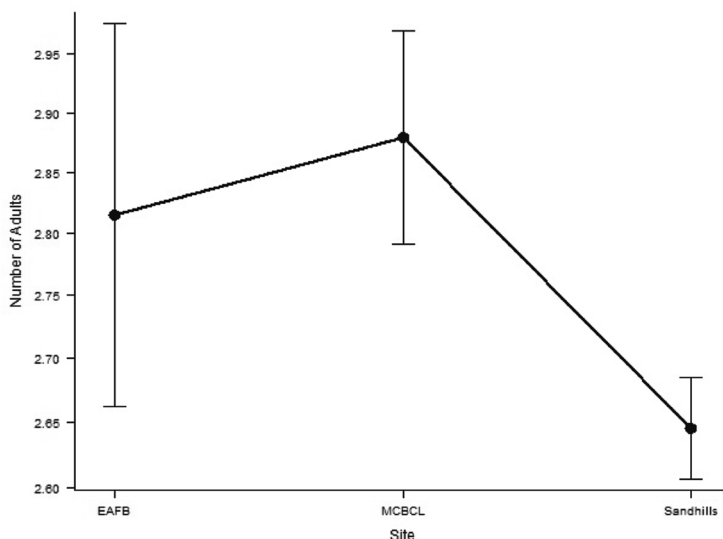
Figure 1. Group sizes (number of adults) were larger at the two coastal sites (Marine Corps Base Camp Lejeune and Eglin Air Force Base) when compared to the inland site (Sandhills). Estimates are predicted values from the highest ranked model with 95% confidence intervals

1. ábra A csoportméret (adult egyedek száma) a két tengerparti területen nagyobb volt (Lejeune haditengerészeti bázis és Eglin légierő bázis), összehasonlítva a kontinentális vizsgálati területtel (homokdombok). A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Lifespan)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Mean Group Size + Sex	**5**	**8579.668**	**0**	**-4284.82**	**1**
Mean Group Size + Sex	3	8658.296	78.628	-4326.14	1
Site + Mean Group Size	4	9136.866	557.198	-4564.42	1
Mean Group Size	2	9228.221	648.552	-4612.11	1
Site + Sex	4	9286.221	706.553	-4639.10	1
Site	3	9856.622	1276.954	-4925.30	1
Sex	2	9881.042	1301.374	-4938.52	1
1	1	10447.000	1867.333	-5222.50	1

Table 2. Comparison of models examining factors that affect Red-cockaded Woodpecker lifespan (n=2,583). All factors were fixed. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

2. táblázat A kokárdás harkály élettartamát (n=2583) befolyásoló faktorokat vizsgáló modellek öszszehasonlítása. Minden faktor fix volt. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
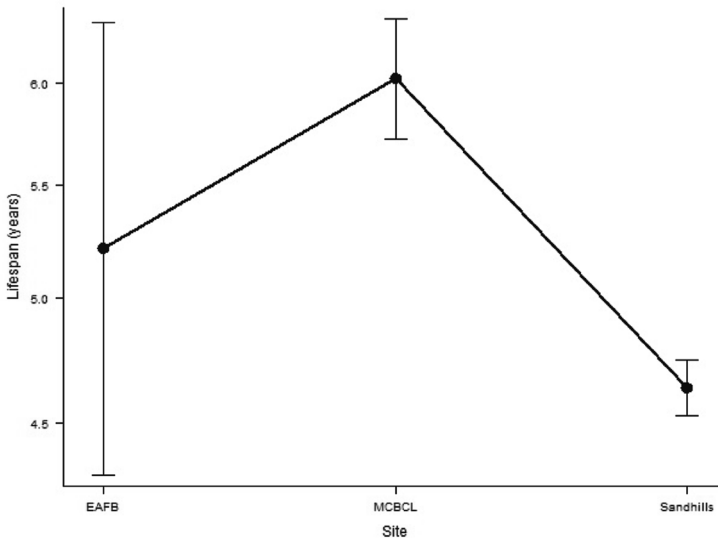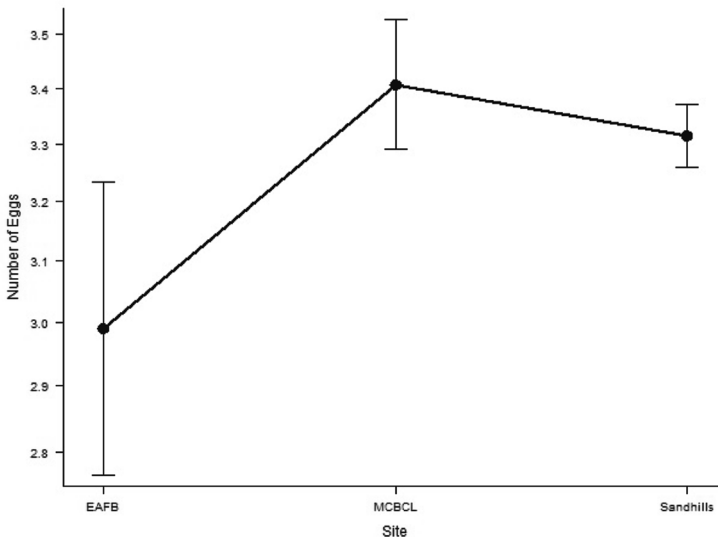

Figure 2. Lifespan was longest at Marine Corps Base Camp Lejeune, and shortest at the inland study site (Sandhills). Estimates are predicted values from the highest ranked model with 95% confidence intervals

2. ábra Az egyedek élettartama a Lejeune haditengerészeti bázis területén volt a leghosszabb, a legrövidebb pedig a kontinentális területen (homokdombok). A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Clutch size)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Group Size + Age + Bird ID	**6**	**1018.886**	**0**	**-503.44**	**0.916027**
Group Size + Age + Bird ID	4	1023.925	5.039	-507.96	0.989784
Site + Age + Bird ID	5	1027.999	9.113	-508.99	0.999401
Age + Bird ID	3	1033.551	14.665	-513.77	1
Site + Group Size + Bird ID	5	1053.968	35.081	-521.98	1
Group Size + Bird ID	3	1059.220	40.334	-526.61	1
Site + Bird ID	4	1070.644	51.758	-531.32	1
Bird ID	2	1076.509	57.623	-536.25	1

Table 3.   Comparison of models examining factors that affect Red-cockaded Woodpecker clutch size (n=5,428). Individual bird identity (Bird ID) was included as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

3. táblázat A kokárdás harkály fészekaljméretét (n=5428) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A madarak egyéni azonosítója (Bird ID) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
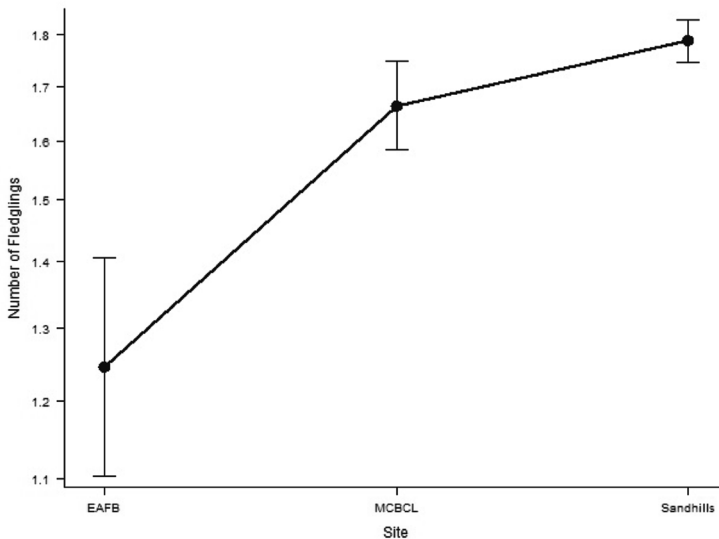

Figure 3.   The number of eggs (clutch size) was larger at the two northernmost sites (coastal Marine Corps Base Camp Lejeune and the inland Sandhills site) compared to Eglin Air Force Base in coastal Florida. Estimates are predicted values from the highest ranked model with 95% confidence intervals

3. ábra   A tojások száma (fészekaljméret) a két északi mintaterületen (Lejeune haditengerészeti bázis és homokdombok) nagyobb volt az Eglin légierő bázisnál tapasztaltakhoz képest. A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Fledglings)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Group Size + Age + Bird ID	**6**	**4885.538**	**0**	**-2436.76**	**1**
Group Size + Age + Bird ID	4	4924.064	38.525	-2458.03	1
Site + Group Size + Bird ID	5	5048.455	162.917	-2519.22	1
Site + Age + Bird ID	5	5061.142	175.604	-2525.57	1
Age + Bird ID	3	5089.991	204.453	-2541.99	1
Group Size + Bird ID	3	5090.812	205.273	-2542.40	1
Site + Bird ID	4	5280.114	394.576	-2636.05	1
Bird ID	2	5307.040	421.501	-2651.52	1

Table 4.   Comparison of models examining factors that affect the number of fledglings produced in Red-cockaded Woodpeckers (n=5,428). Individual bird identity (Bird ID) was included as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

4. táblázat A kokárdás harkály kirepülési számát (n=5428) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A madarak egyedi azonosítója (Bird ID) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti


Figure 4.   The mean number of fledglings was larger at the two northernmost sites (coastal Marine Corps Base Camp Lejeune and the inland Sandhills study site) compared to the coastal site in Florida (Eglin Air Force Base). Estimates are predicted values from the highest ranked model with 95% confidence intervals

4. ábra   A kirepült egyedek átlagos száma magasabb volt a két északi mintaterületen (Lejeune haditengerészeti bázis és homokdombok). A becslések a legjobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Lay Date)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Age + Mate's Age + Microsite	**5**	**2440.191**	**0**	**-1215.09**	**0.891347**
Age + Mate's Age + Microsite	4	2444.400	4.209	-1218.19	1
Site + Mate's Age + Microsite	4	2809.978	369.787	-1400.98	1
Mate's Age + Microsite	3	2813.886	373.695	-1403.94	1
Site + Age + Microsite	4	3407.092	966.901	-1699.54	1
Age + Microsite	3	3410.560	970.369	-1702.28	1
Microsite	2	4045.547	1605.356	-2020.77	1
Site + Microsite	3	4042.444	1602.253	-2018.22	1

Table 5. Comparison of models examining factors that affect Red-cockaded Woodpecker lay date (n=5,215). Microsite (geographic location within each study site) was included as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

5. táblázat A kokárdás harkály tojásrakási dátumát (n=5215) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A vizsgálati területen belüli pozíció (Microsite) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
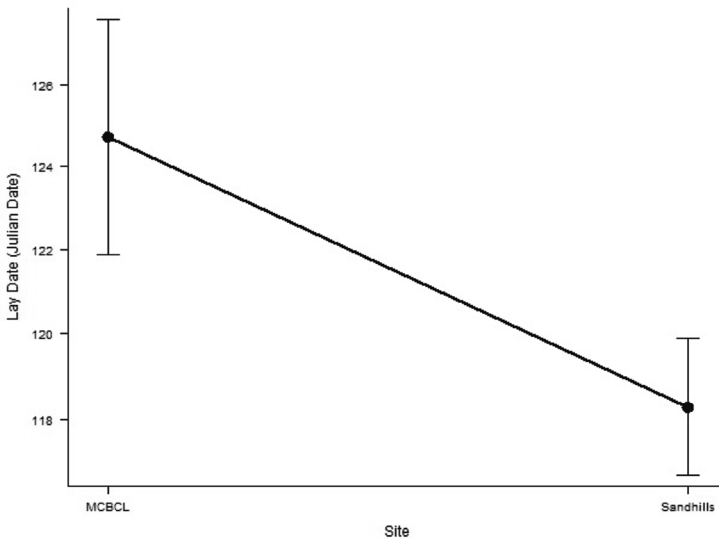
Figure 5. Lay dates were larger (later) at coastal Marine Corps Base Camp Lejeune when compared to the inland study site (Sandhills). Estimates are predicted values from the highest ranked model with 95% confidence intervals

5. ábra A tojásrakás későbbre esett a Lejeune haditengerészeti bázison a homokdombokhoz képest. A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Model (Brood loss)	K	AICc	Delta_AICc	LL	Cum.Wt
Site + Territory	**4**	**5635.964**	**0**	**-2813.98**	**1**
Territory	2	5692.196	56.232	-2844.10	1

Table 6. Comparison of models examining factors that affect Red-cockaded Woodpecker brood loss (n=7,793). Territory was treated as a random factor. LL is the log likelihood, Cum. Wt is the cumulative Akaike weight of each model

6. táblázat A kokárdás harkály fészekalj-veszteségét (n=7793) befolyásoló faktorokat vizsgáló modellek összehasonlítása. A territórium (territory) random faktorként volt kezelve. Az LL log likelihood-ot jelent, a Cum. Wt pedig az egyes modellek Akaike (AIC, Akaike információs kritérium) súlyát jelenti
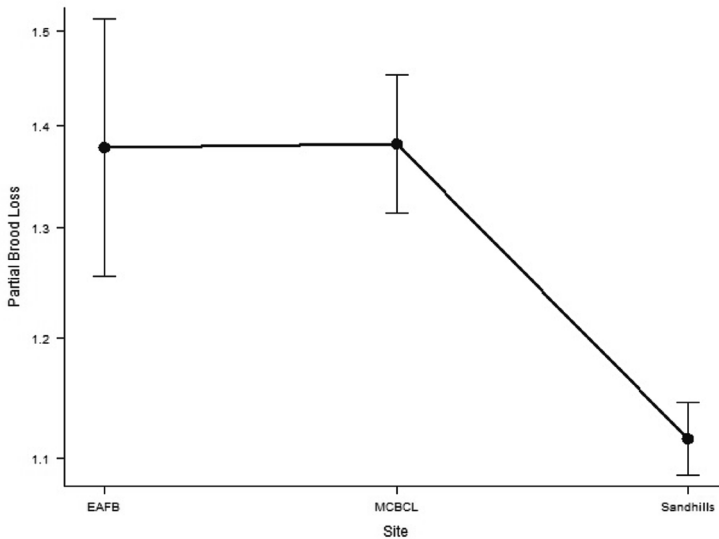
Figure 6. The amount of brood loss was lower at the inland study site (Sandhills) when compared to the two coastal sites (Marine Corps Base Camp Lejeune and Eglin Air Force Base). Estimates are predicted values from the highest ranked model with 95% confidence intervals

6. ábra A fészekalj-veszteség a homokdombok elnevezésű vizsgálati területen alacsonyabb volt a másik két mintaterülethez képest. A becslések a lejobbnak értékelt modellből prediktált értékek, 95%-os konfidencia intervallumokkal. A vízszintes tengelyen olvashatók az egyes mintaterületek: Eglin légierő bázis (EAFB), Lejeune haditengerészeti bázis (MCBCL), homokdombok (SH)

Discussion

Among the three Red-cockaded Woodpecker populations studied, there was ample evidence of life history variation suggesting adaptation to different conditions. The coastal populations had larger group sizes and longer lifespans compared to the inland Sandhills site, suggesting that survival is better in coastal areas than at inland sites. Group size for Red-cockaded Woodpeckers has been found to be positively correlated with fledging success (Conner *et al.* 2004), but the coastal populations experienced high brood loss despite having the largest group sizes. This could indicate that reproduction is more limited by highly variable environmental factors in coastal areas. An increase in parental care is thought to occur in order to prevent reduced survival of offspring due to adverse environmental conditions (Clutton-Brock 1991). This limitation on the number of young that survive could be a direct factor of inclement weather or due to the parents and helpers not being able to exert enough effort to properly feed and care for fledglings so that they all thrive. For example, this could be a matter of reproductive investment, with effort being limited such that fewer young survive when conditions are poorer (i.e. the same effort results in less food brought to the nest under poor conditions). Coastal storms can form from hurricanes, wave developments, depressions, and severe local storms, with the most severe damage coming from hurricanes. The southern states may experience fewer storms than the northern states, but the intensity of storms in the southern states is greater (Mather *et al.* 1964). Engstrom and Evans (1990) reported a 25% mortality in cavity trees during a hurricane year and this mortality rate was expected to be at least an order of magnitude greater than in a year in which a hurricane did not occur. Reduction of available cavities and increase in competition for cavities could force Red-cockaded Woodpeckers to roost outside of cavities and increase exposure to weather and predators, therefore weakening them or increasing chances of mortality (Engstrom & Evans 1990). The late lay date and high brood loss even with a large number of helpers could indicate that environmental factors, such as the highly variable coastal weather at Marine Corps Base Camp Lejeune, limited the number of nestlings that survived to fledging.

The southern, coastal Florida population at Eglin Air Force Base differed from the two northern populations in exhibiting lower clutch sizes and number of young fledged. The two northern populations were similar in these respects, suggesting a north-south gradient, in addition to the coastal-inland gradient discussed above, one that specifically impacts productivity. This suggests a geographic gradient in availability of resources as low food availability favors a smaller clutch and brood sizes (Ricklefs 1980, Badyaev & Ghalambor 2001). Lower food availability may be due to decreased seasonality from north to south (Ricklefs 1980). Eglin Air Force Base contains more old growth forest compared to the other sites (Varner & Kush 2004), suggesting that poor habitat is not responsible for this pattern. However, Eglin Air Force Base is known to be a low productivity site in terms of forestry metrics, so this likely is a factor (Provencher *et al.* 2001). Nevertheless, we cannot draw firm conclusions about how latitudinal gradients affect Red-cockaded Woodpecker traits given the limited number of sites in our study.

Lay dates were earlier in the Sandhills site compared to Marine Corps Base Camp Lejeune, which suggests differences in spring arrival between inland and coastal areas, as has been found elsewhere (Nilsson & Källander 2006). Group sizes were the smallest and

lifespans were shortest at the inland site (Sandhills), which may indicate that there is increased predation on adults or otherwise harsher conditions away from the coast.

These three sites in the southeastern United States have shown how different the needs of isolated populations can be within a species. To effectively manage populations, each site would benefit from conducting a study about the specific life history trade-offs a population employs. Knowing and monitoring life history traits for these managed populations can allow management efforts to be assessed by how they affect traits, or managers can focus on improving certain traits. For example, number of adults per group is associated with territory quality (Heppell *et al.* 1994, Conner *et al.* 2001, McKellar *et al.* 2014) and may be used as a secondary measure of quality, along with habitat data. Additionally, adding new territories and cavities can temporarily decrease group sizes as helpers move to the new territories (Walters 1991), so keeping track of group sizes can help managers assess the need for new territories. Many studies monitor reproductive traits such as clutch size or number fledged, and these traits can help explain population dynamics and be indicators of overall population health.

Acknowledgements

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Parental care by Black-backed Woodpeckers in burned and unburned habitats of eastern Canada

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Abstract Nest care is an important parental contribution to offspring. In woodpeckers, males often have an equal or greater contribution to parental care, including nest sanitation. The Black-backed Woodpecker *(Picoides arcticus)* is a North American boreal woodpecker for which both parents are highly involved in parental care. By modifying their territory size in optimal and suboptimal habitat (e.g. burned vs unburned habitats), this species seems to have a large tolerance to variation in prey abundance at a landscape scale, and could provide a useful biological model to investigate the adaptability of parent care, particularly to relative contribution of each sex. We investigated sex- and habitat-specific parental care behaviour of Black-backed Woodpeckers at 9 nests by daily monitoring during the nestling period. Specifically, we examined two different aspects of parental care: 1) time spent at the nest, and 2) food delivery. We also compared relative contribution between sexes to nest sanitation. Despite our small sample sizes, our results show that males are more involved in nest sanitation and spend longer at the nest, and both sexes exhibit higher food delivery rates and spend less time at the nest in burned habitat. This latter result may suggest that greater effort is needed to provision Black-backed Woodpecker nestlings in unburned habitat compared to burned habitat.

Keywords: food delivery, nest sanitation, parental provisioning, *Picoides arcticus*, woodpecker

Összefoglalás Az utódgondozás fontos szülői tevékenység. A harkályoknál a hímek szülői ráfordítása gyakran egyenlő mértékű vagy nagyobb a tojókéhoz képest. Ennek egy fontos eleme az odú tisztántartása. Az észak-amerikai, boreális elterjedésű harkályfaj, a feketehátú hőcsik *(Picoides arcticus)* esetében mindkét szülő nagy arányban részt vesz az utódgondozásban. A revírek mérete változhat annak függvényében, hogy az adott élőhely optimális vagy szuboptimális-e (pl. leégett vagy le nem égett élőhely). Úgy tűnik, hogy a vizsgált faj jól tolerálja a prédafajok abundanciájának tájléptékű variabilitását. Jó biológiai modellként szolgálhat az utódgondozás adaptibilitásának vizsgálatához, főként az egyes ivarok ráfordítási arányát tekintve. Naponta monitoroztuk a faj ivar- és élőhelyspecifikus utódgondozási viselkedését 9 fészek esetében a fiókanevelés időszakában. Két aspektust vizsgáltunk: 1) a fészeknél töltött időt és 2) a táplálékellátás gyakoriságát. Ezek mellett összehasonlítottuk az ivarok relatív hozzájárulását is az odú tisztántartásához. A kis mintaszám ellenére eredményeink megmutatják, hogy a hímek nagyobb részt vállalnak az odú tisztántartásában, illetve több időt töltenek az odúnál, mint a tojók. Mindkét ivar nagyobb mennyiségű táplálékot hord az odúba, és kevesebb időt tölt a fészeknél a leégett élőhelyen. Az utóbbi eredményből arra következtethetünk, hogy a le nem égett élőhelyen nagyobb mértékű szülői ráfordítás szükséges a feketehátú hőcsikektől a leégett élőhelyhez képest.

Kulcsszavak: etetés, fészektisztítás, szülői gondoskodás, *Picoides arcticus*, harkály

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Introduction

Reproductive strategies in birds are globally dichotomous (Ricklefs 1983). Birds with pre-cocial strategies produce young able to walk, thermoregulate and find their food rapidly (Ricklefs 1983). This strategy requires the production of eggs containing sufficient resour-ces for a longer period of development (Gill 2007), and in many cases, only one parent is in-volved in parental care (Emlen & Oring 1977, Oring 1986). At the opposite end, an altricial strategy produces naked young completely dependent on parents for food, thermoregulation and sanitation (Ricklefs 1983). Eggs contain less resources which results in a shorter incu-bation period (Gill 2007), but nestlings generally benefit from care by both parents (Lack 1968, Black 1996). For altricial birds generally, most species show greater contributions by females (Clutton-Brock 1991), but in woodpeckers, males have an equal or greater contri-bution to parental care (Wiktander *et al.* 2000, Michalek & Winkler 2001, Kozma & Kroll 2013) including nest sanitation (Chazarreta *et al.* 2011), and nocturnal incubation, which is generally rare in birds (Ligon 1993).

The Black-backed Woodpecker *(Picoides arcticus)* is a boreal woodpecker found exclu-sively in North America, and produces altricial nestlings where both parents are highly in-volved in parental care (Dixon & Saab 2001). Black-backed Woodpeckers feed by excavat-ing almost exclusively on dying or recently dead coniferous trees (Tremblay *et al.* 2010, Nappi *et al.* 2015) and eating predominantly wood-boring larvae of Cerambycidae (Mur-phy & Lehnhausen 1998, Nappi & Drapeau 2009), but also Buprestidae, Curculionidae (Scolytinae) and Tenebrionoidea larva (Ibarzabal *et al.* in prep.). Although Black-backed Woodpeckers occur at high densities in recently burned forests (Hutto 1995, Murphy & Lehnhausen 1998, Nappi & Drapeau 2009), they also occur at low densities in unburned fo-rest stands, where they are mainly associated with mature or old-growth forests (Setterring-ton *et al.* 2000, Tremblay *et al.* 2009, 2015), or with forests damaged by insect outbreaks (Goggans *et al.* 1989, Bonnot *et al.* 2008, Rota *et al.* 2014). Home-range sizes of breeding Black-backed Woodpeckers vary considerably from 20 ha in burned habitats (Nappi & Dra-peau 2009) to more than 150 ha in old, unburned coniferous forests (Tremblay *et al.* 2009). The principal cause of this variation is prey density and Tremblay *et al.* (2009) showed that Black-backed Woodpecker home range size increased with the distance between preferred foraging habitat patches in unburned habitats. Furthermore, Tremblay *et al.* (2014) report that the amount of old coniferous habitat positively influenced weight gain in Black-backed Woodpecker nestlings.

Since this species seems to have a large tolerance to variation in prey abundance at the landscape level (burned vs. unburned habitats), it could provide a good biological model to investigate the adaptability in parent care, particularly to relative contribution of each sex. It is likely that low resource availability has a greater impact on females since they need to

produce eggs and thus, it is possible that male Black-backed Woodpeckers contribute more to parental care in unburned than in burned habitats. In contrast, when food resources are high, as in a recently burned habitat, females may have a greater ability to contribute equally to parental care.

Only a few studies exist on nestling care by Black-backed Woodpeckers and these tend to report observations from individual nests (Kilham 1966, Short 1974, Kilham 1983). To the best of our knowledge, this study is the first to address parental care by Black-backed Woodpeckers in the context of habitat types that may support different food resource availability. The main objective of this study is to provide insight into the influence of habitat and sex on parental care by the Black-backed Woodpecker in eastern Canada, with a specific focus on three different responses: 1) time spent at the nest, 2) food delivery and 3) nest sanitation.

Material and Methods

Study area

We conducted field work from June 14th to 22nd, 2006 in Québec, eastern Canada *(Figure 1)*. The study area was located within the black spruce *(Picea mariana)* moss forest of the Canadian boreal forest ecological domain (Saucier *et al.* 1998). Forest stands were composed mainly of black spruce, or black spruce mixed with jack pine *(Pinus banksiana)*, balsam fir *(Abies balsamea)*, white birch *(Betula papyrifera)*, aspen *(Populus tremuloides)* and occasionally, tamarack *(Larix laricina)*. The topography is undulating and wildfire is the major natural perturbation. Forest management began at the end of the 1990s and created a mosaic of logged and residual forest blocks across the landscape.

Parental care of Black-backed Woodpecker pairs were observed in two habitat types: burned and unburned forest stands. Burned habitat was created by a wildfire that occurred from May 31th to June 23rd 2005, and 30% of the area was composed of high-severity burn (Ministère des Forêts, de la Faune et des Parcs of Québec) (unpublished data). Salvage logging occurred in the burned habitat and we monitored Black-backed Woodpecker nests in unmanaged sections of high-fire severity areas. Unburned habitat is composed of the interspersion of old coniferous stands (>90 years old) and harvested stands (see Tremblay *et al.* 2009, 2015 for more detailed information on habitats).

Nest searching

We used two different methods to locate nests between habitat types, mainly because of relative high and low densities of Black-backed Woodpeckers in burned and unburned habitats respectively. In burned areas, we established transects and played recordings of the Black-backed Woodpecker's rattle call (used in conspecific disputes) (Dixon & Saab 2000) to attract individuals and follow them to their nest. In the unburned habitat, we located birds using roadside surveys with 20 minute (or less if detection occurred) playbacks of Black-backed Woodpecker calls and drumming (Ibarzabal & Desmeules 2006) during the end of
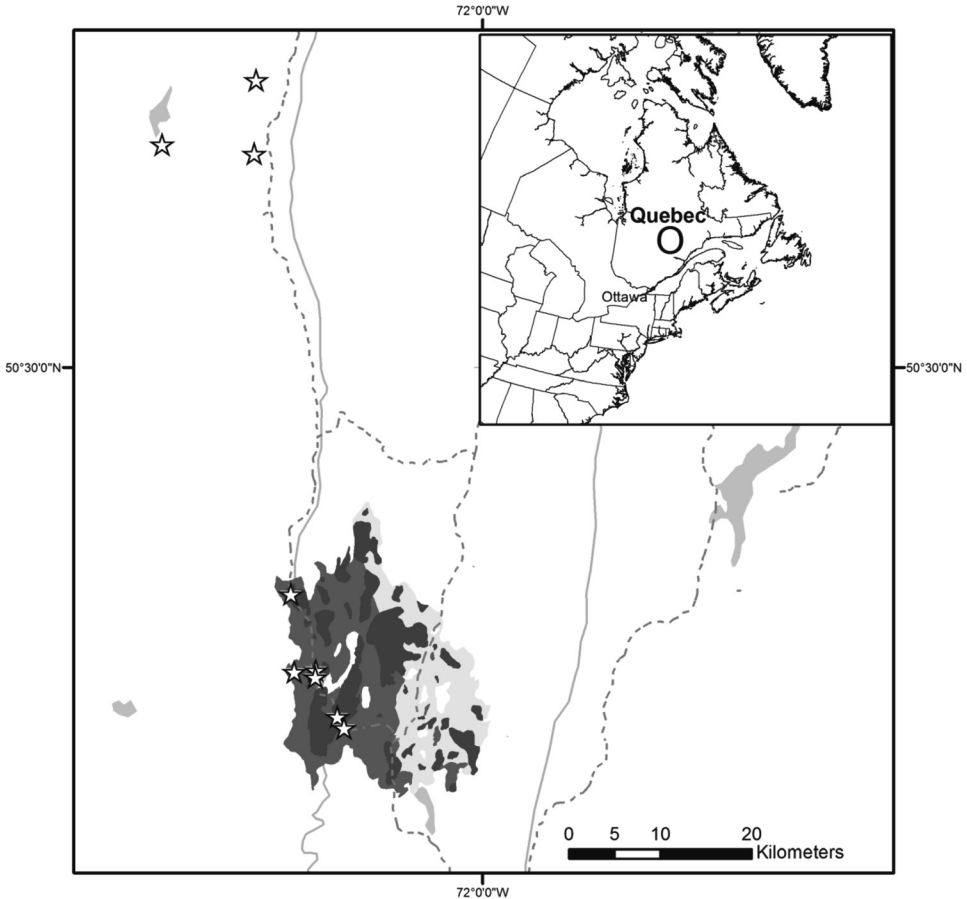
Figure 1. Location of the study area and nests (white stars) investigated for parental care by Black-backed Woodpecker in eastern Canada. Burned habitat was classified according to the burn severity and color intensity is related to fire severity

1. ábra A feketehátú hőcsik szülői utódgondozásáról szóló vizsgálatban a vizsgált terület és a költőodúk (fehér csillagok) elhelyezkedése Kelet-Kanadában. A leégett élőhelyen az erdőtűz intenzitását a különböző árnyalatok jelölik

May through the first third of June. We used mist nets to capture woodpeckers and we fitted a 2.3g radio-transmitter (Model PD-2, Holohil Systems Ltd., Carp, Ontario) at the base of the two central rectrices on individuals showing signs of breeding (i.e. a brood patch). Nests of released birds were located using telemetry by homing methods (Mech 1983).

We recorded nest location coordinates using a global positioning system (GPS Garmin Legend, Garmin Corporation, Olathe, Kansas), and we marked the location using flagging tape placed at least 3m from the nest tree. Age of nestlings was monitored using a wireless camera mounted on a telescopic pole and images were captured on a video recorder for later visualizations. We developed, during our global study on Black-backed Woodpecker (Tremblay *et al.* 2014, 2016), a developmental chart of nestlings based on nest histories

and nestling observations from 37 nests (unpublished data) which enabled us to age nestlings precisely. Nests in unburned habitat were at least 20 km from those in burned habitat *(Figure 1)*.

Observations at nest

One observer was hidden at about 20 m from the nest and recorded time (hour/minute/second) for each arrival and departure of a woodpecker; sex was determined by the yellow crown of the male. Nestlings were aged between 8 and 21 days during observation periods, and weather conditions were favourable (no precipitation and mean min.-max. temperature of 9.6 and 22.4 °C; Environment Canada 2013). Time spent at the nest was split between time spent outside and inside the cavity. Food deliveries and nest sanitation were noted for all visits. Two different individuals made these observations from 06.00 to 16.00, and observations were recorded on a dictaphone to enhance recording speed, and ensure we did not miss any behavioral event. From these observations, we determined the following parental care measures: time spent at nest (outside, inside the nest, and total), rate of food delivery (number of food delivery per hour), nest sanitation (% of visits with transportation of fecal bag), number of visits/hour, and interval duration between consecutive visits.

Statistical analysis

We used a combination of linear models and descriptive statistics to assess the relative influence of variables that may influence parental care of Black-backed Woodpeckers. Time spent at nest and rate of food delivery were examined using a generalized linear mixed model where woodpecker ID was included as a random variable to account for replicate observations per individual. After a preliminary exploratory analysis, we limited our set of explanatory variables to three ("habitat type", "number of nestlings" and "sex") in order to be parsimonious. We specifically used GLMM for zero-truncated count data using *glmer.nb* function in the lme4 package (Bates *et al.* 2015). This approach is suitable when the data cannot included zero. As "Time spent at nest" showed some evidence of over-dispersion, we subsampled with a cut-off value of 500s. Homogeneity of residuals was assessed by plotting residuals against fitted values, and normality of residuals was checked by visual inspection.

Considering our low sample size, we limited our set of biologically relevant models to single variables and an intercept-only model, resulting in a set of 4 models. We used Akaike's Information Criterion (AIC) to evaluate the set of candidate models (Burnham & Anderson 2002). For each model, we calculated ΔAIC as the difference between that model and the model with the lowest AIC value in the candidate set. We also examined the AIC weights (w_i), which are a measure that indicates the probability that the model is the best in the set. We assumed all models within 2 ΔAIC units of the top model as having support but we also considered support for each variable by comparing it against the same null model with only an intercept. In this case, when that model has a lower AIC despite the additional parameter we can infer support for the inclusion of that variable (Burnham & Anderson 2002).

We only report descriptive statistics to compare time spent at nest between sexes and habitats, between the time spent inside and outside the nest, rates of food delivery in relation to the number of nestlings and between habitats, nest sanitation between habitats, and lastly, duration of intervals between consecutive visits between habitats. For each comparison we report the mean±SE and 95% confidence limits uncorrected for repeated measurements.

All statistical tests were done using R version 3.2.0 (R Core Team 2015).

Results

Parental care of 9 Black-backed Woodpecker pairs were monitored in this study; 6 pairs in burned (2.9±0.2 nestlings/nest) and 3 pairs in unburned forests (2.3±0.3 nestlings/nest), for a total of 41.2 and 40.3 hours of observation in each habitat respectively and a total of 710 observations.

A model with sex was the most supported model for time spent at nest with an AIC weight of 0.66, although habitat also had a weaker influence with a drop in AIC of 1.92 units relative to the intercept only model *(Table 1)*. Visit durations were longer in males (79.4±8.7 sec) than in females (29.4±3.3 sec) *(Table 2)*, primarily because females do not enter the nest cavity as often as males. It seemed to have two peeks of time spent at nest during the day, one on the morning and the other in the afternoon *(Figure 2)*. Time spent at the nest tended to be higher in unburned (97.9±13.7 sec) than in burned habitat (36.5±3.4 sec) *(Table 2)*.

Model	log(L)	AIC	ΔAIC	w_i	K	Variance of the random factor
Time spent at nest						
Sex	-3122.24	6252.47	0	0.66	2	0.390
Habitat	-3123.40	6254.78	2.31	0.21	2	0.444
Intercept-only	-3125.35	6256.70	4.23	0.08	1	0.558
Number of nestlings	-3124.86	6257.71	5.24	0.05	2	0.526
Rate of food delivery						
Number of nestlings	-419.62	847.23	0	0.66	2	0.110
Habitat	-420.31	848.63	1.40	0.33	2	0.139
Intercept-only	-424.99	855.98	8.75	0.01	1	0.328
Sex	-424.96	857.92	10.69	<0.01	2	0.328

Table 1.   Model selection results for parental care of 9 pairs of Black-backed Woodpecker (6 in burned and 3 in unburned habitats) during the nestling period. Analyses were conducted using generalized linear mixed-effects models (GLMM for zero-truncated count data) which contained "woodpecker ID" as a random effect to control for repeated observations

1. táblázat   A modell szelekció eredményei 9 feketehátú hőcsik költőpár esetében (6 pár a leégett, 3 pár a le nem égett élőhelyen) a fiókanevelési időszakban. Az analízisek során általánosított lineáris kevert modellt alkalmaztunk (GLMM for zero-truncated count data), amely tartalmazta az egyedek azonosítóját „woodpecker ID", mint random hatást az ismételt megfigyelések figyelembe vételére

Response variables	Mean	SE	95% Confidence limits	
			Lower	Upper
Interval durations between visits (minutes)				
Burned	8.2	0.5	6.8	9.6
Unburned	17.6	1.2	12.3	22.9
Nest sanitation (%)				
Female	1.1	0.6	0.7	1.6
Male	27.8	2.4	26.0	29.7
Rate of food delivery (visits per hour)				
2 nestlings	2.0	0.4	0.0	3.9
3 nestlings	5.5	0.5	4.1	6.9
Burned	5.3	0.6	3.8	6.8
Unburned	2.4	0.3	1.0	3.7
Time spent at nest (seconds)				
Female	29.4	3.3	21.8	37.0
Male	79.4	8.7	59.2	99.5
Burned	36.5	3.4	27.9	45.2
Unburned	97.9	13.7	39.0	156.7
Inside	86.9	11.3	60.8	113.0
Outside	35.6	3.4	27.8	43.4

Table 2. Mean, SE and 95% Confidence limits of response variables investigated in parental care of 9 pairs of Black-backed Woodpecker (6 in burned and 3 in unburned habitats) during nestling period

2. táblázat 9 pár feketehátú hőcsik (6 pár a leégett, 3 pár a le nem égett élőhelyen) szülői utódgondozását leíró változók átlaga, standard hibája és 95%-os konfidencia-intervallumai a fiókanevelési időszakban

Time spent inside the cavity (86.9±11.3 sec) was significantly longer than time spent on the nest tree (35.6±3.4 sec) *(Table 2)*.

Models with number of nestlings and habitat had the highest support for food delivery rate of Black-backed Woodpecker pairs with an AIC weight of 0.66 and 0.33 respectively *(Table 1)*. Indeed, food delivery rates tended to be higher for nests with 3 nestlings (5.5±0.5 deliveries/hour/adult) than for nests with 2 nestlings (2.0±0.4 deliveries/hour/adult), and to be different among habitats with a mean of 5.3±0.6 and 2.4±0.3 deliveries/hour/adult in burned and unburned habitats respectively *(Table 2)*. Accordingly, interval durations between visits were significantly different among habitats with a mean of 8.2±0.5 and 17.6±1.2 min between visits in burned and unburned habitats respectively *(Table 2)*. Parents had food in most of the visits in both habitats (97.1% and 94.1% of the visits in burned and unburned habitats respectively).

Males removed fecal bags more frequently (27.8±2.4% of visits) than females (1.1±0.6%) *(Table 2)*, where males removed almost exclusively fecal bags (98 removals by males and only 4 by females).
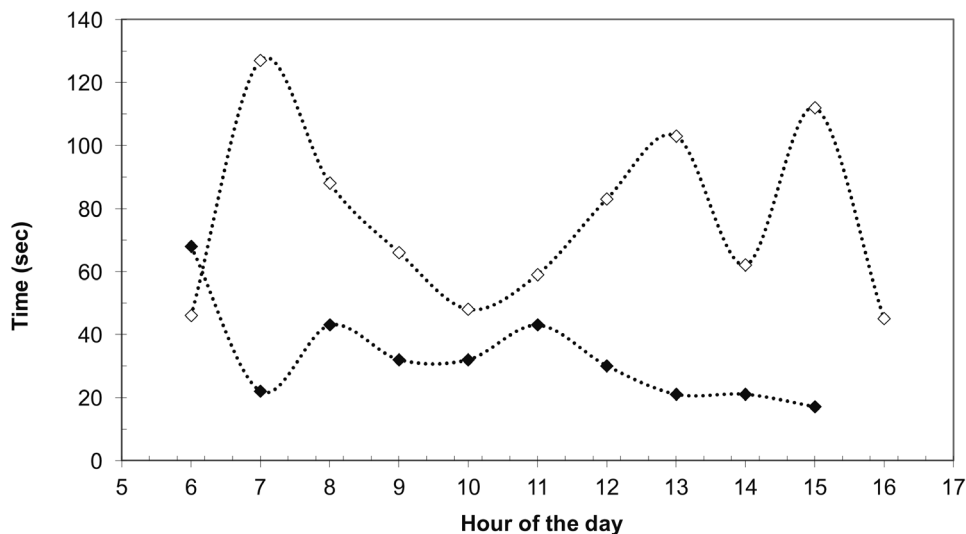
Figure 2. Mean time passed at nest (sec) during hour of the day by 9 pairs of Black-backed Woodpecker (6 in burned and 3 in unburned habitats) during nestling period (white: males, black: females)

2. ábra A nap adott órájában a 9 pár (6 pár a leégett, 3 pár a le nem égett élőhelyen) feketehátú hőcsik által, fiókanevelési időszakban, a fészeknél eltöltött átlagos idő (másodpercben) (fehér négyzet: hímek, fekete négyzet: tojók)

Discussion

Our study is based on a limited sample size, but offer first insights into the relative influence of both parental sex and habitat on parental care by Black-backed Woodpecker. Further research with larger sample sizes is needed to verify our results and to investigate the patterns we found in greater detail. Our results show that the sexes differ in the parental contribution to nest care in this species with males being more involved in nest sanitation and time spent at the nest. We also found that habitat is an important variable in explaining rates of food delivery, after taking into account the number of nestlings in the cavity.

Black-backed Woodpeckers showed high rates of food delivery with more than 94% of visits with prey in both habitats of the study area. Recently burned habitats are known to have a high density of xylophagous insect larvae (Saint-Germain *et al.* 2004, Boulanger & Sirois 2007) that offers abundant foraging opportunities for woodpeckers such as the Black-backed Woodpecker, and prey availability influences rate of food delivery (Naef-Daenzer *et al.* 2000). Such greater abundance of prey may explain the higher rates of food delivery by Black-backed Woodpeckers observed in burned habitat, where rates were more than 2 times higher in burned habitat. However, in burned habitat food delivery rates observed in this study are lower than those reported for the species by Short (1974) in an unburned habitat of northeastern United States (NY) where a mean of 12.4 feedings/hour was observed during 5 consecutive days at a single nest (perhaps 5 nestlings based on Short (1974). This may be explained by the fact that observations of Short (1974) come from forest stands flooded

by recent damming activities by beaver, where favorable habitat conditions may have been generated for wood-boring larvae (Soto *et al.* 2002). Nevertheless, times between visits were longer in unburned habitats as prey may be spatially more dispersed. In an exploratory study, Tremblay *et al.* (2014) reported that amount of unburned old coniferous habitat (food availability) within the home range positively influenced weight gain in Black-backed Woodpecker nestlings. Consequently, interval durations between visits and rates of food delivery may reflect more disperse food availability in the home range. More studies should be done to examine this relationship.

In our study, the number of nestlings seemed to influence rate of food delivery by Black-backed Woodpecker parents, following by habitat. Accordingly, we observed a higher rate of food delivery for nests with more nestlings with 4.0 and 11.0 deliveries/hour for nests containing 2 and 3 nestlings respectively. This rate corresponds to 2.0 and 3.7 feedings/nestling/hour. These results are quite surprising as we expected to observe a decrease in food delivery rate/nestling with an increase in the number of nestlings per nest as reported for Northern Flickers *(Colaptes auratus)* (Gow *et al.* 2013). No comparable study exists for the Black-backed Woodpeckers. Kozma and Kroll (2013) studied provisioning rates for Hairy *(Picoides villosus)* and White-headed Woodpeckers *(Picoides albolarvatus)*, two species that take advantage of burned habitats and frequently feed on wood-boring larvae (Raphael & White 1984, Covert-Bratland *et al.* 2006, Kozma & Kroll 2013) as in the Black-backed Woodpecker. For these two species, mean provisioning rates of about 4 and 3.5 feedings/nestling/hour were observed in nests with 2 and 3 nestlings respectively for Hairy Woodpeckers and about 3.6 and 3.0 feedings/nestling/hour in nests with 2 and 3 nestlings respectively for White-headed Woodpeckers. Thus, the rate of food delivery we observed for Black-backed Woodpecker nests with 3 nestlings is comparable with Hairy and White-headed Woodpeckers while delivery rates for nests with 2 nestlings was lower. This difference may be explained by habitat types as 2 of 3 nests monitored in unburned habitat had 2 nestlings while 5 of 6 nests monitored in burned habitat had 3 nestlings although this interaction did not perform well in our model selection. We have previously found that productivity per nest in the Black-backed Woodpecker is on average 0.9 nestlings/nest higher in burned than in unburned habitats (Tremblay *et al.* 2016).

Studies on food deliveries by Black-backed Woodpecker report that females feed nestlings more frequently than males (Kilham 1966, Short 1974; two and one nest respectively). Sex was not an important variable influencing food deliveries in our study, but was important for time spent at nest and nest sanitations were almost exclusively made by males. Indeed, females rarely entered the cavity and our results show that visits inside the cavity were about 2.5 times longer than visits where the parent remained at the cavity entrance. Time spent inside the nest may not only include time searching for fecal sacs, but also other activities such as pecking walls inside the cavity to add fresh layers of woodchips to cover debris/feces, to stimulate nestling defecation (Backhouse 2005), or thermoregulate when nestlings are too young to thermoregulate themselves. Our results are congruent with those of Short (1974) reporting, for one nest, that the female removed fecal sacs on only 3 percent of her 234 visits, and the male remove 12 times more sacs overall than the female. An important variable that may explain the predominance of males in nest sanitation is the aggressiveness

of nestling Black-backed Woodpeckers. Indeed, during our study nestlings had attacked parents in many occasions and were also reported in other studies (Short 1974, Kilham 1983). Such aggressiveness does not seem to be a frequent behavior in woodpeckers, and was not reported in American Three-toed Woodpecker (*Picoides dorsalis* – reported as *P. tridactylus* at this time) nestlings by Short (1974).

Although time spent at the nest/visit was longer by a factor of 2.7 in unburned habitat, mean time spent at the nest/hour (time spent at nest/visit*nb of visits/hour) was shorter by only a factor of 1.2 in unburned habitat (4.2 min/hour vs 3.4 min/hour in unburned and burned habitats respectively). Thus parents may compensate for their fewer visits in unburned habitat by a longer duration of the visit and total time spent at nests were comparable between both habitats.

Conclusion

Although our study is based on limited sample size and needs to be supported by further studies, it represents one of the only existing studies on parental care in Black-backed Woodpecker. Overall, our results show that males are more involved in nest sanitation and time spent at the nest, and both sexes exhibit higher food delivery rates and seemed to spent less time at the nest per visit in burned habitat. Parent activities while away from the nest are unknown but our results suggest that raising nestlings, at least feeding them, in unburned habitat requires greater effort than in burned habitat, ultimately leading to fewer fledged young than in burned habitat (Tremblay *et al.* 2016). With our limited data, we observed difference in parental care between sexes, except for food delivery, but our results gave no indication of female disengagement, neither in burned habitat, a high food resource habitat for Black-backed Woodpecker, nor in unburned habitat, a lower resource habitat. Nevertheless, more intensive studies are needed to support our findings, acknowledging that it may be challenging to monitor more nests of Black-backed Woodpecker in unburned habitats during the same breeding season.

Acknowledgements

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Nest site characteristics of the Great-spotted Woodpecker in a bottomland riparian forest in the presence of invasive tree species

Gábor Ónodi* & Dániel WINKLER

Abstract This study was carried out in Hungary, in an old unmanaged riparian poplar-willow forest during the breeding seasons of 2014 and 2015. The occurrence of two invasive tree species, the green ash and boxelder, is significant in the study area, which influences negatively the populations of native riparian tree species in Central Europe. We studied Great-spotted Woodpecker nest sites in the presence of these invasive species. Throughout the study period, eight and twelve nesting cavity trees were mapped. Trees were recorded in 20-20 circular plots of 0.05 ha both for each mapped nest trees and random plots as well. Species, diameter at breast height and condition were recorded for each tree. Composition and diversity of nest site and random plots were compared. Distributions and preferences were calculated for nest tree use. Most of the recorded trees were invasive. Nest site plots had more native trees compared to random plots. Nest site showed higher diversity in terms of all three variables. Decayed and dead willow and white poplar hybrid trees were preferred for nesting. Diameter at breast height of nest trees was between 30–90 cm. Studies about cavity excavators in transformed habitats have high importance for nature conservation of riparian forests.

Keywords: Picidae, breeding, alluvial forest, green ash, boxelder maple

Összefoglalás A vizsgálatot 2014–2015-ben, egy kezeletlen folyó-menti fűz-nyár ártéri erdőben végeztük. A területen két invázziós fafaj fordul elő, az amerikai kőris és a zöld juhar. A két faj Közép-Európa szerte negatívan befolyásolja az ártéri erdőkben őshonos fafajok állományait. A nagy fakopáncs költőterületét vizsgáltuk az említett invázziós fafajok jelenlétében. A vizsgálati periódusban 8, illetve 12 költőodút térképeztünk fel. A fás vegetációt 0,05 hektáros, kör alakú mintaterületeken mértük fel 20 költőhelyen, illetve 20 random mintaterületen. Rögzítettük a fák faját, mellmagassági átmérőjét, kondícióját. A költő- és random mintaterületek összetételét és diverzitását hasonlítottuk össze. Mind a költőhelyeken, mind a random mintaterületeken a legnagyobb arányban a két invázziós faj volt jelen, ám a költőterületeken gyakoribbak voltak az őshonos, és ritkábbak az invázziós fajok a random mintaterületekhez képest. A költőhelyeken az idősebb, korhadt, illetve holt fák nagyobb elegyarányban voltak jelen. A költőhelyek diverzitása mindhárom vegetációs változó esetében nagyobb volt. A vizsgált faj egyedei költőodúk készítésére a korhadó, valamint holt fűz és szürke nyárfákat részesítették előnyben. Ezek mellmagassági törzsátmérője 30–90 cm-es között változott. Az odúkészítő fajokról szóló vizsgálatok az átalakult ártéri élőhelyeken nagy jelentőségűek a megfelelő természetvédelmi kezelések kidolgozásához.

Kulcsszavak: Picidae, költés, ártéri erdők, amerikai kőris, zöld juhar

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Introduction

Riparian forests maintain high natural and conservational value. These forests provide source-rich habitats for a high diversity of species. Alluvial forests also serve as green corridors for forest associated species to maintain their opportunities for dispersing. These habitats are highly threatened by river control management and inter alia invasive plant species. Numerous European rivers were regulated for economic reasons and their river beds were transformed to more straight statuses. In lowland Central Europe, riparian forests have two main distinguished types: the willow-poplar forests (softwood gallery forests), situated closer to the river bed; and further away, the oak-ash-elm forests (hardwood gallery forests). Distribution of hardwood gallery forests has drastically decreased as a result of river control, dam management or forest clearing for agricultural land use. Most softwood gallery forests of Hungary are composed of poplar and willow species with dominant native species like white poplar *(Populus alba)*, black poplar *(Populus nigra)*, white willow *(Salix alba)* and crack willow *(Salix fragilis)*. Because of their high genetic similarity, the Hungarian distribution of aspen *(Populus tremula)* and white poplar overlap; thus, hybrids with high variability and introgressive populations of poplars are present in the riparian forests. Due to the extensive distribution of planted hybrid poplar *(P. × euramericana)*, nowadays the majority of trees that resemble black poplar in these forests are most likely hybrids of black poplar and the planted Euamerican poplars (Haraszthy 2001, Gencsi & Vancsura 2002).

Floodplain forests are especially at risk of alien plant invasion because of the permanent propagulum supply and the presence of moist, nutrient-rich disturbed habitats which are very suitable for new establishment. Among the invasive tree species the green ash *(Fraxinus pennsylvanica)* and boxelder *(Acer negundo)* are the most notable mainly in the under- and midstorey level. Due to their abundant and effective dispersed fruits, rapid growth and good regenerative capacities, they have a strong transformative effect on the species composition of floodplain forests by hindering the renewal of native species, of which very few seedlings and saplings can be found in such forests. They influence the chemical traits of the soil and also develop a second canopy layer under the canopy of native trees and thus increasingly shade the ground preventing the saplings of the autochtonous trees from growing properly (Csiszár & Bartha 2008, Udvardy 2008, Erfmeier *et al.* 2011).

In North America, the green ash and the boxelder maple are considered to be mid-successional species as they live in an intermedier lane between the early-successional willow-poplar and the late-successional ash-elm riparian forests. Our focal species are present in the midstorey and the lower canopy layer of the two above-mentioned habitats. They tolerate the higher ground water levels and floods less and the droughts more than the willow and poplar species (Rumble & Gobeille 1998). In addition to the above-mentioned habitat preferences of the two species, the river control managements happened to be beneficial for the green ash and the boxelder maple as the floods are scarcer and the level of ground water is deeper. These species survive more successfully in the shade and grow better at the clearings of the source-rich European riparian forests, than the European willow and poplar species (Saccone *et al.* 2010, Porté *et al.* 2011). These species also produce allelopathic chemicals that can prevent the saplings of native species from developing properly (Csiszár 2009, Csiszár *et al.* 2013). As a result, there

are very few saplings of the native species in the study area, making these habitats more homogenous than one and a half century ago. Nowadays, aging poplar and willow trees and various generations of these two invasive species can be found simultaneously in these forests. This is a widespread environmental problem in the bottomland riparian forests of Central Europe (Mihály & Botta-Dukát 2004, Erfmeier *et al.* 2011).

Picid birds (Picidae) can be considered as keystone species playing key role in forest ecosystems (Gorman 2011). A total of 277 species are known worldwide, while only 11 species are native to Europe (9 of them are breeding in Hungary) (Lammertink 2014). These species live in woody habitats and feed mainly on arthropods. Cavity-excavator species can only breed in habitats where trees are old and thick enough to allow for the production of cavities within them (Gorman 2004). A high number of animal species depend on tree cavities. Among others, cavity-excavators can provide nesting opportunities for other cavity-dwelling species. Cavity-nester birds include ducks (Anatidae), owls (Strigidae), doves (Columbidae), flycatchers (Muscicapidae) and tits (Paridae) etc., while the most frequent mammalian cavity-dweller species are rodents (Rodentia) and bats (Chiroptera) (Bai *et al.* 2005, Politi *et al.* 2010). Apart from vertebrates, we can also find several examples for secondary cavity-dwelling invertebrates including wasps (Hymenoptera) or butterflies (Lepidoptera).To maintain the diversity of cavity-dwellers, it is essential to protect the cavity-excavators as well. Woodpeckers can be considered as umbrella species since through their protection it is possible to protect other species. Each woodpecker species has distinct habitat preferences in terms of both foraging and nesting. Habitat utilization studies of cavity excavator species can support the conservation of their secondary cavity-dweller species as well (Ross *et al.* 1997, Mazgajski 1998, Martin & Eadie 1999, Adkins Giese & Cuthbert 2003, Melletti & Penteriani 2003, Kosiński & Winiecki 2004, Martin *et al.* 2004, Kosiński *et al.* 2006, Pasinelli 2007, Roberge *et al.* 2008a, 2008b, Vaillancourt *et al.* 2008, Wan *et al.* 2008, Hebda 2009, Kozma 2009, Edman *et al.* 2011, Gorman 2011, Cooke & Hannon 2012).

Numerous works have examined the nest site use of certain woodpecker species (Mazgajski 1998, Kosiński & Winiecki 2004, Pasinelli 2007, Hebda 2009, Kozma 2009). Nevertheless, one can barely find any such studies that took place in habitats highly transformed by invasive plant species. There is an increasing need for such studies, as there are altered habitats worldwide with actual range expansion. According to climate change scenarios, habitat transformations will spread around the globe (Starzomski 2013).

There is a huge lack of knowledge about the mentioned, altered riparian habitats, though this environmental problem is considered to be widespread in Central Europe. Beyond the changes in vegetation characteristics, the fauna and so the cavity-nesting communities happened to be affected by this problem. The Great-spotted Woodpecker *(Dendrocopos major)* is the most common woodpecker species in Europe, being present with high densities in most woody habitats, thus making the most cavities. As a generalist species could have a crucial role in such altered communities as the main cavity-excavating species. For further understanding, it is important to study the habitat use of this species in such transformed habitats (Ónodi & Csörgő 2013, 2014).

The questions of our study were the following: Are there any compositional differences between the characteristics of nest site and random plots? What detailed characteristics do nest trees have?

Material and methods

Our study area was a 60–70-year old unmanaged riparian poplar-willow forest (cc. 35 ha) (N 47º04' E 20º11' – N 47º02' E 20º11') situated in the Central-Tisza Landscape Protection Area, which belongs to the Hortobágy National Park, in the floodplain area of the river Tisza *(Figure 1)*. The following native tree species were recorded: white poplar, black poplar, white willow, crack willow. Among the overstorey species, there are some introduced tree species in the area: green ash, boxelder maple, white mulberry *(Morus alba)* and common hackberry *(Celtis occidentalis)*. Among them, the green ash and the boxelder maple are known to be invasive plants as well. The midstorey consisted mainly of the saplings of the above mentioned invasive species. The other scrub layer species are European dewberry *(Rubus caesius)* and, at the edges, the North-American bastard indigobush *(Amorpha fruticosa)*.

Apart from the study species, the Great-spotted Woodpecker, three other woodpecker species are breeding in lower densities in the area: the Lesser-spotted Woodpecker *(Dryobates minor)*, the Green and the Black Woodpecker (*Picus viridis* and *Dryocopus martius*).

Bird census

Great-spotted Woodpecker nest trees were mapped in the breeding seasons of 2014 and 2015, as we followed the chirping begging calls of the nestlings (Kosiński & Winiecki 2004, Kosiński *et al.* 2006, Pasinelli 2007). 8 and 12 cavity trees were mapped, respectively. None of the nest trees of the latter year were reused from the former year.

Figure 1. Map of the study area (N47º04'; E 20º11' – N47º02'; E20º11')
1. ábra   A vizsgált terület térképe (N47º04'; E 20º11' – N47º02'; E20º11')

Vegetation survey

Characteristics of habitat were measured in 12.62 m radius circular plots (0.05 ha) centred on 20 active woodpecker nest trees and on 20 points, randomly selected from 32 semi-random plots on a 100 m by 100 m grid. Tree species, DBH (diameter at breast height) and condition of each tree were recorded in every plot. Only trees with DBH greater than 3 cm were recorded, because this value is supposed to be the minimum diameter of trees that support prey species for the Great-spotted Woodpecker (Gorman 2004).

Tree species were recorded according to the following categories: willow species (W.), black poplar and its hybrids (Pb.), white poplar and its hybrids (Pw.), green ash (A.), box-elder maple (M.), white mulberry (Mb.) and common hackberry (H.). In parallel with the current study, we have been gathering data on foraging microhabitat use of the studied species all year round. So that, both willow species were listed in one single category due to the very similar architecture and bark structure which makes difficult to identify the exact species when the branches are covered with snow.

Vegetation parameters were recorded after earlier studies on woodpecker nest site utilization (Hogstad 1971, Pettersson 1983, Török & Csorba 1986, Morrison & With 1987, Török 1990, Aulén & Lundberg 1991, Suhonen & Kuitonen 1991, Engstrom & Sanders 1997, Osiejuk 1998, Imbeau & Desrochers 2002, Pechacek 2006, Hogstad 2009, Czeszczewik 2010). Diameter at breast height was recorded in 10 cm intervals. The category for the thickest trees was ">100 cm". Condition of trees was assigned in three categories: living trees (less than half of their branches are decayed), decaying trees (more than half of their branches are decayed, but still have living branches) and dead trees (the whole tree and all of the branches are dead). The thickness of the utilized part of tree was assigned to one of the following six categories: <10.1 cm, 10.1–20 cm, 20.1–30 cm, 30.1–40 cm, 40.1–50 cm, 50 cm<. We estimated the thickness of the branch relative to the biometric measures of the study species (length 21–23 cm, wingspan 34–39 cm) (Cramp 1985). We gathered data on the condition of the used substrate in three categories: "Living", "Decaying" and "Dead".

Data analyses

Chi-square test was used to compare the distributions in species, DBH and condition between nest site and random plots.

Shannon diversity index was calculated for tree species, DBH and condition in the case of each plot. Diversity indices of nest site and random plots were compared through Hutcheson's diversity t-test (Hutcheson 1970, Poole 1974).

The ratio of the number of native trees to the pooled number of native and invasive trees was calculated for each plot. Values of nest site and random plots were compared with two-sample t-test with Welch correction.

According to the availability of each category of the three dimensions measured at random plots, frequency distributions and Jacobs' selectivity indices were calculated to examine which type of trees were used and preferred for nesting cavity excavation. This index can result in values from −1 to +1, where negative values are referring to avoidance

Tree species	Nest site (680)	Random (566)
Willow	17.79%	9.01%
White poplar hybrid	13.09%	10.78%
Black poplar hybrid	9.85%	3.89%
Green ash	24.71%	29.86%
Boxelder maple	28.68%	41.87%
White mulberry	5.29%	3.89%
Common hackberry	0.59%	0.71%

Table 1. Frequency distributions of tree species in the nest site and random plots
1. táblázat Az egyes fafajok gyakoriság-eloszlásai a költőhelyen, illetve random plotokban. Fafajok fentről lefelé: fűz, fehér nyár hibridek, fekete nyár hibridek, amerikai kőris, zöld juhar, fehér eper, nyugati ostorfa

and positive values are referring to preference. For these measures, we only worked with trees of a DBH greater than 10 cm.

Analyses were carried out with PAST 2.17c (Hammer *et al.* 2001). Tables were managed with Microsoft Office Excel 2007 software.

Results

The most frequent tree species were the invasive species, among them the most abundant is the boxelder maple, while native tree species were less abundant. At the random

Tree diameter at breast height	Nest site (680)	Random (566)
3.1–10 cm	32.35%	45.41%
10.1–20 cm	23.82%	21.73%
20.1–30 cm	14.26%	13.78%
30.1–40 cm	8.97%	5.48%
40.1–50 cm	6.91%	4.95%
50.1–60 cm	3.97%	2.65%
60.1–70 cm	3.38%	1.59%
70.1–80 cm	2.06%	2.30%
80.1–90 cm	1.47%	0.88%
90.1–100 cm	1.32%	0.53%
100 cm<	1.47%	0.71%

Table 2. Frequency distributions of tree diameter at breast height in the nest site and random plots
2. táblázat Az egyes mellmagasságban mért törzsátmérő kategóriák gyakoriság-eloszlásai a költőhelyen, illetve random plotokban

Tree condition	Nest site (680)	Random (566)
Living	30.88%	39.93%
Decaying	58.24%	53.71%
Dead	10.88%	6.36%

Table 3. Frequency distributions of tree condition in the nest site and random plots
3. táblázat Az egyes fakondíció kategóriák gyakoriság eloszlásai a költőhelyen, illetve random plotokban (kondíció kategóriák fentről lefelé: élő, korhadó, holt)

plots, white poplar hybrids were the most abundant native trees, while willow trees were the most frequent in the nest site plots. White mulberry and common hackberry trees happened to be sporadic species. Nest site plots had less invasive trees and more native trees than random plots *(Table 1)*. Chi² test showed significant difference between the two distributions ($X^2=53.955$, df=6, P<0.0001).

Both plot types had gradually less trees in the greater DBH categories, although thinner, younger trees were represented in lower proportions in the nest sites *(Table 2)*. Chi² test showed significant difference between the two distributions ($X^2=29.885$, df=9, P<0.0001).

Decaying trees were represented the most and dead trees the least at both types of plots, although nest site plots had more decaying and dead trees and less living trees *(Table 3)*.

Plot	Nest site (680)	Random (566)
1	1.18	1.16
2	1.46	1.18
3	1.54	0.91
4	0.88	0.44
5	1.09	1.10
6	1.59	1.29
7	1.03	1.08
8	1.45	1.41
9	1.36	1.04
10	1.20	1.44
11	1.34	1.15
12	1.11	1.17
13	1.22	1.15
14	1.26	1.47
15	1.37	1.42
16	0.85	1.24
17	1.16	1.45
18	1.43	1.08
19	1.24	1.03
20	1.45	1.23
Mean	1.26	1.17
SD	0.20	0.23

Plot	Nest site (680)	Random (566)
1	27.98	81.87
2	138.30	108.73
3	76.79	50.75
4	55.51	122.25
5	38.55	135.69
6	95.09	36.75
7	139.54	58.83
8	38.85	72.58
9	89.55	26.32
10	18.30	59.42
11	25.98	2.77
12	65.28	41.87
13	84.82	41.82
14	96.59	8.32
15	37.20	24.46
16	78.66	88.60
17	67.85	82.99
18	49.14	52.85
19	68.93	49.99
20	26.86	41.39
Mean	65.99	59.41
SD	34.93	35.60

Table 4. Tree species diversity (Shannon) in the nest site and random plots
4. táblázat Shannon diverzitási értékek a fafajok esetében a költőhelyen, illetve random plotokban

Table 5. Shannon diversity indices in the case of tree diameter at breast height in the nest site and random plots
5. táblázat Shannon diverzitási értékek mellmagasságban mért törzsátmérő esetében a költőhelyen, illetve random plotokban

Chi^2 test showed significant difference between the two distributions (X^2=15.505, df=2, P<0.0001).

Nest site plots showed higher diversity values in the case of tree species *(Table 4)*, diameter at breast height *(Table 5)* and tree condition *(Table 6)*. Diversity t-test showed significant differences between nest site and random plots in terms of Shannon diversity indices of tree species (t=5.607, df=953.43, P<0.0001) and diameter at breast height (t=4.8318, df=1116, P<0.0001). The t-test did not show significant differences for tree condition (t=1.4687, df=1223.7, P=0.14218).

According to the two-sample t-test with Welch correction, nest site plots had significantly higher values for ratio of the number of native trees to the pooled number of native and invasive trees, compared to the random plots *(Table 7)* t(Welch)=3.5591, p(Welch t)=0.0014.

Plot	Nest site (680)	Random (566)
1	41.28	97.72
2	179.59	123.18
3	121.67	56.42
4	85.11	150.93
5	63.16	164.61
6	118.83	38.03
7	165.95	82.90
8	54.21	96.39
9	123.48	36.95
10	33.34	72.58
11	48.04	6.59
12	103.83	56.37
13	97.02	63.93
14	137.23	26.38
15	53.58	30.26
16	115.89	119.46
17	95.07	115.84
18	85.11	52.51
19	93.81	81.82
20	44.40	61.30
Mean	93.03	76.71
SD	41.39	42.40

Plot	Nest site (680)	Random (566)
1	0.65	0.39
2	0.38	0.21
3	0.46	0.08
4	0.56	0.16
5	0.92	0.18
6	0.39	0.18
7	0.12	0.35
8	0.27	0.30
9	0.42	0.20
10	0.15	0.19
11	0.33	0.29
12	0.38	0.38
13	0.27	0.32
14	0.53	0.38
15	0.39	0.21
16	0.92	0.24
17	0.37	0.35
18	0.45	0.13
19	0.33	0.36
20	0.35	0.14
Mean	0.43	0.25
SD	0.21	0.10

Table 6. Shannon diversity indices in the case of tree condition in the nest site and random plots

6. táblázat Shannon diverzitási értékek a fakondíció esetében a költőhelyen, illetve random plotokban

Table 7. Ratio values for the number of native trees to the sum of the number of native and invasive trees in the nest site and random plots

7. táblázat Őshonos fák aránya az őshonos és invázios fák összegéhez képest a költőhelyen, illetve random plotokban

12 nests out of 20 were made in willow trees, 7 nests were made in white poplar hybrids and one nest was made in a boxelder maple tree, which means 60%, 35% and 5%, respectively. According to Jacobs' selectivity indices, birds showed preference for willows and white poplar hybrids. The highest preference value was observed for willow trees. All other trees were avoided by the studied species, but boxelder maple showed slightly lower avoidance *(Table 8)*.

For cavity excavation, a wide range of DBH was utilized from trees between 10.1 and 20 cm to trees of maximum 90 cm thickness. Most of the nest trees were between 30.1 and 50 cm thick. According to their availability, the preferred trees were ranged from 30.1 to 70 cm, but 80.1–90 cm DBH trees were also preferred. Other categories were avoided *(Table 9)*.

Tree species	Utilization frequencies	Jacobs' selectivity indices
Willow	60%	0.77
White poplar hybrid	35%	0.38
Black poplar hybrid	0%	-1.00
Green ash	0%	-1.00
Boxelder maple	5%	-0.81
White mulberry	0%	-1.00
Common hackberry	0%	-1.00

Table 8. Utilization frequencies and Jacobs' selectivity indices for species of nest trees

8. táblázat Az egyes fafajok gyakoriság-eloszlásai és ezek Jacobs szelektivitási index értékei a költőfák esetében. Fafajok fentről lefelé: fűz, fehér nyár hibridek, fekete nyár hibridek, amerikai kőris, zöld juhar, fehér eper, nyugati ostorfa

Tree condition	Utilization frequencies	Jacobs' selectivity indices
Living	10%	-0.55
Decaying	75%	0.28
Dead	15%	0.24

Table 10. Utilization frequencies and Jacobs' selectivity indices for condition of nest trees

10. táblázat Az egyes fakondíció kategóriák gyakoriság-eloszlásai és ezek Jacobs szelektivitási index értékei a költőfák esetében (kondíció kategóriák fentről lefelé: élő, korhadó, holt)

Substrate condition	Utilization frequencies
Living	10%
Decaying	75%
Dead	15%

Table 12. Frequency distributions of substrate condition at nesting cavities

12. táblázat Az egyes fakondíció kategóriák gyakoriság-eloszlásai a költőodúknál (kondíció kategóriák fentről lefelé: élő, korhadó, holt)

Tree diameter at breast height	Utilization frequencies	Jacobs' selectivity indices
10.1–20 cm	0%	-1.00
20.1–30 cm	10%	-0.50
30.1–40 cm	35%	0.66
40.1–50 cm	25%	0.54
50.1–60 cm	10%	0.37
60.1–70 cm	15%	0.71
70.1–80 cm	0%	-1.00
80.1–90 cm	5%	0.52
90.1–100 cm	0%	-1.00
100 cm<	0%	-1.00

Table 9. Utilization frequencies and Jacobs' selectivity indices for diameter at breast height of nest trees

9. táblázat Az egyes mellmagasságban mért törzsvastagság kategóriák gyakoriság-eloszlásai és ezek Jacobs szelektivitási index értékei a költőfák esetében

Diameter at nest height	Utilization frequencies
0–10 cm	0%
10.1–20 cm	5%
20.1–30 cm	60%
30.1–40 cm	25%
40.1–50 cm	5%
50 cm<	5%

Table 11. Frequency distributions of tree diameter at nest height

11. táblázat Az egyes költőodúknál becsült törzsvastagság kategóriák gyakoriság-eloszlásai

75% of nest trees were in "decaying" condition. 15% of the utilized trees were dead and 10% were living. The preferred condition stages were the "decaying" and the "dead", where decaying trees were more preferred. Living trees were avoided *(Table 10)*.

60% of nesting cavities were excavated in parts of trees with the diameter at nest height of 20.1–30 cm. Other categories were represented less and less *(Table 11)*. 75% of nesting cavities were excavated in decaying substrates *(Table 12)*.

Discussion

Within the literature one can rarely find studies on nest site use of the Great-spotted Woodpecker in riparian forests. These studies were carried out mostly in oak-ash-elm forests *(Fraxino-Ulmetum)* (Kosiński & Winiecki 2004, Kosiński *et al.* 2006), while none of them took place in willow-poplar alluvial forests *(Populo-Salicetum)*. Besides, we could not find any example of woodpecker nest site studies in habitats transformed by invasive tree species. There is a huge lack of knowledge on these topics so far.

Among native trees, nest site plots had more trees from all of the available three species, but the difference was proportionately bigger in terms of willow and black poplar hybrid trees, than white poplar hybrids. In one of our earlier studies made in the same study area, through weekly standard, year-round foraging observations, we found, that invasive tree species were avoided (Ónodi & Csörgő 2014). In spite of that, among other tree species, the rough barked native willow and black poplar hybrids were the most preferred trees for foraging (Ónodi & Csörgő 2014). The green ash and boxelder maple were scarcely used for foraging by the study species (Ónodi & Csörgő 2014). This could be due to that these tree species have very few prey items in them. Both non-native species have anti-herbivore secondary metabolic products in their tissues, in the leaves and in the living wood as well (Csiszár & Bartha 2008, Udvardy 2008, Csiszár 2009). Among the few insect species that can inhabit the wood of green ash, the most common is the Ash Bark Beetle (*Leperisinus fraxini*, Scolytidae) that lives in the bark of the trees (Udvardy 2008). According to the literature, there is not any documented wood boring insect species, which could inhabit the wood of boxelder in Europe (Csiszár & Bartha 2008).

Foraging woodpeckers preferred bigger, older native trees, which could be the reason why nest site plots had more abundant thicker, older trees and less young trees than random plots. This phenomenon is similar to the results of Kosinski and Winiecki (2004). They found in *Quercus-Fraxinus-Ulmus* and *Quercus-Carpinus* stands in Poland, that Great-spotted Woodpeckers used nest sites with proportionately bigger and older trees of higher total basal area.

Most trees were decaying at both nest site and random plots. Nest site plots had more decaying and dead trees and less living trees. Although living trees were preferred by the foraging birds, nest site plots had proportionately less living trees than random plots. This could be from the fact that most of the living trees in the study area are invasive and thus avoided by the foraging birds for both foraging and nesting (Ónodi & Csörgő 2014).

According to our results, nest site plots had higher diversity in terms of all three studied variables, as birds chose nest sites with more thick, decaying or dead native trees, while the

overall characteristics of this transformed habitat are less diverse, due to the high frequencies of young, living invasive trees.

As there are so few studies on the nest site utilizations of the Great-spotted Woodpecker and we could not find any studies held in poplar-willow riparian forests so far, it is hard to compare their nest tree utilizations as well. In other studies, willow trees were not among the preferred nest trees, although these trees were sporadically present in those study sites (Kosiński & Winiecki 2004, Kosiński *et al.* 2006). Willow trees were only mentioned by Kosiński *et al.* (2006) as highly preferred nest tree species for the Middle-spotted Woodpeckers. In our study area, these tree species provide the most suitable, 20–30 cm thick substrates with the proper volume of soft decaying wood. As white poplar hybrid trees are hybrids of white poplar and aspen trees, our studied woodpeckers used these trees similarly to Aspens that were used in other studies as well. Aspens were preferred by Great-spotted Woodpeckers for example in Bialowieza National Park in Poland (Wesolowski & Tomialojc 1986), in Norway (Hagvar *et al.* 1990) and in Sweden (Hansson 1992). The used aspen cavity trees were described as dead and decaying trees in case of Bialowieza, but were considered to be living trees in both the Norwegian and Swedish studies. Such high preference could be related to its soft wood, which can mean less effort for excavation (Kosiński & Kempa 2007). The other preferred trait of this species is its smooth bark. The latter trait could lower the success of scansorial nest predators such as Pine Marten *(Martes martes)* and Stone Marten *(M. foina)* (Glue & Boswell 1994, Walankiewicz & Czeszczewik 2005).

Great-spotted Woodpecker chose dead and decaying trees for nesting in other studies as well (Glue & Boswell 1994, Smith 1995, Smith 1997, Kosiński & Winiecki 2004, Smith 2007), although, among other European woodpecker species, the Great-spotted Woodpecker use living trees the most. In some studies the species used near exclusively living trees for nesting (Kosiński & Kempa 2007). Compared to other *Dendrocopos* species, like the dead wood specialist White-backed Woodpecker *(D. leucotos)* which has a slightly greater body size and considerably greater bill length (Gorman 2004), the Great-spotted Woodpecker's shorter and deeper bill occurred to be more efficient for excavating nesting cavities in hard, living trees (Aulén & Lundberg 1991). According to the condition of such transforming riparian habitats, high proportion of native trees suitable for nesting are in decaying or dead condition as well. Older willow and white poplar hybrid trees are mostly decaying under these soil water conditions. In contrary to other studies in which cavities were found in old, larger trees with 50–60 cm diameter at breast height (Kosiński & Winiecki 2004), our study birds mainly excavated their nesting cavities in medium diameter trees of 30–40 cm. These trees represented 10% of the available stems applicable for cavity excavation by Great-spotted Woodpecker. Equivocally with other studies, our studied species made cavities in substrates between 20 and 30 cm diameter at nest height (Glue & Boswell 1994).

In their native habitats, in particularly in green ash woodlands, green ash and boxelder maple support a high diversity of forest bird species, including cavity-nesting species (Rumble & Gobeille 2008). According to our results, we predict that the population decrease of native, alluvial tree species could lead to a suboptimal habitat for numerous members of riparian forest communities (Magura *et al.* 2008). In that case, the density of woodpecker

species could decrease. As the main cavity excavator, the Great-spotted Woodpecker plays a key role in riparian forest ecosystems. Its decrease in density caused by habitat alteration would supposedly have a considerable influence on the cavity-dwelling community. Among the secondary cavity-nesters of this species we can find tits (Paridae), nuthatches (Sittidae), sparrows (Passeridae), starlings (Sturnidae) and flycathcers (Muscicapidae) (Kotaka & Matsuoka 2002), even though the Great-spotted Woodpecker is one of the most important nest predators for cavity-nesting species, for example in the Bialowieza National Park, where certain species even avoid nesting in woodpecker cavities (Wesolowski 2007). Decaying processes of natural cavities could be initiated by the foraging excavations of woodpeckers, as they can inoculate wood-decaying fungi. Such holes, within decades can become nesting cavities. The wood of the invasive tree species is much harder, so these trees can produce hollows slower than willow and poplar trees; thereby, the importance of nesting and foraging cavities made by the generalist Great-spotted Woodpecker will undoubtedly rise (Jackson & Jackson 2004).

Through their above mentioned processes, green ash and boxelder maple are considered to be such transforming species. In the making of conservation management plans, it is adequate to use the "novel ecosystem" approach. Certain transforming species can change fairly entire ecosystems in irreversible ways. The restoration of such habitats could be impossible or so resource intensive, that it could even cause great harm to the processes of the ecosystem. In our case, these invasive tree species support the essential midstorey and secondary canopy layer as important microhabitats for various forest-dwelling species. Managers should secure the current processes of such altered ecosystems while taking efforts to conserve the indigenous habitat as much as possible (Milton 2003, Hobbs *et al.* 2006, Lindenmayer *et al.* 2008, Hobbs *et al.* 2013).

As the green ash and boxelder maple are considered to be mid-successional species in their North-American, native alluvial habitats (Iverson *et al.* 2008, 2009), through river control managements the more straight, deeper riverbeds of Central Europe happened to be more optimal for these species, than the native riparian tree species. The conditions of native riparian woodland ecosystems could be mitigated by the restoration of natural, meandering and flooding processes of such riverbeds (Scott *et al.* 1997, van Turnhout *et al.* 2010), though this consideration is yet to be an utopistic approach due to inter alia economic reasons.

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Picidae in the European fossil, subfossil and recent bird faunas and their osteological characteristics

Jenő (Eugen) KESSLER

Jenő (Eugen) Kessler 2016. Picidae in the European fossil, subfossil and recent bird faunas and their osteological characteristics. – Ornis Hungarica 24(1): 96–114.

Abstract This paper presents the European fossil, subfossil and recent representatives of the Picidae family. Following the list of fossil and subfossil remains, the author analyzes and presents images of the osteological characteristics of the order's 10 recent European species.
Skeletal parts that are usually present both in the fossil and subfossil material were examined (*mandibula, coracoideum, scapula*, *humerus*, *ulna*, *metacarpus*, the first phalanx of the second finger of the wing, *femur*, *tibiotarsus*, *tarsometatarsus* and *distal phalanx*). The text is complemented with the bibliography concerning the fossilized material, tables and figures and a size chart.

Keywords: paleornithology, osteology, Paleogene, Neogene

Összefoglalás A dolgozatban a harkályok rendjének európai fosszilis, szubfosszilis és recens képviselőit mutatja be a szerző. A fosszilis és szubfosszilis maradványok felsorolását követően a szerző a rend 10 európai recens fajának csonttani jellegeit elemzi és mutatja be képeken is. A vázrészek közül azok kerülnek vizsgálatra, amelyek a fosszilis és szubfosszilis anyagban is rendszerint jelen vannak (alsó állkapocs, hollócsőrcsont, lapocka, felkarcsont, singcsont, kézközépcsont, a szárny II. ujjának első ujjperce, combcsont, lábszárcsont, csüd és karomcsont). A szöveget kiegészíti a fosszilis anyagot felölelő könyvészeti jegyzék, 8 táblakép és egy mérettáblázat.

Kulcsszavak: paleornitológia, csonttan, paleogén, neogén

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Introduction

Representatives of the order Picidae were present in Europe already in the beginning of the Paleogene, represented by species of the presently exclusively tropical family (Capitonidae) or the now extinct family (Zygodactylidae). These are, for example, the *Primozygodactylus eunjoae* Mayr and Zelenkov, 2009 (Mayr 2005c, 2006, Mayr & Zelenkov 2009), from the Middle Eocene of Messel Grube, Germany, the *Zygodactylus luberonensis* Mayr, 2008, from the Lower Ogliocene of France (Mayr 2005b, 2008) and multiple findings from the Miocene of France and Germany (*Zygodactylus ignotus* Ballmann, 1966, and *Capitonides europaeus* Ballmann, 1966, from the Middle Miocene of Wintershof (West) bei Eicstätt, *Z. grivensis* Ballmann, 1969, and *Z. gaudryi* (Depéret 1887), from the Middle Miocene of La Grive-Saint-Alban) (Ballmann 1966, 1969a, 1969b). The small *Rupelramphastoides kopfi* Mayr, 2005 from the Lower Oligocene site of Freuenweiler, Germany, is thought to belong to the Ramphastidae family (Mayr

2005a). *Picavus litencicensis* Mayr and Gregorova (2012) described from the Litenčice site of the Czech Republic also comes from the Lower Oligocene (Mayr & Gregorova 2012).

The recent Picidae, however, are only known from the Neogene of Europe in quite scarce numbers and without exception represented by modern genera:

– *Picus peregrinabundus* Umans'ka, 1981 from the Upper Miocene of Novoelisavetovka, Ukraine (MN 11-12) (Umanska 1981, Mlikovský 2002)

– *Picus pliocaenicus* Kessler, 2013 from the Lower Pliocene of Beremend 26, Hungary (MN 15) (Kessler 2013)

– *Dendrocopos praemedius* Jánossy, 1974 from the Upper Pliocene of Villány 3, Hungary (MN 16-17) (Jánossy 1974) and subsequently from site Beremend 26 (Kessler 2009, 2013)

– the extinct *Dendrocopos submajor* Jánossy, 1974 was described by Dénes Jánossy (1974) from the Upper Pleistocene of Hundsheim, Austria, but Mlikovský (2002) synonymized the latter with the species *D. major* as he did the former with the recent *D. medius*. Given that the author identified both species from the much older site of Beremend 26, we are on the opinion that according to the sizes and characteristics, the former should be viewed as a valid species, while the latter as a subspecies *(D. major submajor)*.

The marking of the recent *Pogoniulus* genus belonging to the Ramphastidae family by Mlikovský (2002) from the Upper Miocene of Austria is also worth mentioning (Kohfidisch – Gyepüfüzes).

Recent species of the Picidae family are only specific to the Pleistocene and Holocene of Europe:

– *Jynx torquilla* Linnaeus, 1758
Known from the Lower Pleistocene: Betfia 2 (Kormos 1913, Čapek 1917) and Upper Pleistocene of the Carpathian Basin: the shelter cave of Hámor-Puskaporos (Lambrecht 1912, 1916, 1933, Jánossy 1977, 1986), as well as the Middle Pleistocene of France and the Upper Pleistocene of Austria, the Czech Republic, France, Croatia, Germany, Switzerland and Romania (Tyrberg 1997).

– *Picus viridis* Linnaeus, 1758
Known from the Lower Pleistocene: Betfia 9 (Gál 2002), Somssich Hill 2 (Jánossy 1981a, 1982b, 1983, 1986), Middle Pleistocene: Tarkő 1-16 (Jánossy 1977) and Upper Pleistocene: Varbó-Lambrecht Kálmán Cave (Jánossy 1977), the Holocene: Kazánszoros-Töröklik Cave (Kessler 1974), Körösbánlaka Cave (Kessler 1982), Vársonkolyos-Izbîndiş Cave, (Kessler 1977, Gál 2002), the caves of Vársonkolyos (Kessler 1982), as well as the Middle Pleistocene of France, Italy, Spain and the Upper Pleistocene of England, Austria, the Czech Republic, France, Croatia, Germany, Italy and Spain (Tyrberg 1997).

– *Picus canus* Linnaeus, 1758
Known from the Upper Pleistocene of the Carpathian Basin: Felsőtárkány-Peskő Cave (Lambrecht 1912, 1933, Jánossy 1977), Nándor-Nándori Cave (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Óruzsin-Antal Cave (Nehring 1880, Róth 1881, Lambrecht 1912, 1933), shelter cave I. of Pilisszántó (Lambrecht 1915, 1933,

Jánossy 1977, 1986), Répáshuta-Balla Cave (Lambrecht 1912, 1933), Varbó-Lambrecht Kálmán Cave (Jánossy 1977), Velika Pecina (V. Malez 1975, 1984, 1988), Velika pec na Lipi (V. Malez 1975, 1984, 1993, V. Malez-Bačić 1975), the Holocene: Felsőtárkány-Petény Cave (Jánossy 1977), as well as the Middle Pleistocene of the Czech Republic, France and the Upper Pleistocene of Austria, the Czech Republic, France, Germany, Italy and Switzerland (Tyrberg 1997).

– *Picus* sp.
Known from the Upper Pleistocene of the Carpathian Basin: the shelter cave of Hámor-Puskaporos (Lambrecht 1912, 1916, 1933, Jánossy 1977, 1986), as well as the Upper Pleistocene of Luxemburg and Germany (Tyrberg 1997).

– *Dryocopus martius* (Linnaeus, 1758)
Known from the Upper Pleistocene of Georgia, France and Poland (Tyrberg 1997).

– *Dendrocopos major* (Linnaeus, 1758)
Known from the Middle Pleistocene: Vindija (M. Malez 1961, V. Malez 1973, 1988, 1991), and Upper Pleistocene: Bajót-Jankovich Cave (Lambrecht 1933, Jánossy 1977), Budapest-Remetehegy Shelter Cave (Kormos & Lambrecht 1914, Lambrecht 1933, Jánossy 1977, 1986), the shelter cave of Hámor-Puskaporos (Lambrecht 1912, 1916, 1933, Jánossy 1977, 1986), Hámor-Herman Ottó Cave (Lambrecht 1915, 1933), Merkenstein (Wettstein & Mühlhofer 1938), shelter cave I. of Pilisszántó (Lambrecht 1915, 1933, Jánossy 1977, 1986), Szegyestel-Măgura Cave (Kessler 1982, 1985, Gál 2002), Szilvásvárad-Istállóskő Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1977), Tatabánya-Szelim Cave (Jánossy 1977), Velika Pecina (V. Malez 1975, 1984, 1988) and from the Holocene of Ecsegfalva n. 23 (Pike-Tay *et al.* 2004, Gál 2007b), Felsőtárkány-Petény Cave (Jánossy 1977), Legény Cave (Lambrecht 1914), the shelter cave of Répáshuta-Rejtek (Jánossy 1977), Teufelslucken (Soergel 1966), as well as the Lower Pleistocene of France and Spain, the Middle Pleistocene of the Czech Republic, France, Croatia, Germany, Italy, Spain, and the Upper Pleistocene of England, Bosnia and Herzegovina, the Czech Republic, France, Ireland, Poland, Germany, Italy, Spain, Switzerland and Ukraine (Tyrberg 1997).

– *Dendrocopos medius* (Linnaeus, 1758)
Known from the Lower Pleistocene: Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1977, Gál 2002), Middle Pleistocene: Hundsheim (Jánossy 1974), Tarkő 4, 11 (Jánossy 1977) and Upper Pleistocene, Óruzsin-Antal Cave (Nehring 1880, Róth 1881, Lambrecht 1912, 1933), Velika Pecina (V. Malez 1975, 1984, 1988), as well as the Lower Pleistocene of Ukraine, the Middle Pleistocene of France, the Upper Pleistocene of France, Germany, Italy and Ukraine (Tyrberg 1997).

– *Dendrocopos minor* (Linnaeus, 1758)
Known from the Lower Pleistocene of the Carpathian Basin: Betfia 9 (Gál 2002), as well as the Lower Pleistocene of England, middle Pleistocene of France, and Upper Pleistocene of England, France and Croatia (Tyrberg 1997).

– *Dendrocopos leucotos* (Bechstein 1803)
Known from the Holocene of the Carpathian Basin: Felsőtárkány-Petény Cave (Jánossy 1977), as well as the Middle Pleistocene of France, Italy, and the Upper Pleistocene of Austria, Belgium, France, Greece and Italy (Tyrberg 1997).

– *Picoides tridactylus* (Linnaeus, 1758)
Known from the Middle Pleistocene of France and the Upper Pleistocene of Germany (Tyrberg 1997).

Palaeoecological conclusions

The changes in climate across Europe by the end of the Miocene, seasonal cooling and warming were not favorable for fruit-eating types (Coliiformes, Musophagiformes, Psitaciformes, beside Trogoniformes from among the families of Piciformes (the representatives of Capitonidae, Ramphastidae and Zygodactylidae) – thus, these receded back to tropical areas. Members of the Picidae family in the Piciformes order were able to withstand the seasonal changes in temperature as insectivores, mostly specializing on invertebrates living under tree bark. The sole exception is the less specialized Eurasian wryneck with beaks incapable of carving, which is the only migrating species of the family and not only does it not show any specialization in its skull, but also its flight capabilities and tail feathers are unlike those of other species.

   For the latter, the thickening of the parietal bones, the rather strong lower and upper jaws, the remarkably long tongue, the flight feathers capable of weight support all had significant effects on flight capabilities, and consequently the shape and size of the wings. The distinctively wavelike trajectory and low flight speed would not allow for longer migration at this point, which they do not need in their woodland habitats, however, it serves perfectly well motion in this environment. The geographic spread of the approximately 300 species of the family supports the above statement, since they were unable to reach Oceania, Madagascar, Australia and New-Zealand. An extremely complex, data-rich study appeared recently (Winkler 2015), which perfectly complements this work.

Osteological characteristics of Picidae

From an osteological perspective, their skeletal parts can easily be identified, but the current paper only takes into account those that easily remain, fossilize and can be identified up to species level. These are the mandible, the coracoid bone of the pectoral girdle, the scapula, bones of the upper and lower limbs (apart from the radial bone, fibula and certain phalanges), so we do not examine neither the otherwise typical skull, sternum and pelvis, nor the vertebrae, ribs and furcula *(Plate 1)*.
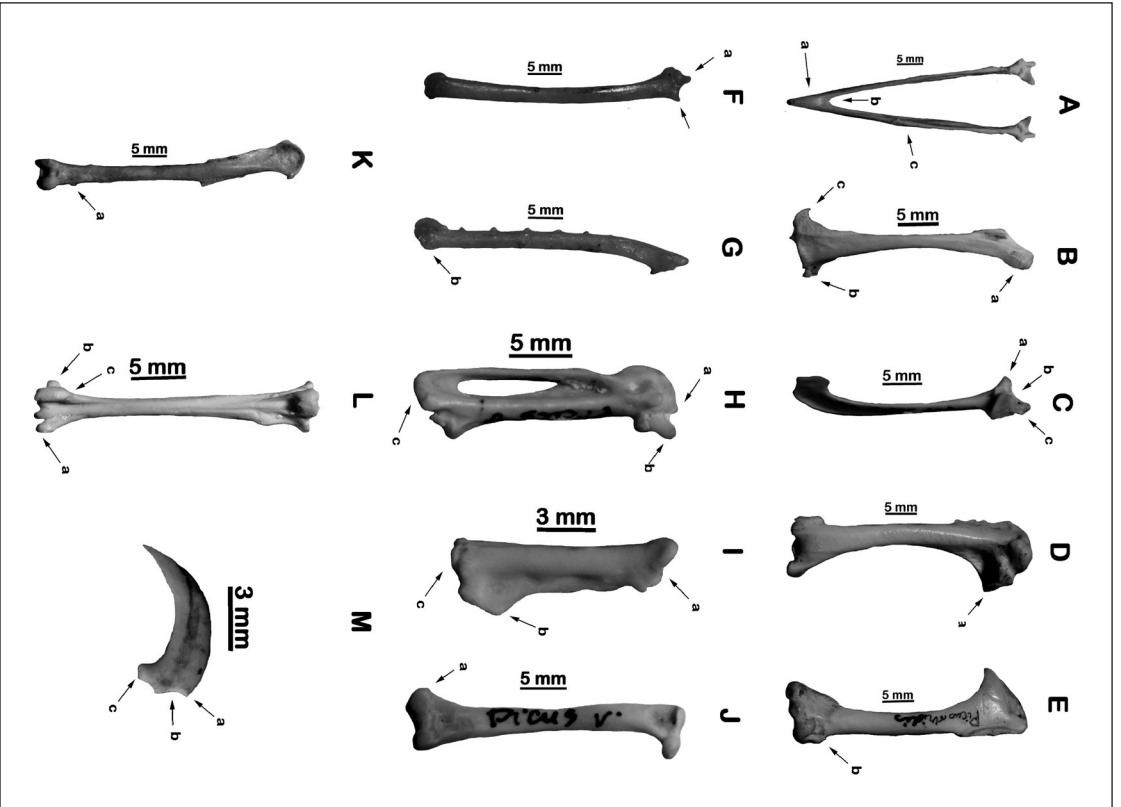
Plate I. Picus viridis Linnaeus, 1758 osteology characters: A. Mandible – a. te end of the beak; b. the recess between the stems; c. the stems. B. Coracoideum – a. the processus acrocoracoidalis; b. the medial part of the sternal end; c. the lateral part of the sternal end. C. Scapula – a. the lateral projection; b. the dorsal projection. D.E. Humerus – a. the crista bicipitalis; b. the processus supracondylaris dorsalis. F.G. Ulna – a. oleocranon; b. cotyla dorsalis; c. tuberculum carpale. H. Carpometacarpus – a. the trochlea carpalis; b. the processus extensorius; c. the distal end of the metacarpus major. I. Phalanx proximalis digiti majoris – a. the proximal end; b. the distal end; c. the distal end of the dorsal side. J. Femur – a. the condylus lateralis. K. Tibiotarsus – a. the tuberositas retinaculi. L. Tarsometatarsus – a. trochlea metatarsi I. M. Distal phalanx metatarsi IV.; c. trochlea metatarsi II.; b. trochlea – claw – a. the tuberculum extensorium; b. the cotyla articularis; c. the tuberculum flexorium.

Táblakép I. Picus viridis Linnaeus, 1758 csonttani jellegek: A. Alsó állkapocs – a. a csőr vége; b. a csőr szárai közti mélyedés; c. a csőr szárai. B. Hollócsőrcsont – a. processus acrocoracoidalis; b. a mellcsonti rész mediális vége; c. a mellcsonti rész laterális vége. C. Lapocka – a. oldalsó nyúlvány; b. dorsális nyúlvány. D.E. Felkarcsont – a. crista bicipitalis; b. processus supracondylaris dorsalis. F.G. Singcsont – a. oleocranon; b. cotyla dorsalis; c. tuberculum carpale. H. Kézközépcsont – a. trochlea carpalis; b. processus extensorius; c. a metacarpus major disztális vége. I. A nagy kézujj első ujjperce – a. proximális vég; b. disztális vég; c. a disztális vég dorsális része. J. Combcsont – a. condylus lateralis. K. Lábszárcsont – a. tuberositas retinaculi. L. Csüd – a. trochlea metatarsi I. M. Karomcsont – a. tuberculum extensorium; b. cotyla articularis; c. tuberculum flexorium.
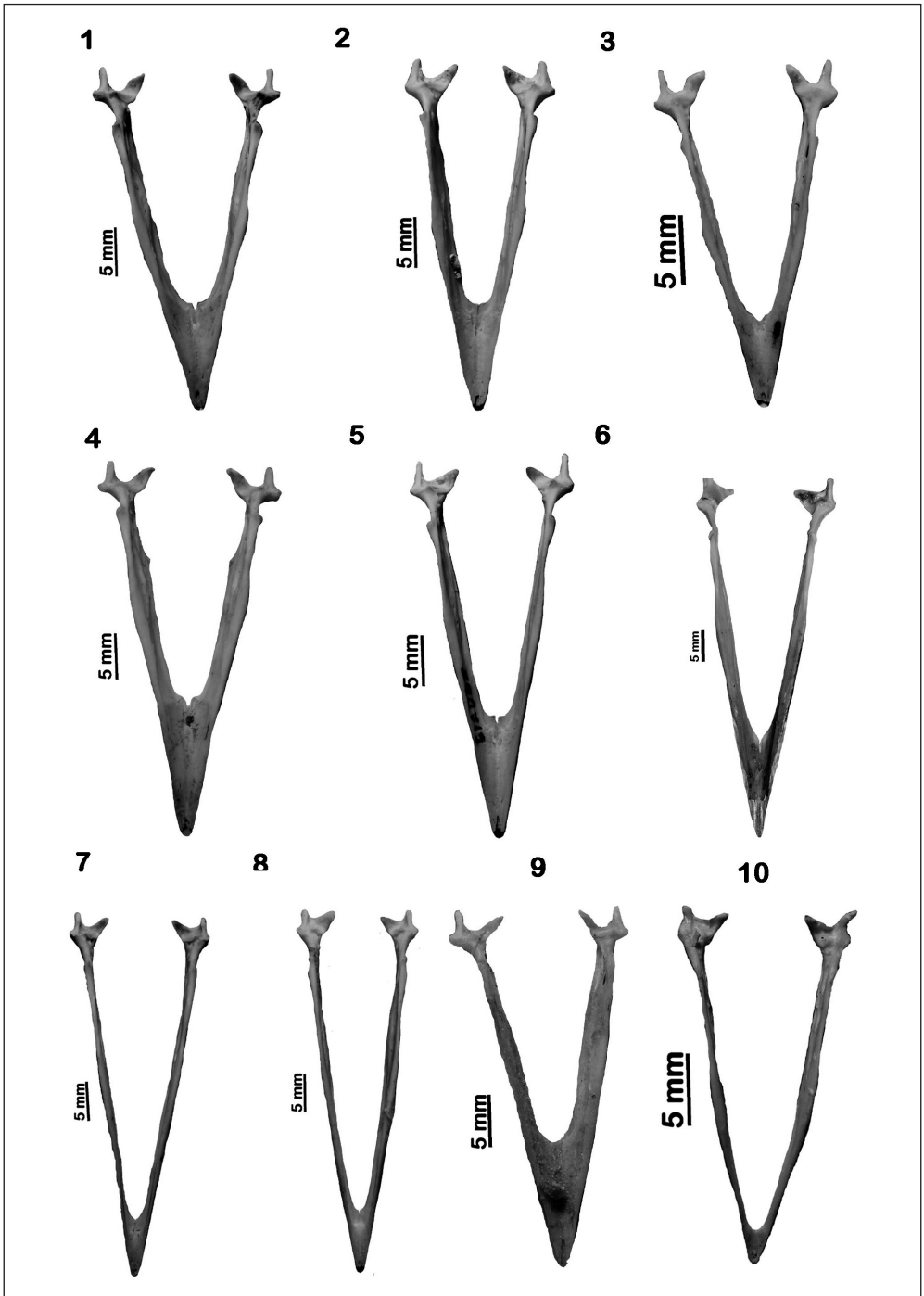
Plate 2.   *Mandibula,* dorsal aspect: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*
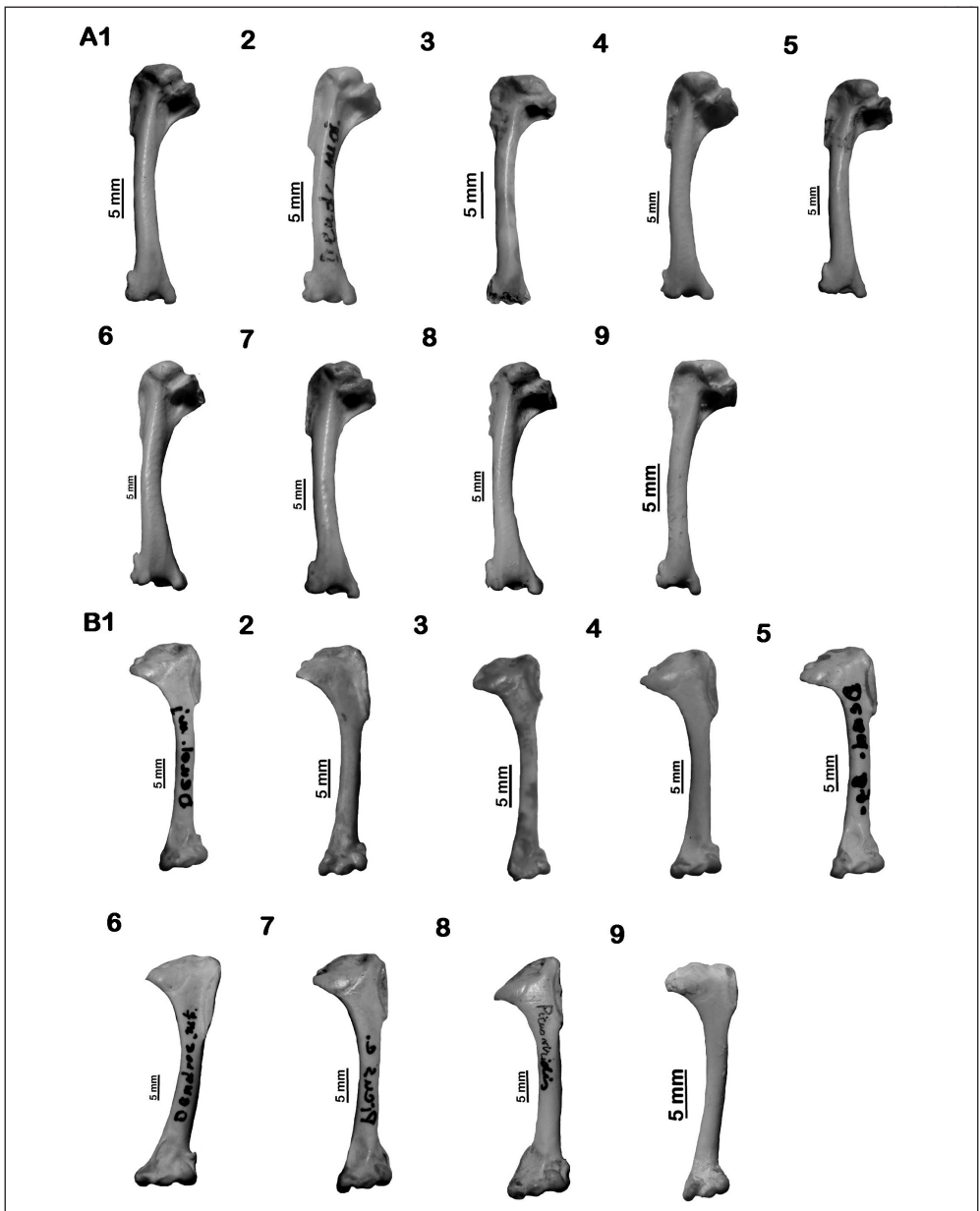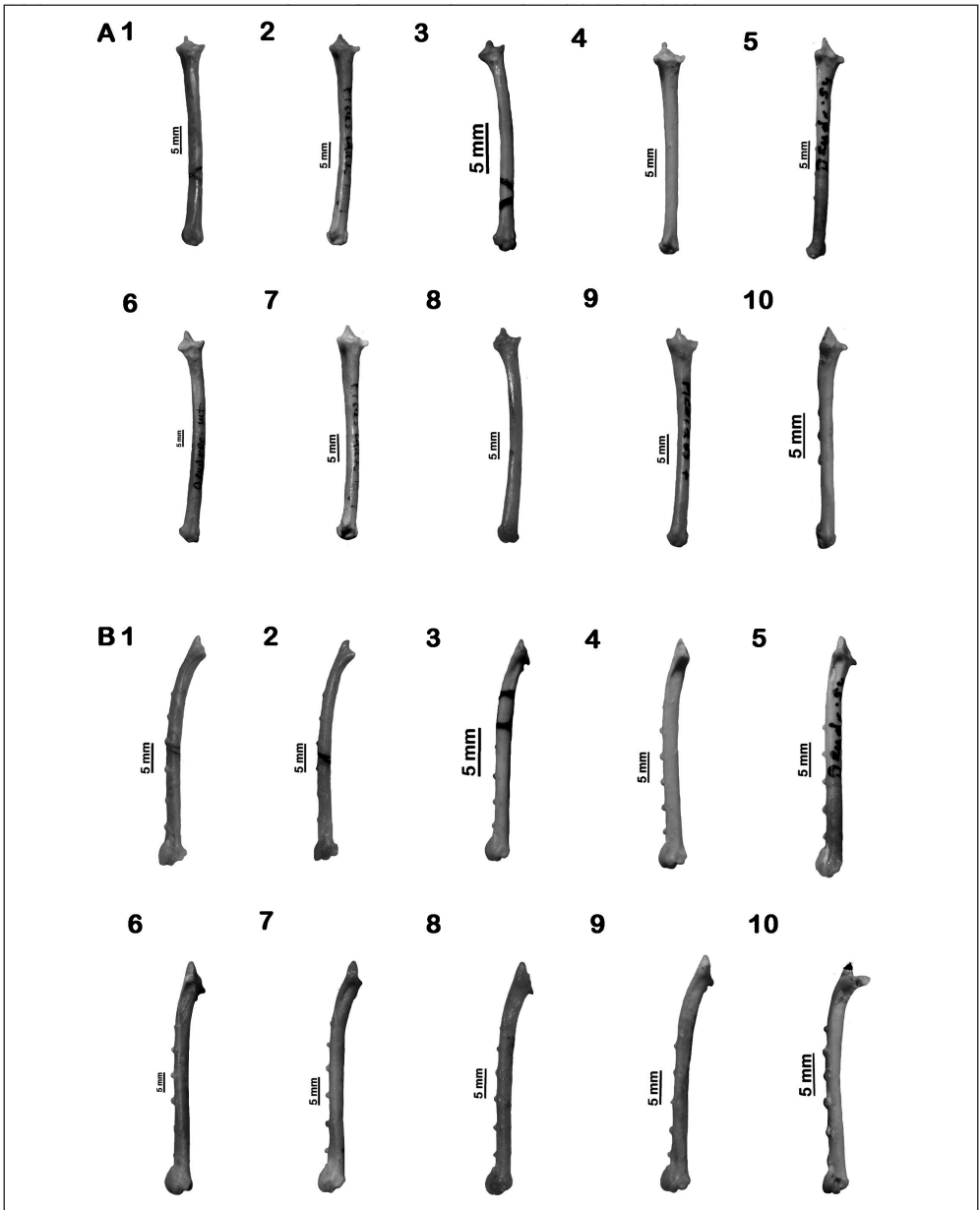
Táblakép 2.   Alsó állkapocs, dorsális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*
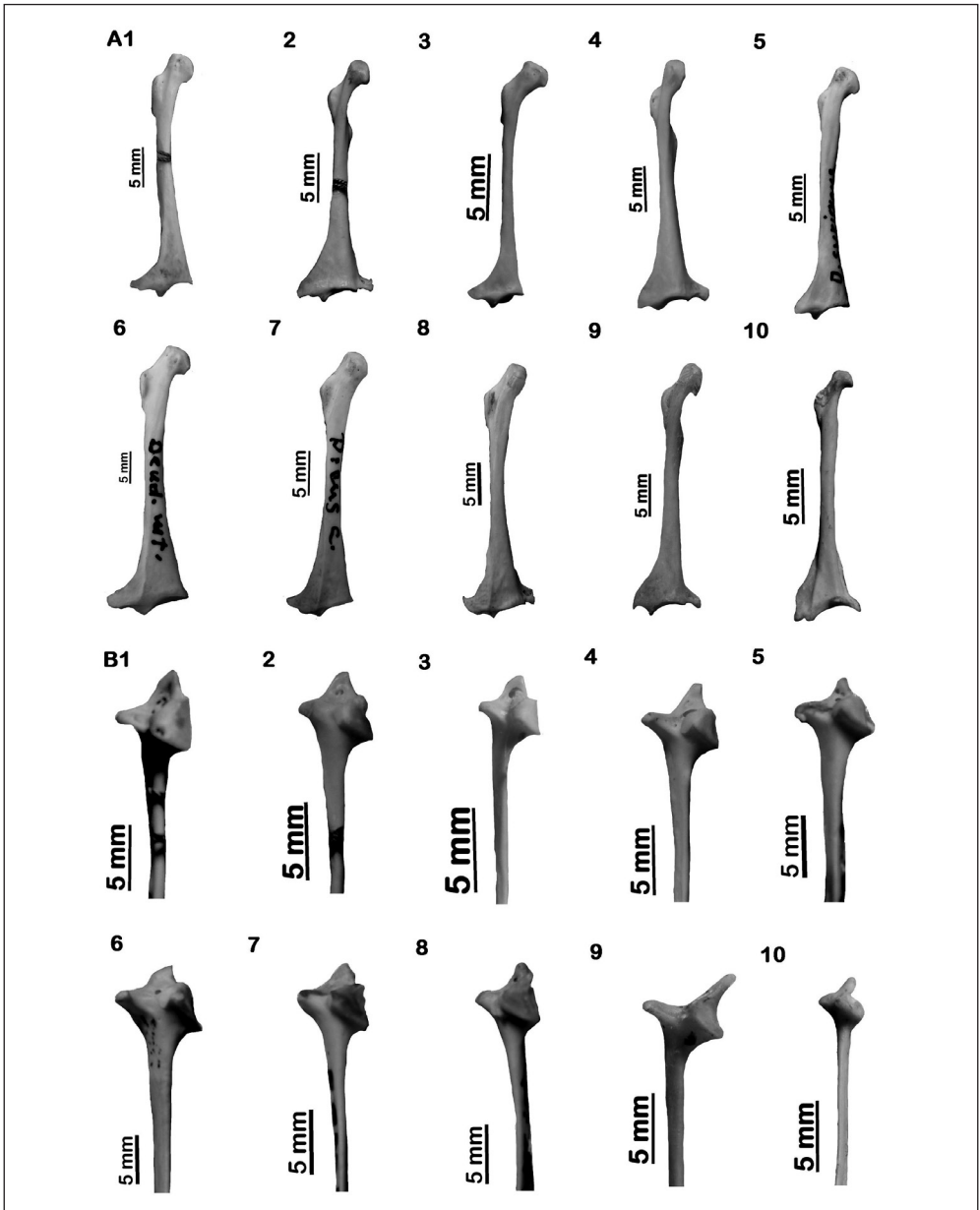
Plate 3.   A. *Coracoideum*, right side, ventral surface: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*
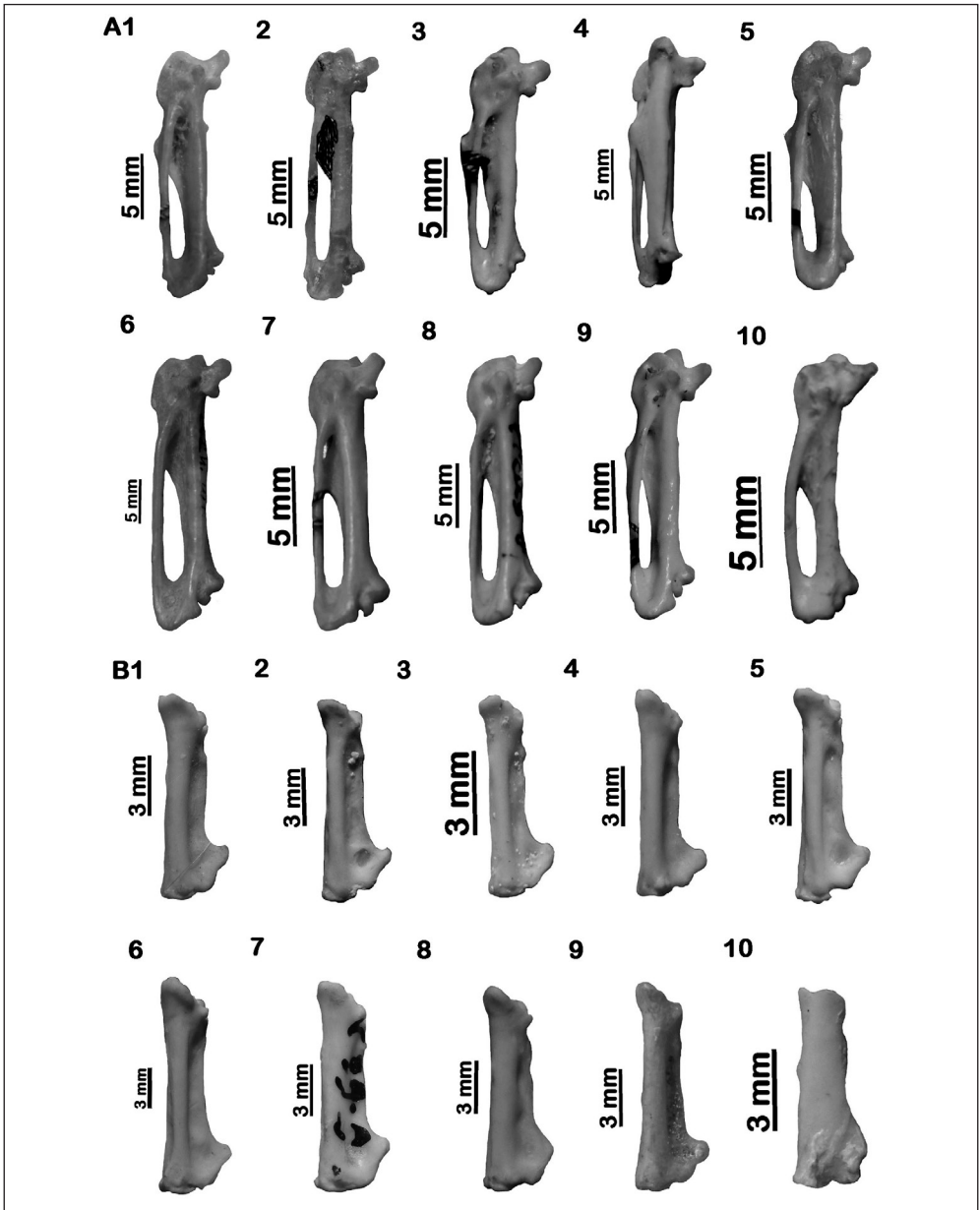
B. *Scapula*, left side, medial surface: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

Táblakép 3.   A. Hollócsőrcsont, jobboldali, ventrális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*.

B. Lapocka, baloldali, mediális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*
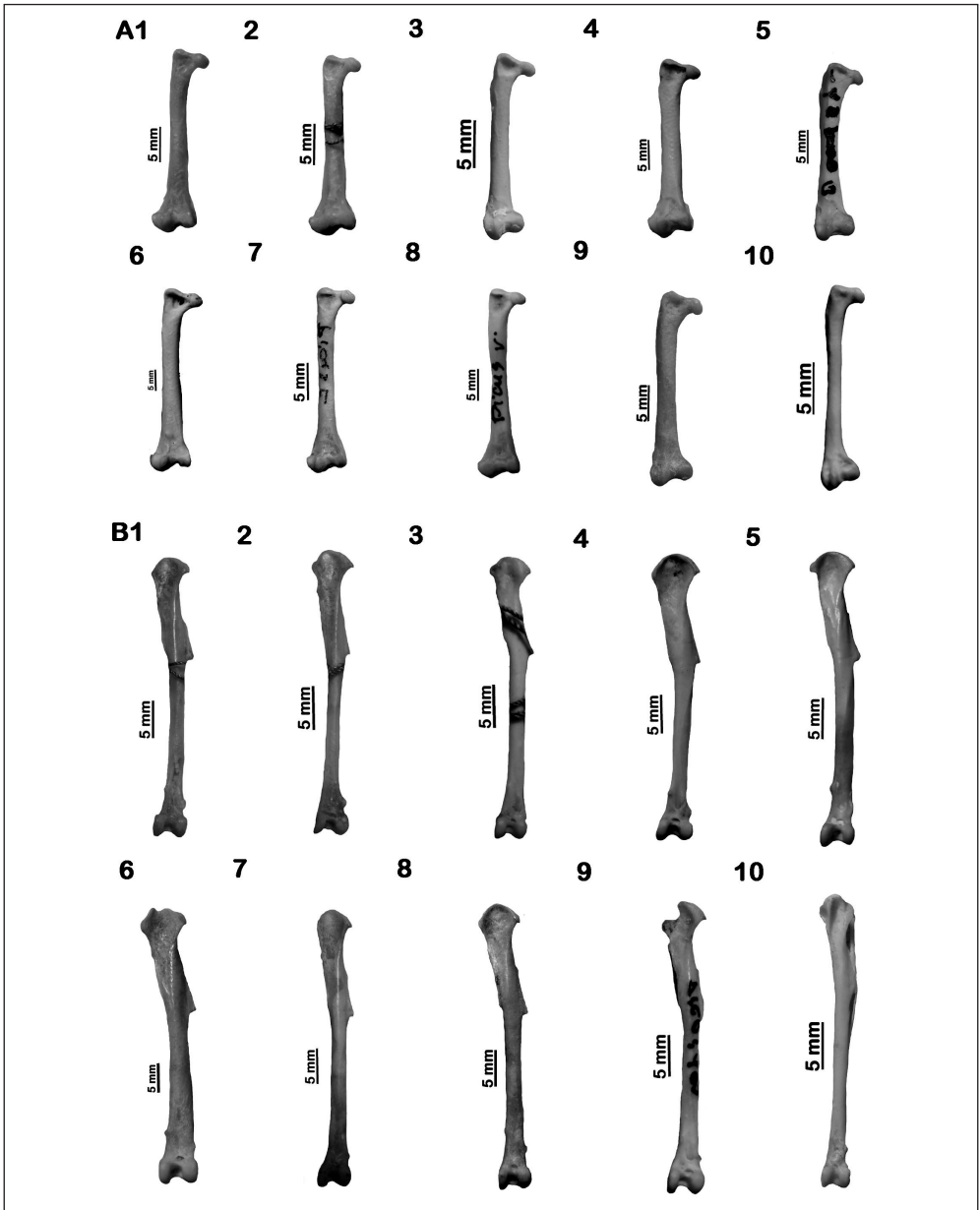
Plate 4.   A. *Humerus*, left side, caudal surface: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Jynx torquilla*.
B. *Humerus*, left side, cranial surface: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Jynx torquilla*

Táblakép 4.   A. Felkarcsont, baloldali, caudális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Jynx torquilla*.
B. Felkarcsont, baloldali, craniális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Jynx torquilla*

Plate 5. A. *Ulna*, right side, dorsal surface: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

B. *Ulna*, right side, medial surface: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

Táblakép 5. A. Singcsont, jobboldali, dorsális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*
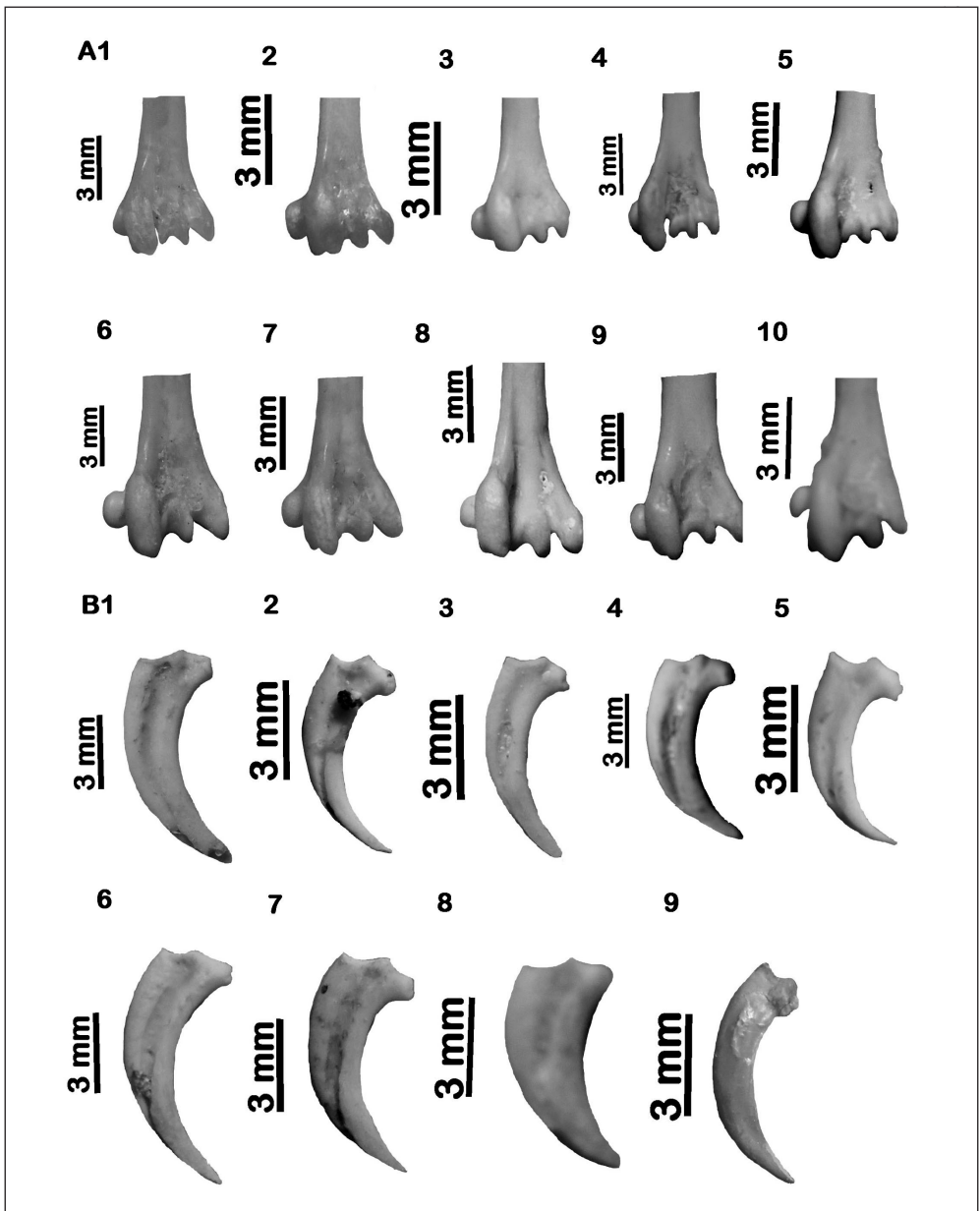
B. Singcsont, jobboldali, mediális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

Plate 6.   A. *Carpometacarpus*, left side, ventral aspect: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*.
B. *Phalanx proximalis digiti majoris*, left side, dorsal aspect: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

Táblakép 6.   A. Kézközépcsont, baloldali, ventrális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*.
B. II. jj, 1.ujjperc, baloldali, dorsális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

Plate 7. A. *Femur*, left side, caudal aspect: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

B. *Tibiotarsus*, left side, cranial aspect: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

Táblakép 7. A. Combcsont, baloldali, caudális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

B. Lábszárcsont, baloldali, craniális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*

Plate 8.   A. *Tarsometatarsus*, left side, dorsal aspect: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*
                    B. Claw, lateral aspect: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Picus canus*; 7. *Picus viridis*; 8. *Picoides tridactylus*; 9. *Jynx torquilla*

Táblakép 8.   A. Csüd, baloldali, dorsális nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Dryobates martius*; 7. *Picus canus*; 8. *Picus viridis*; 9. *Picoides tridactylus*; 10. *Jynx torquilla*
                    B. Karomcsont, oldalsó nézet: 1. *Dendrocopos major*; 2. *Dendrocopos medius*; 3. *Dendrocopos minor*; 4. *Dendrocopos leucotos*; 5. *Dendrocopos syriacus*; 6. *Picus canus*; 7. *Picus viridis*; 8. *Picoides tridactylus*; 9. *Jynx torquilla*

Respectively to skeletal parts, their characteristics are the following:

1. Mandibula (Plate 2):
  – a. the tip of the beak is:
    – very short: *Jynx*
    – short: *Picus*
    – long: *Dendrocopos, Dryobates, Picoides*
  – b. the recess between the stems is:
    – ovoid: *Jynx, Picoides, Picus*
    – ovoid, with recess in the middle: *Dendrocopos, Dryobates*
  – c. the stem is:
    – very long: *Jynx*
    – long: *Picus*
    – short: *Dendrocopos, Dryobates, Picoides*

2. Coracoideum (Plate 3A):
  – a. the processus acrocoracoidalis is:
    – straight, clublike: *Picus*
    – medially protuberant: *Dendrocopos, Dryobates*
    – medially pointening in a hook shape: *Jynx, Picoides*
  – b. the medial part of the sternal end is:
    – short and pointed: *Dendrocopos major*, *D. minor*, *D. syriacus*, *Dryobates*
    – shortly protrusive: *Picus*
    – protractedly protrusive: *Dendrocopos leucotos*, *D. medius*, *Jynx, Picoides*
  – c. the lateral part of the sternal end:
    – curves downward sharply: *Picoides*
    – curves upward sharply: *Picus*
    – curves downward bluntly: *Dendrocopos leucotos*, *D. medius*, *Jynx*
    – straight: *Dendrocopos major*, *D. minor*, *D. syriacus*, *Dryobates*

3. Scapula (Plate 3B):
  – a. the lateral projection is:
    – cone-shaped: *Dendrocopos*
    – curved, sharp: *Dryobates*
    – thick, with a cut-off end: *Picus*
    – narrow, long: *Jynx, Picoides*
  – b. the dorsal projection is:
    – cone-shaped: *Dendrocopos, Dryobates, Jynx, Picus*
    – long, narrow: *Picoides*

4. Humerus (Plate 4):
  – a. the crista biccipitalis is:
    – rounded: *Dendrocopos*

– cone-shaped: *Dryobates, Jynx, Picus*
   – b. the processus supracondylaris dorsalis is:
      – rounded: *Jynx, Picus*
      – slightly protruding cone shape: *Dendrocopos*
      – strongly protruding cone shape: *Dryobates*

5. Ulna (Plate 5):
   – a. olecranon:
      – pointed cone: *Dendrocopos medius, D. syriacus, Jynx*
      – blunt cone: *Dendrocopos minor, Dryobates, Picoides, Picus*
      – straight: *Dendrocopos major, D. leucotos*
   – b. cotyla dorsalis:
      – pointed cone: *Dendrocopos, Dryobates, Picoides, Picus*
      – straight: *Jynx*
   – c. the tuberculum carpale is:
      – rounded: *Dendrocopos minor, D. syriacus, Picus*
      – strongly protruding: *Dendrocopos major, D. medius*
      – slightly protruding: *Dendrocopos leucotos, Dryobates, Jynx, Picoides*

6. Carpometacarpus (Plate 6A):
   – a. the trochlea carpalis is:
      – simple: *Dendrocopos*
      – double: *Dryobates, Jynx, Picoides, Picus*
   – b. the processus extensorius is:
      – straight, with a rounded end: *Dendrocopos leucotos*
      – straight blunt cone: *Jynx*
      – oblique with a cut-off end: *Picus*
      – oblique with a rounded end: *Dendrocopos major, D. medius, D. minor,*
         D. syriacus, Dryobates, Picoides
   – c. the distal end of the metacarpus major is:
      – straight, wavy*: Dendrocopos leucotos, Jynx*
      – rounded: *Dendrocopos major, D. medius, D. minor, D. syriacus*
      – oblique: *Dryobates, Picoides, Picus*

7. Phalanx proximalis digiti majoris (Plate 6B):
   – a. the proximal end is:
      – straight, wavy: *Jynx*
      – oblique: *Dendrocopos, Dryobates, Picoides, Picus*
   – b. the distal end is:
      – straight: *Picus canus*
      – protruding: *Dendrocopos, Dryobates, Jynx, Picoides, Picus viridis*
   – c. the distal end of the dorsal side is:
      – rounded: *Jynx*

– cone-shaped: *Picus viridis*
– straight: *Dendrocopos leucotor, D. syriacus, Dryobates, Picoides, Picus canus*
– oblique: *Dendrocopos major, D. medius, D. minor*

8. Femur (Plate 7A):
– a. the condylus lateralis is
– laterally rounded: *Dendrocopos minor, D. syriacus, Jynx, Picoides*
– laterally protruding: *Dendrocopos leucotos, D. major, D. medius, Dryobates, Picus canus, P. viridis*

The morphological homogeneity is significant in the case of this skeletal part. What differs is the relative length of the diaphysis: it is long and slim in the *Jynx*, medium length in the *Picus*, while shorter in other genera.

9. Tibiotarsus (Plate 7B):
– a. the tuberositas retinaculi is:
– well-developed: *Dendrocopos leucotos, D. major, D. medius*
– moderately developed: *Dryobates, Jynx, Picoides, Picus*
– undeveloped: *Dendrocopos minor, D. syriacus*

Homogeneity is significant in the case of this skeletal part. In case of *Dendrocopos syriacus* and the *Dryobates,* a protrusion can be located above the epicondylus medialis. The diaphysis of the *Jynx* is long and slim, that of the *Dryobates,* however, is relatively short and thickset, whereas in case of the other genera, it is medium-size.

10. Tarsometatarsus (Plate 8A):
– a. trochlea metatarsi II:
– pointed: *Dendrocopos major, D. medius, D. minor, Dryobates, Picoides*
– rounded: *Dendrocopos leucotos, D. syriacus, Jynx, Picus*
– b. trochlea metatarsi IV.:
– semicircular: *Dendrocopos minor, D. leucotos, Picoides, Picus*
– ovoidal: *Dendrocopos major, D. medius, D. syriacus, Dryobates, Jynx*

This bone is the most typical skeletal part of the Picidae, i.e. on the distal end of the caudal side of the tarsometatarsus and on the medial side of the trochlea, a well-developed, spur-like rowel can be found. This is none other than the trochlea metatarsi I. (c). In case of other bird species, the I. metatarsus holding the first finger is not grown to the tarsometatarsus, while for the Picidae, it is, and its trochea leans forward between trochlea metatarsi II. and III. This is also valid for the *Picoides* and the *Jynx*, even though the *Picoides* have three fingers.

11. Distal phalanx (Plate 8B):
– a. the tuberculum extensorium:

– leans toward the apex: *Dendrocopos major, D. minor, D. leucotos. Picoides*
– leans forward: *Dendrocopos medius, D. syriacus, Picus, Jynx*
    – b. the cotyla articularis is:
        – symmetrically concave: *Dendrocopos medius, D. minor, D. leucotos,*
            D. syriacus, Picus, Jynx
        – asymmetrically concave: *Dendrocopos major, Picoides*
    – c. the tuberculum flexorium is
        – cone-shaped: *Picoides*
        – protruding, rounded: *Dendrocopos leucotos, D. medius*
        – protruding, prismatic: *Dendrocopos major, D. minor, D. syriacus, Picus*
        – flattened: *Jynx*

The fact that the distal phalanges of the 4 toes can differ in size and somewhat in appearance has to be taken into account. Thus, the characteristics presented here are provided for information purposes only, as well as their lengths in the size chart. The *Picoides* only has 3 distal phalanges respectively to the three toes. We did not have the opportunity to examine the distal phalanges of the *Dryobates*, since they were not present on the single skeleton found in the collection.

Name	TL-mand.	TL-corac.	TL-scap.	TL-hum.	TL-ulna	TL-cmcp.	TL-ppdm.	TL-fem.	TL-tibts.	TL-tmts.	TL-p.ung.
Dryobates martius	71.12	40.41	32.41	53.81	62.51	31.41	18.52	42.51	51.31	35.31	
Dendrocopos major	35.65	27.21	22.51	33.51	40.31	20.31	10.94	25.61	38.61	25.51	6.44
Dendrocopos medius	34.11	21.01	19.41	28.81	34.21	18.31	10.56	20.21	32.31	21.06	6.61
Dendrocopos minor	20.47	17.06	13.53	20.01	24.01	11.41	6.77	16.06	24.31	15.01	5.05
Dendrocopos syriacus	35.88	27.24	22.48	32.57	40.69	18.51	9.94	23.59	35.84	24.01	5.23
Dendrocopos leucotos	39.58	31.81	25.91	38.65	43.81	22.58	10.53	29.29	40.66	27.55	6.82
Picus viridis	55.21	31.21	27.01	35.71	44.06	21.51	12.96	28.81	41.71	26.31	9.64
Picus canus	51.03	30.21	27.02	36.21	42.41	20.42	11.06	28.51	41.21	26.51	9.31
Picoides tridactylus	36.41	25.96	20.71	30.01	35.61	18.53	9.98	24.63	33.89	22.71	7.66
Jynx torquilla	25.84	20.81	24.31	23.21	26.08	16.12	9.07	19.88	31.63	19.73	6.65

Table 1. Size table of recent woodpeckers
Abbreviations: TL-mand. – total lenght of mandible in mm; TL-corac. – total lenght of coracoid; TL-scap. – total lenght of scapula; TL-hum. – total lenght of humerus; TL-uln. – total lenght of ulna; TL-cmcp. – total lenght of carpometacarp; TL-ppdm. – total lenght of *phalanx proximalis digiti majoris*; TL-fem. – total lenght of femur; TL-tibts. – total lenght of tibiotars; TL-tmts. – total lenght of tarsometatars; TL-p.ung. – total lenght of *phalanx ungularis*
1. táblázat A recens harkályok mérettáblázata
Rövidítések: TL-mand. – állkapocs teljes hossza mm-ben; TL-corac. – hollócsőrcsont teljes hossza; TL-scap. – lapocka teljes hossza; TL-hum. – felkarcsont teljes hossza; TL-uln. – singcsont teljes hossza; TL-cmcp. – kézközépcsont teljes hossza; TL-ppdm. – II. kézujj, 1 ujjpercének teljes hossza; TL-fem. – combcsont teljes hossza; TL-tibts. – lábszárcsont teljes hossza; TL-tmts. – csüd teljes hossza; TL-p. ung. – karomcsont teljes hossza

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DE GRUYTER OPEN

A test on within-individual changes in risk-taking behaviour due to experience to predation in the Collared Flycatcher (*Ficedula albicollis*)

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Summary Different experiences from the past may have influence on individual's behaviour through feedback mechanisms that can weaken or preserve the within-individual consistency of behavioural traits. Here, we aimed to find evidence for such feedback mechanisms that may operate on risk-taking behaviour via the effect of former experience to potential predation events in male Collared Flycatchers *(Ficedula albicollis)*. We predicted that risk-taking of males would decrease after experiencing a predator's attack in previous breeding seasons (negative feedback). We assessed risk-taking by flight initiation distance (FID) that is the distance at which an individual flees from an approaching predator, which was estimated for 234 individuals from different breeding seasons. Information on predation experience (i.e. occurrence of nest predation, the incidence of capture by human observers) was available from our long-term database on individual life histories. In a horizontal approach, we found no difference in FID when comparing males with former experience to predation with males naive to predators. A longitudinal approach relying on the repeated tests of the same individuals from different years yielded analogous results, we could not show a significant change in the risk-taking behaviour of the males as a consequence of experience to predation in past years. However, we found that individuals systematically took less risk over the years, which might be a consequence of acquiring general experience with age.

Keywords: feedback mechanisms, predation, human handling, flight initiation distance

Összefoglalás A különböző múltbéli tapasztalatok visszacsatolásos mechanizmusokon keresztül hatással lehetnek az egyedek személyiségére, mert az ilyen visszajelzések gyengíthetik vagy konzerválhatják az egyedek viselkedésének konzisztenciáját. Kutatásunkban visszacsatolásos mechanizmusok létezésére kerestünk bizonyítékot a múltbéli predációs események egyedek kockázatvállaló viselkedésére gyakorolt hatásának vizsgálatával hím örvös légykapók *(Ficedula albicollis)* esetén. Predikciónk szerint a korábbi predációs tapasztalattal rendelkező hímek kockázatvállalása csökken a predációs eseményt követő költések során (negatív visszacsatolás). Az egyedek kockázatvállaló viselkedését a menekülési távolsággal (FID, Flight Initiation Distance) becsültük meg, ami azt a távolságot jelenti, amelynél a madár elrepül az őt megközelítő ragadozó elől. Az egyedek predációs múltjának feltérképezéséhez a hosszú távú költési adatbázisunkat használtuk. Összehasonlítva a predációs múlttal rendelkező és nem rendelkező hímek FID adatait (horizontális megközelítés), eredményeink alapján a predációs tapasztalattal bíró egyedek és naiv társaik kockázat vállalásában nem tudtunk különbséget kimutatni. Az egyedek különböző évekből származó ismételt mérésén alapuló vizsgálatai (longitudinális megközelítés) esetében sem tudtunk szignifikáns különbséget kimutatni a predációs tapasztalat alapján elkülönülő egyedek kockázatvállaló viselkedése között. Azonban azt találtuk, hogy az egyedek szisztematikusan kisebb kockázatot vállalnak az évek múlásával, ami a korral történő általános tapasztalatszerzésnek lehet a következménye.

Kulcsszavak: visszacsatolásos mechanizmusok, predáció, emberi kezelés, menekülési távolság

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Introduction

In the field of behavioural ecology, recent studies have discovered that there are consistent differences in behaviour among individuals within a population. Such variations describe animal personality, and have important evolutionary implications (Bell 2007). Behaviour can be considered consistent within an individual if it reacts similarly and displays more or less the same behavioural responses in different temporal and environmental contexts (Sih *et al.* 2004, 2012). However, behaviours can also vary within individuals, and such flexible responses could help animals to cope adaptively with the changing environmental conditions (behavioural plasticity, Dingemanse *et al.* 2009).

Animal personality and behavioural plasticity could be influenced by experiences through feedback mechanisms (Stankowich & Blumstein 2005). The future state of the individual could be affected by its current behaviour through experience, either in a negative or a positive way by further weakening or preserving the consistency of the given behaviour (Luttbeg & Sih 2010). For instance, if an individual is bolder, it may show more courage to protect the nest from an approaching predator. By defending the nest successfully, the individual could increase its reproductive success which permits the maintenance of the bold behaviour towards other predators (positive feedback, Sih 2011). However, being bolder may lead to injuries when defending the nest from predators thus jeopardizing the future survival of the offspring and the individual as well (negative feedback). Therefore, relying on past experiences, an individual has to optimise the expression of its particular behaviour in order to find the balance between the benefits and the costs in predatory situations.

In behavioural ecology, different behavioural traits can be classified into categories according to the underlying ecological challenge (Reale *et al.* 2007). One of these major domains is the risk-taking domain, which defines how individuals react in a predatory or in other risky situations, and it bears with a strong evolutionary and ecological significance. Risk-taking behaviour has been shown to have fitness consequences between individuals (Smith & Blumstein 2008). Bolder individuals in various species have higher reproductive success than their shier conspecifics, but they have a shorter lifespan (Reale *et al.* 2000, Korhonen *et al.* 2001). Like other behavioural traits, risk-taking behaviour can be consistent and plastic at the same time within individuals. Individuals depict behavioural reaction norms, which show how behaviour changes within individuals along an environmental gradient. The slope of these reaction norms indicates plasticity, while a systematic difference in their intercepts signifies consistent behavioural differences among

individuals. The most common influential factors that have been identified to trigger plastic risk-taking behaviour are predation (e.g. density of predators, Brown *et al.* 2005), the phase of the breeding season (Montgomerie & Weatherhead 1988) and the physiological condition of the individual such as parasite infections (Møller & Nielsen 2007) or testosterone level (Martins *et al.* 2007). As risk-taking behaviour can show remarkable plasticity, it can be hypothesized that former experiences induced by different stimuli influence the future risk-taking strategies of individuals through feedback mechanisms. Positive experiences may facilitate the maintenance of the current risk-taking behaviour as the individual can benefit from it, while experiences decreasing future reproductive success will alter the individual's risk-taking decisions.

Individual risk-taking can be measured as flight initiation distance (FID, Ydenberg & Dill 1986, Blumstein 2003) in different taxa, which is an inverse scale quantifying the distance at which a prey individual starts to flee when a predator is approaching. Collared Flycatchers *(Ficedula albicollis)* are proven to be a good model species to study risk-taking behaviour, as FID varies at the between-individual level, and individual-specific estimates of FID correlate with other behavioural traits like aggression in a Hungarian population (Garamszegi *et al.* 2015). In contrast to considerable within-year repeatability, between-year repeatability appeared to be low, which raises the question whether individuals can adaptively change their risk-taking behaviour from one year to the next, and such plasticity in FID can be attributed to former experiences to predation.

The aim of the present study was to explore the relationship between the risk-taking behaviour of male flycatchers and former experience to predation based on two different approaches (Gil *et al.* 2001, Van De Pol & Verhulst 2006). First, in a horizontal approach, we compared FID across individuals based on the presence or absence of former experience to predation. Such a horizontal approach, based on individual-specific (phenotypic) mean estimates does not allow discriminating the within-individual and between-individual effects statistically (Dingemanse & Dochtermann 2013, Garamszegi *et al.* 2013). Therefore, second, we also applied a longitudinal approach, in which we compared FID within the same males that were tested more than once during the study years, prior and after a predation event. We considered two stressful stimuli that can potentially contribute to the experience to predation. We distinguished i) whether individuals experienced any predation event at their nests during their life; and ii) whether individuals experienced any stress due to capturing and handling by humans during the standard ringing protocols. For the horizontal approach, we predicted that if former experience works as negative feedback, then males with experience to any of the two stimuli would take less risk compared to their naive conspecifics, so their FID would be higher. In case of the longitudinal analysis, we predicted that males experiencing nest predation or human handling between the two behavioural tests will generally take less risk in the second test compared to naive males.

Material and Methods

Study area and model species

Our research was carried out in the Pilis Mountains, Hungary. The study area is within an unmanaged, mainly oak-dominated, continuous woodland, which is protected by the Duna-Ipoly National Park. There are around 800 nest boxes on the study plots, where our model species, the Collared Flycatcher breeds together with other hole-nesting passerines such as the Great Tit *(Parus major)* and the Blue Tit *(Cyanistes caeruleus)*. The populations of these small passerine birds have been regularly monitored since 1983 (Török & Tóth 1988). The Collared Flycatcher nests naturally in tree cavities, and is a long-distance migratory species arriving to our breeding site from Africa in the middle of April. Male Collared Flycatchers arrive earlier than females, and compete for the best territories. Males and females do not differ in size, but they show sexual dimorphism in terms of feather colouration. Both sexes bear white wing patches, which are condition-dependent ornaments signalling individual quality (Török *et al.* 2003, Hegyi *et al.* 2008), while only males have a white forehead patch, which also has a signal function. It signals the physical condition of the individual, and it plays an important role in mate choice (Hegyi *et al.* 2010). Males with bigger forehead patches tend to find a mate earlier during courtship than males with smaller forehead patches.

Field work

For this study, we used data from nine years, from 2007 to 2015, in which we assessed the risk-taking behaviour of males by measuring FID (Garamszegi *et al.* 2009). We collected data only from males, because during courtship only their behaviour can be assessed around the nest-box, while a similar procedure cannot be established for females. The assessment of risk-taking started with provoking the focal male into a territorial dispute by placing a decoy male flycatcher in a small cage as an intruder on the focal male's territory (by doing so we achieved that each focal bird was engaged in the same background behavioural activity before assessing FID). When the focal male was observed on the stimulus cage, the observer began to approach it from about 30 m, until it took notice of the presence of the potential predator, and flew away from the decoy's cage. If the resident male returned to continue the territorial dispute within 1 minute, the experimenter proceeded walking towards the focal bird. The process was repeated up to the point where the focal male did not come back anymore to the cage within a minute (all individuals returned at least once). FID was measured by the number of steps (approx. 1 m) between the decoy's cage and the last position of the observer where the male did not return. After the behavioural tests, we caught the males at their nest boxes by using conventional spring traps and ringed them for long-term identification.

We considered two different stressful stimuli as components of predation experience in the analyses. In one hand, we specified whether the tested individual suffered nest predation (former experience to predators). We considered a nest predated if any of the following

events were detected during the standard nest box monitoring between egg laying and chick-feeding period: nest structure was disarranged and/or nest material was pulled out of the nest box and/or torn feathers covered the surroundings. The most common nest predators of flycatchers are stoats, weasels, martens and woodpeckers (Lundberg & Alatalo 1992). On the Hungarian study site, flycatcher nests are mainly predated by small mammalian nest predators such as weasels, martens and cats. On the other hand, we defined whether the male flycatcher experienced any incidence of human handling prior to the behavioural test. Every male wearing a ring for identification was considered experienced to handling, as males always have to be captured for ringing. We used our long-term database to determine the history of these events within each male's lifetime.

Statistical approaches

We studied the relationship between experience to predation (true predator or human handling) and risk-taking behaviour using two different approaches. In the horizontal approach, we aimed to capture the presence of the feedback mechanism by comparing FID of males with former experience to predation or human handling to FID estimates of males naive to predators or humans, sampling the whole population. In this case, we could utilize a larger sample size (N=234). In the longitudinal approach, we focused on males, for which we had repeated FID estimates from different years. In this sample, we determined how the FID value changed between the two tests of the same individuals. Furthermore, we assessed whether this change differed between experienced and naive males with respect to predation. In the case of experience to nest predation, the sample size was 16, while the sample size was 19 when the former experience was related to human handling. In these longitudinal tests, we used different groups of individuals for each type of experience (naive to either nest predation or human handling), as control reference (N=10 and N=7 respectively).

We used general linear mixed models to determine the possible role of a life-threatening experience on individual risk-taking decisions. We used the log10-transformed form of FID in all statistical analysis to ensure the normal distribution of model residuals. We run three different statistical models. In the horizontal approach, the model contained the experiences to predation and human handling, the age of the individuals and the day when the test was carried out as predictors. We included random factors in the model to control for the hierarchical structure of the data. We used the same decoy bird in several experiment to provoke aggressive behaviour before the assessment of FID, thus we used the ring number of decoy males as a random factor (N=36 decoy males). In a few cases, we had multiple data from the same individual, thus we also entered the ring number of tested males to control for pseudoreplication (note that within-individual and temporal order effects are tested in the longitudinal model). Finally, we considered observer and year effects to partition variance components in the model via the appropriate random factors. In our dataset, there were several naive males not experiencing any predation events (N=211) that could all be used as controls, but these controls could have different association with males experiencing nest predation. We discriminated between historical and true controls (Kramer & Font 2015) based on whether they were tested on the same day as the experienced males. To achieve this we

created a new binary variable, named 'day code', characterising whether naive individuals in the analysis were tested on the same day or not with regard to the experienced males. This variable was used as random factor to model historical and true controls. In the longitudinal approach, we defined two models based on the type of experience, which contained the experience itself, the relative order of the two behavioural tests, and the age of the males as predictors. We entered the same random effects in these models than in the previous one.

We used likelihood ratio tests to determine χ^2 and p-values corresponding to particular predictors (achieved by comparing models including and lacking the respective predictor). As the main question of our research was to investigate whether former experience has any effect on the risk-taking behaviour of the males when controlling for the effects of potentially interfering factors, primarily we were interested in the full model and accordingly we did not perform further model selection for the fixed effects (we note however that if we exclude non-significant terms from our models, the main findings of the study do not change with respect to those we report below). Concerning the random effects, we simplified our final models by excluding terms that had lower variances than 0.001.

Before interpreting the model outputs, we performed appropriate model diagnostics to determine whether all the necessary model assumptions were valid by checking the normal distribution of model residuals with q-q plots, checking the normality of the random effects and inspecting multicollinearity by calculating VIF (O'Brien 2007). All statistical analyses were performed in R statistical environment (R Development Core Team 2015) using '*lme4*' package (Bates *et al.* 2015).

Results

Horizontal approach

The results of the statistical model built to test the effects of former experience on risk-taking behaviour are given in *Table 1*. We found no significant difference in FID between males with and without former experience to predation. Males experiencing nest predation at least once in their lifetime did not take less risk during the tests than their conspecifics that were naive to predators. The experience to human handling also had no significant effect on FID. Ringed males did not tend to be more cautious than males without experience to humans. Similarly, the date of the test had no significant effect on risk-taking behaviour. On the other hand, the FID estimates depended significantly on the age of the individuals, older males taking less risk than younger conspecifics. We excluded the ring of the tested males, the observer and the day code from the random factors because of their low variance (<0.001).

Longitudinal approach

Studying the relationship between experience to predation and risk-taking behaviour of repeatedly tested males, we found no significant effect of former experience on FID *(Figure 1,*

Predictor variables	β(SE)	t	LRT χ2	P
experience to predation	0.031 (0.069)	0.447	0.185	0.667
experience to handling	0.019 (0.045)	0.265	0.094	0.759
date	0.0003 (0.004)	0.073	0.001	0.977
age	**0.036 (0.017)**	**2.158**	**4.826**	**0.028**

Random effects	Variance	Standard deviation
male decoy	0.004	0.066
year	0.005	0.070
residual	0.077	0.278

Table 1.   The results of the horizontal analysis representing the relationship between flight initiation distance (FID) and the examined predictor variables: the experience to predation and human handling, the day when the tests were carried out and the age of the males. The random factors in this model were the ring of the male decoys and the year when the tests were carried out. P-values are shown based on likelihood ratio tests (LRT). N=234

1. táblázat A múltbéli tapasztalatok és a menekülési távolság (FID) közötti kapcsolat horizontális megközelítés esetén. A modellben magyarázó változóként szerepel a predációs múlt, az emberi kezelésből származó tapasztalat, a tesztek dátuma (nap) és a hímek kora. Random változóként a csali hím gyűrűszáma és a kísérlet éve szerepel. A P-értékek a likelihood-hányados tesztekből (likelihood ratio test) származnak. N=234

Table 2). However, the order of the tests was a significant predictor of risk-taking in case of experience to predation with increasing FID values from year to year. In this model, the FID estimates did not depend significantly on the age of the individuals. We excluded the ring of the decoy male, the year, the observer and the day code as their variance was lower than 0.001. The results of the other model studying experience to human handling showed that males experiencing human handling did not take significantly less risk than their conspecifics without experience *(Figure 2, Table 3)*. Neither the order of the tests, nor the age of the individuals correlated significantly with the FID estimates. We excluded the ring of the decoy male, the year, the observer and the day code because of their low variance (<0.001).

Discussion

In this study, we investigated the relationship between former experiences to potentially life-threatening stimuli and risk-taking behaviour in male Collared Flycatchers. The main hypotheses were that individuals with experience to predation or human handling would take less risk than their naive conspecifics. We found no evidence that former experience to predation had any effect on the risk-taking decisions, neither in the horizontal, nor in the longitudinal approaches. When studying the effect of experience to human handling, we got the same results as mentioned above. However, in the horizontal analysis the risk-taking behaviour of the males depended on their age.
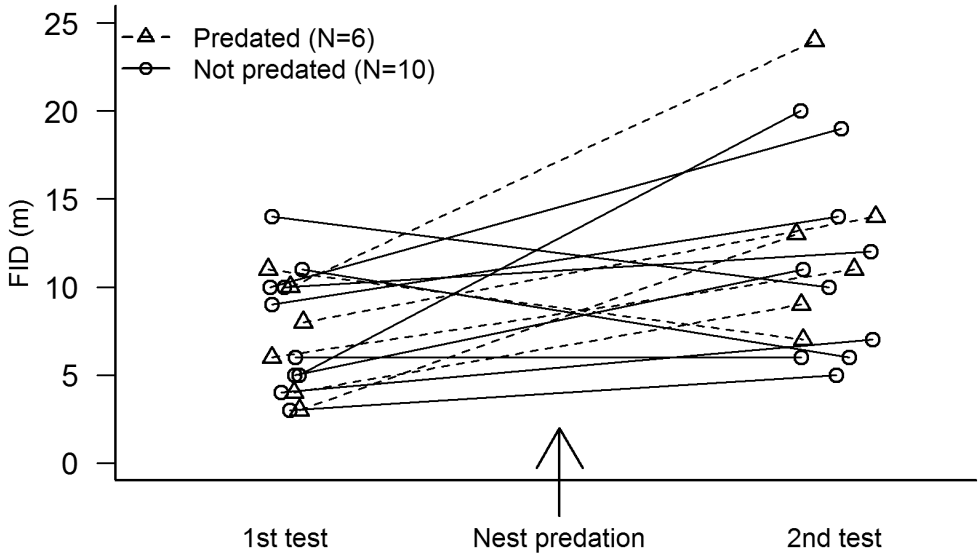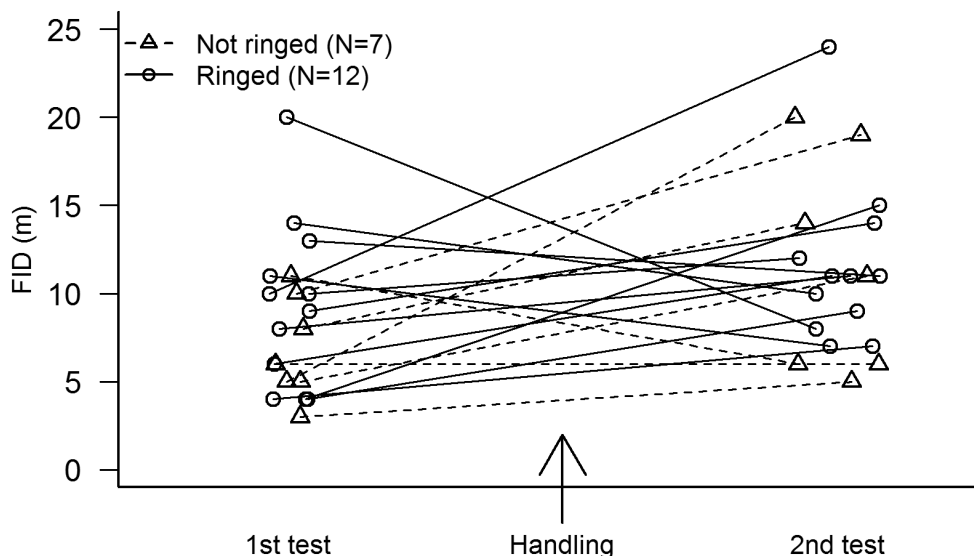
Figure 1.   The changes in the flight initiation distance (FID) of flycatcher males that were repeatedly tested in two consecutive years. The triangles and dashed lines represent males with experience to predation, while the circles and continuous lines describe individuals naive to predators

1. ábra   A FID változása a két különböző évben elvégzett teszt között. A predációs múlttal rendelkező egyedeket háromszöggel és szaggatott vonallal, a predációs múlttal nem rendelkező egyedeket pedig körrel és folytonos vonallal jelöltük

Predictor variables	β(SE)	t	LRT χ2	P
experience to predation	0.037 (0.090)	0.406	0.188	0.664
order	**0.181 (0.079)**	**2.302**	**4.446**	**0.035**
age	0.011 (0.028)	0.389	0.229	0.632

Random effects	Variance	Standard deviation
ring	0.012	0.111
residual	0.034	0.184

Table 2.   The results of the longitudinal analysis representing the relationship between flight initiation distance (FID) and the examined predictor variables: the experience to predation, the chronological order of the tests and the age of the males. The random factor in this model was the ring of the tested males. P-values are shown based on likelihood ratio tests (LRT). N=16

2. táblázat   A predációs múlt és a menekülési távolság (FID) közötti kapcsolat az egyedek ismételt mérése esetén. A modellben magyarázó változóként szerepel a predációs tapasztalat, a tesztek sorrendje és a hímek kora. Random változóként a tesztelt hím azonosítója szerepel. P-értékek a likelihood-hányados tesztekből (likelihood ratio test) származnak. N=16

Figure 2. The changes in the flight initiation distance (FID) of flycatcher males that were repeatedly tested in two consecutive years. The triangles and dashed lines represent naive males with no experience to human handling, while the circles and continuous lines describe experienced individuals

2. ábra A kockázatvállaló viselkedés változása a két különböző évben elvégzett teszt között. A gyűrűvel nem rendelkező egyedeket háromszöggel és szaggatott vonallal, a gyűrűvel rendelkező egyedeket pedig körrel és folytonos vonallal jelöltük

Predictor variables	β(SE)	t	LRT χ2	P
experience to handling	0.135 (0.077)	1.738	3.263	0.071
order	0.127 (0.074)	1.722	3.129	0.077
age	-0.0004 (0.023)	-0.018	0.0002	0.988

Random effects	Variance	Standard deviation
ring	0.001	0.028
residual	0.037	0.193

Table 3. The results of the longitudinal analysis showing the relationship between flight initiation distance (FID) and the examined predictor variables, the former experience to human-handling, the chronological order of the tests and the age of the males. In this model the random factor was the ring of the tested males. P-values are shown based on likelihood ratio tests (LRT). N=19

3. táblázat Az emberi megfogásból származó tapasztalat és a menekülési távolság (FID) közötti kapcsolat a longitudinális elemzés esetén. A modellben magyarázó változóként szerepel a múltbéli tapasztalat emberrel, a tesztek sorrendje és a hímek kora. Random változóként a tesztelt hím azonosítója szerepel a modellben. P-értékek a likelihood-hányados tesztekből (likelihood ratio test) származnak. N=19

In the horizontal approach, we investigated the between-individual component of the phenotypic change in risk-taking behaviour. Using all available data, we could operate with a bigger sample size and thus we were able to search for patterns in risk-taking behaviour in general based on former experience. As the horizontal approach could not give information about within-individual changes, we applied a longitudinal approach to separate the between- and within-individual effects of the risk-taking behaviour. In this case, we could focus on the within-individual changes but we had to operate with a smaller sample size. Despite of the two different statistical approaches, neither proved that a negative feedback mechanism via former experience to predation or human handling would mediate the risk-taking behaviour of male flycatchers, as individual experience to any of the two stimuli did not predict FID estimates.

For the lack of any effect of the experiences on risk-taking behaviour, we suggest the following explanations. In case of experience to predation, a possible reason behind our observations may be that the influence of a single predation event (that we considered in our study) is too small to be detected in our sample by using observational data instead of performing targeted experiments. For example, one event of nest predation can have no detectable influence on the risk-taking decisions, because the males may need repeated stimuli to alter their behaviour as it was shown in mice (Kinsey *et al.* 2007). Additionally, experienced males may not necessarily take less risk than their conspecifics naive to predation but may also increase risk-taking (Oosten *et al.* 2010). Based on our observations, predators do not always destroy the whole nest, which could be a consequence of successful nest defence of the focal male. Saving part of the nestlings could encourage the male to take greater risk next time when encountering a predator to save even more of its offspring. Note that in the longitudinal approach, we operated with a relatively small sample size, so it remains plausible that if we could collect more data from repeatedly tested males in the next few years, the relationship between risk-taking behaviour and experience to predation would turn significant.

We note that some of the non-significant effects in relation to human handling involved biologically meaningful tendencies that fall in the expected direction (which were close to statistical significance). This may suggest that we would need a larger sample size by repeatedly testing the same male in different years to make strong conclusions about these effects. In any case, this also implies that our analysis for human handling may partially suffer from insufficient statistical power. As an explanation, it is possible that one encounter with humans at the ringing procedure is not a sufficient stimulus to alter individual risk-taking decisions, just like in case of real predation. Another reason for the failure of finding a significant effect is that males were ringed far from their nest boxes at our field station, and the ringing process did not have serious impact on the birds, thus such an experience may serve as a weaker stimulus. It is possible that the stress connected with the ringing procedure was not sufficient enough to alter considerably the future risk-taking behaviour of ringed males.

We found a significant relationship between the FID and the age of male flycatchers in the horizontal approach, similarly to another study (Jablonszky *et al.* 2016 submitted) showing that older individuals have higher FID values and are more cautious than their younger conspecifics. Moreover when studying the effect of the experience to predation in

the longitudinal approach, we were able to show within-individual changes in risk-taking behaviour, individuals taking less risk during the second than in the first tests. In the background of these observed patterns, the following causes may stand. The relationship between risk-taking decisions and age could be explained through the process of aging. With age, the physiology of the individual alters and its physical condition decreases (Vleck *et al.* 2011). For an older individual, it might be more important to pursue an energy saving strategy (Lecomte *et al.* 2010) thus avoiding acting bolder (Patrick *et al.* 2013). On the other hand, experiences collected through the years could stand in the background of the relationship as well (Dill 1974, Ydenberg & Dill 1986). An older male may be more skilful detecting the approaching predator than its younger conspecifics, so it flees away earlier to avoid the rush (Blumstein 2010).

Furthermore, the results could also be mediated by effects due to aging or experience that are acting on aggression and not on risk-taking *per se*. In another study of our Hungarian population, a relationship has been shown between the aggressive behaviour and the age of male flycatchers. The latency of the first attack of the focal male on the cage of the stimulus male was shorter in yearlings than in adult individuals, which means that older individuals were less aggressive (Garamszegi *et al.* 2006). Huntingford and his colleagues (2012) showed a positive relationship between territorial aggression in the breeding season and risk-taking behaviour, aggressive Three-spined Stickleback *(Gasterosteus aculeatus)* males being significantly bolder than their unaggressive conspecifics. If aggression and risk-taking behaviour depends on each other in a positive way, and aggression decreases with age, than it is possible that risk-taking behaviour shows a similar decreasing pattern with age. Moreover, since we brought each individual into a territorial conflict prior to the assessment of FID, it is also plausible that older/experienced individuals that did not invest heavily into aggressive territorial defence could notice the approaching predator earlier. This mechanism mediated by the detection of the predator would also result in longer FID in older males.

In conclusion, we did not find any significant influence of former experience to predation or human handling on the risk-taking behaviour of male Collared Flycatchers, thus we were unable to provide support for a negative feedback mechanism. However, in the horizontal approach, we found an age effect indicating that older individuals decrease their risk-taking over the years, which might be a consequence of aging or experience.

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Migration routes and stopover sites of the Eurasian Spoonbill *(Platalea leucorodia)* between the Carpathian Basin and wintering areas

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Abstract Understanding the migration routes of the Central European Spoonbill population is important for their conservation. Here we analysed movements of 3186 individuals of Eurasian Spoonbills marked with colour rings in the Carpathian Basin (Hungary, Croatia and Serbia) between 2003 and 2015, and a satellite tagged individual, which was equipped in Italy in 2013, and later moved to the Carpathian Basin. Migration routes of these Spoonbills predominantly followed the Adriatic Flyway, however, some birds were also found to both east and west from this flyway. We identified 59 stopover sites, 55 of which were located along the Adriatic Flyway. Colour-ringed juveniles (1cy), on average, spent 4.0±0.9 (SE) days on the stopover sites along the Adriatic Flyway during autumn migration, while non-juveniles (> 1cy) spent 2.6±1.0 (SE) days during autumn and 2.1±0.4 (SE) days during spring migration there. These durations were not significantly different. Duration of stops of the satellite tracked individual was between 7 and 15 days during autumn and between 1 and 12 days during spring migration. Our results indicate the existence of two alternative routes of the Adriatic Flyway between the Carpathian Basin and the wintering areas in southern Italy and the central part of coastal North-Africa. The North-Adriatic Flyway includes stopover sites in north-eastern Italy at the river mouth of River Isonzo, Lagunes of Venice and wetlands around River Po. The South Adriatic Flyway leads through the Balkan Peninsula, with stopover sites at the karst lakes of Bosnia and Herzegovina, mouth of the river Neretva (Croatia), Ulcinj Salinas (Montenegro) and wetlands in Gulf of Manfredonia (Italy). This hypothesis was also supported by the migration of the satellite tagged individual, the paths of which was described here in detail. The average coordinates of spring and autumn stopover sites were located at different parts of the flyway: it was in south-western Italy during autumn migration, while it was close to the western coast of the Balkan Peninsula during spring migration. We found examples for Spoonbills using the same migration paths along the same route year by year on both spring and autumn migration, but also noticed shifts between routes. Some observations indicate that individuals may show site fidelity to stopover sites between years, although the sample size was low for statistical significance.

Keywords: colour ring, GPS tracking, nature conservation, Black Sea/Mediterranean Flyway, Adriatic Flyway

Összefoglalás A kanalasgémek vonulási útvonalának ismerete lényeges a védelmük szempontjából. Ebben a dolgozatban 3186 színes gyűrűvel jelölt és egy jeladós kanalasgém vonulását elemeztük. Ezeket a madarakat 2003 és 2015 között a Kárpát-medencében (Magyarországon, Horvátországban és Szerbiában) gyűrűzték, míg a jeladót 2013-ban Olaszországban helyezték fel, ez a madár később a Kárpát-medencében is felbukkant. A Kárpát-medencei kanalasgémek vonulásuk során elsődlegesen az adriai vonulási utat követték, de kisebb számban ettől keletre és nyugatra is megjelentek. Összesen 59 megállóhelyet határoztunk meg, melyből 55 az adriai vonulási útvonalon található. A színes gyűrűs fiatalok ősszel átlagosan 4,0±0,9 (SE) napot töltöttek a megállóhelyeken az adriai

vonulási útvonal mentén, míg az ettől öregebb madarak ősszel 2,6±1,0 (SE), illetve tavasszal 2,1±0,4 (SE) napra álltak meg. Ezek az értékek nem különböztek szignifikánsan. A jeladós madár ősszel 7–15, míg tavasszal 1–12 napra állt meg. Az adriai vonulási úton belül két alternatív út létezik a Kárpát-medence, illetve a dél-olaszországi és észak-afrikai telelőhelyek között. Az észak-adriai ág megállóhelyei Északkelet-Olaszországban az Isonzó torkolatánál, a Velencei-lagúnákon és a Pó körüli vizes élőhelyeken találhatóak. A dél-adriai ág a Balkán-félszigeten vezet át, megállóhelyei a Bosznia-Hercegovina területén elhelyezkedő karszt-tavakon, a Neretva torkolatában (Horvátország), az Ulcinj (Montenegró) melletti sólepárlókon találhatóak és a Manfredóniai-öböl (Olaszország) vizes élőhelyein. Ezt a mintázatot a jeladós madár követése is alátámasztotta. Az őszi és a tavaszi koordináták átlagai eltérnek: ősszel Délnyugat-Olaszországra, míg tavasszal a Balkán-félsziget nyugati partvidékére esnek. A madarak egy része évről-évre ugyanazon a vonulási ágon vonul ősszel és tavasszal is, de ismert olyan egyed is, ami két szezonban különböző ágon vonult. Vannak a megállóterület-hűségre utaló adatok, de a mintaszám alacsony volt a statisztikai különbségek kimutatásához.

Kulcsszavak: színes gyűrű, GPS nyomkövetés, természetvédelem, fekete-tengeri/mediterrán vonulási út, adriai vonulási út

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Introduction

Avian migration is a regular, endogenously controlled, seasonal movement of birds between breeding and non-breeding areas. Migration includes two trips: from breeding grounds to non-breeding grounds and back (Salewski & Bruderer 2007). These journeys are repeated in the same time of the year (Newton 2008).

Three major flyways used by shorebirds have been recognised between Eurasia and Africa together with the Middle East (Stroud *et al.* 2004). The East Atlantic Flyway runs along the Atlantic coasts of Europe and Africa (Stroud *et al.* 2004, Triplet *et al.* 2008). The West Asian/East African Flyway links the central Siberian tundra to the Caspian Sea, the Middle East (especially the Gulf Region) and eastern and southern Africa (Stroud *et al.* 2004, Schneider-Jacoby 2008). The Black Sea/Mediterranean Flyway joins arctic and boreal regions with final destinations in the Mediterranean Basin and West Africa (Stroud *et al.* 2004). The Black Sea/Mediterranen Flyway is used not only by shorebirds, but also by several other waterbird species during their migration. This flyway is the only one that crosses the Mediterranean Basin. Part of the Black Sea/Mediterranean Flyway is referred to as the Adriatic or Central European Flyway, which is one of the most important flyways for Central European waterbirds (Schneider-Jacoby 2008, Stumberger & Schneider-Jacoby 2010). The wintering areas of waterbirds along the Adriatic Flyway are found at the Mediterranean coast, mainly in Tunisia, but large number of birds may continue the migration to

the Niger Basin after crossing the Sahara (Schneider-Jacoby 2008, Stumberger & Schneider-Jacoby 2010).

Birds usually do not choose the most direct and shortest routes during their migration, but rather fly along detours (Alerstam 2001). For example, birds preferably migrate along detours to avoid crossing large barriers (desert, large mountains, sea) (Alerstam 2001, Alerstam *et al.* 2003). Several other factors affect the decision to take detours, including differences in wind and weather conditions, availability of stopover sites, risk of predation and starvation, drift and disorientation (Alerstam 2001).

A number of sites between breeding and non-breeding areas, called stopover or staging sites, connect migratory paths during bird migration (Navedo *et al.* 2010b, Warnock 2010). These are important for birds as feeding, drinking, moulting and resting sites (Kirby *et al.* 2008, Navedo *et al.* 2010b, Warnock 2010). These are also used during stochastic adverse weather events as emergency sites as these areas often provide shelter for migrating birds (Overdijk & Navedo 2012). There are three main strategies in the use of stopover or staging sites, regarding the duration of stay and the distance between sites: hopping, skipping and jumping. Birds employing hopping or skipping strategies have short stops (often only for few of days) and relatively short subsequent flights to the next stop with relatively low fuelling rates and fuel loads. The distance between sites can be as large as hundreds of kilometres, with the distance covered by hoppers being shorter than that covered by skippers. Areas used by birds with hopping or skipping strategies have been referred to as stopover areas (Warnock 2010). In contrast, jumpers that cross barriers during their migration, where there is little chance of stopping, usually carry large amount of fuel that exceeds the optimally predicted amounts. To accumulate this fuel, birds usually stay on staging sites for longer periods (often for weeks), and they usually fly thousands of kilometres after departure (Warnock 2010).

Migratory waterbirds usually find only some patchily scattered stopover and staging areas and, the distances among these are usually relatively large. This is especially true for long-distance migrants (Navedo *et al.* 2010a, 2010b). A large number of bird species and individuals use these sites during an energetically demanding part of their annual cycle, therefore, it is important to identify and protect these stopover and staging sites. Additionally, conditions experienced at stopover or staging sites may affect not only the success of migration, but also future individual survival and reproduction, often referred to as carry-over effect, with potential consequences for population dynamics (Navedo *et al.* 2010b, Warnock 2010).

The Eurasian Spoonbill *(Platalea leucorodia)* has a large breeding area spanning between the Atlantic coast of Europe and the Pacific coast of Asia with two small populations in sub-Saharan Africa (Triplet *et al.* 2008). The Spoonbill is a specialist waterbird, largely depending on the presence of wetlands with water of suitable depth, as they are able to forage only in shallow water (Pigniczki & Végvári 2015).

A part of the Central European Spoonbill population breeds in the Carpathian Basin with the largest population located in Hungary. Large numbers (100+ pairs) of breeders are also found in Austria, Croatia and Serbia, while only small populations exist in Slovakia, and irregular breeders in small numbers occur in western Romania (Pigniczki & Végvári 2015). Spoonbills also breed regularly in the Czech Republic, from where birds migrate across the

Carpathian Basin (Cepák 2008). Spoonbills from Central Europe winter mainly in Tunisia, with a large number of wintering individuals also found in Italy. Only a few wintering individuals are known from Turkey, Greece, Egypt, Sudan, Libya, Algeria, Morocco, sub-Saharan Africa between Niger and Mauritania, as well as from the Carpathian Basin (Pigniczki 2009, 2010, 2015, Kralj *et al.* 2012, Pigniczki & Karcza 2013).

The Eurasian Spoonbill is a characteristic species of the Adriatic Flyway (Schneider-Jacoby 2008, Pigniczki 2010, Kralj *et al.* 2012), thus Schneider-Jacoby (2008) recommended it as one of the flagship species along this flyway to improve the protection of key sites. The Spoonbill is an umbrella species (Pigniczki & Végvári 2015) and this increases the need for the conservation of its habitats used around the entire annual cycle. Although its main stopover sites have already been identified in the northern part of West Balkan between Slovenia and Northwest Albania (Stumberger *et al.* 2013), information on migration routes and other stopover sites are still missing (Schneider-Jacoby 2008) and knowledge of the connectivity among different stopover sites along the flyways is very limited.

The aims of this study were to (1) identify the migration routes, stopover and staging areas of the Central European Spoonbill population using individually marked individuals, and (2) identify the possible connection of those wetlands.

Materials and Methods

We used resights of colour-ringed Spoonbills marked as chicks in the Carpathian Basin for our analyses. The original database consists of 6867 recovery and resight records of 3186 individuals spanning between 2003 and 2015 in 13 cohorts. 1750 individuals were marked in Hungary (54.9%), 751 were ringed in Croatia (23.6%), while 685 were marked in Serbia (21.5%).

The colour-ringing program, started in Hungary, Croatia and Serbia in 2003 (Pigniczki 2010, Kralj *et al.* 2012), has used three different types of colour-ringing schemes: (1) two engraved plastic rings with two characters of an alphanumerical code; some possible combinations of six colours on the two rings; used between 2003 and 2008; (2) colour combinations of six rings with a flag; six possible colours on rings; used between 2007 and 2009, and (3) a white engraved plastic ring with three or four characters of alphanumerical code with a possible use of a bar code; used since 2009.

Further data were obtained from an adult female equipped with a GPS-GSM transmitter (model DUCK 3 produced by Ecotone Telemetry) and ringed with metal and an engraved plastic ring. The bird was captured at the nest in the Comacchio lagoons in Italy in June 2013. The transmitter provided accurate information on the geographical location of the bird once every 0.5–6 h (usually every 2 or 4 h). The sampling intervals were manually changed via an online panel accordingly to season and location to optimise control frequency of SMS delivery and battery usage.

We used the calendar year age category for each record as follows: a bird is one year old (1st calendar year old, hereafter 1cy) in the year of hatching until the 31st of December that year; two years old (in its 2nd calendar year, hereafter 2cy) after the year of hatching, and so

on. We defined five different age-groups: one year old Spoonbills (1cy or juveniles); two and three year old birds (2cy and 3cy or immature); four year old birds (4cy or sub-adults) and finally, birds older than four years (4+ or adults). Our preliminary results suggest that four year old (4cy) Spoonbills in the Pannonian population do not breed or, if they do, they breed in very low proportions (Pigniczki 2010, Pigniczki & Végvári 2015).

Resighting data were collected opportunistically by an international network of amateur and professional birdwatchers and bird photographers scattered along the flyways and across the wintering areas. In addition, six colour-ring-reading expeditions were organised to Tunisia between November and February to find wintering birds in 2010, 2012, 2013 (two times) and 2014 (two times), and one was targeted the western Balkans between late September and mid-October of 2014 to check possible stopover sites. In Tunisia and Libya, during the International Waterbird Census (IWC), special attention was given to look for Spoonbills with colour-rings and to read the combination of colour and code.

We used stopover and wintering records of 1cy as well as records of 2cy birds seen until the end of March, as this is the end of the first-winter period, during which birds undertake their first migration to their wintering areas from the Carpathian Basin. We also used the records of 4cy individuals, and adults (4+), as they return to the natal area in high frequencies. We used all the stopover records of Spoonbills from the age of 4cy, because they return to their general natal or breeding area, the Carpathian Basin. Our observations confirmed this, because a large proportion of subadults and adults was found in the natal area during summer, but birds from these age groups were rarely observed in the stopover zones or wintering sites during breeding time. We only used the records of those immatures that returned to their natal area in the Carpathian Basin. Movements of immature birds (2cy and 3cy), unlike that of adults and subadults, are often not considered migratory: these individuals can stay on the wintering grounds or move northwards, but usually do not reach their natal grounds as they do not breed that year (Pigniczki 2009, 2015, Pigniczki & Végvári 2015). Due to similar reasons, we excluded one record of a 4cy individual from our analysis, because that individual was observed only in western Europe.

We used two approaches to identify migratory paths. The direct approach uses observations from the natal/breeding, stopover and wintering areas collected during the same migratory season from the same year. The indirect approach defines supposed paths as observations from the natal/breeding, stopover and wintering sites of one individual from different years. Spoonbills often show fidelity to their wintering areas after their first winter (Lok *et al.* 2011), and we also found site fidelity to the Carpathian Basin as breeding area (Pigniczki & Végvári 2015), so we assumed those locations are used year by year by the same individuals.

Most of the wintering areas of Spoonbills from the Carpatian Basin are found below the latitude of 42°N (Pigniczki 2015). A Spoonbill was treated as wintering bird in a particular area, if: (1) it was observed between November and January at any age; (2) in the case of 2cy and 3cy birds, we treated data from February and March also as indicators of wintering; and if (3) a subadult or an adult bird was seen in October, but known to be present on the same location for at least 50 days before or after that observation. Similarly, (4) a sub-adult or an adult bird that was seen in February and that stayed for at least 30 days on the same location before or after the observation was also treated as wintering record.

Figure 1. Migration paths (lines) of Spoonbills between the Carpathian Basin (n1, n2, n4) and the wintering location (w1) including stopover sites (s1, s2) during autumn migration within one migration season for each individual. The numbers after the letters indicate the number of individuals

1. ábra Kanalasgémek őszi vonulási útvonalai (vonal) a Kárpát-medence (n1, n2, n4) és a telelőhelyek (w1) között a megállóhelyekkel (s1, s2), egy vonulási szezonon belüli megfigyelések alapján, egyedenként. A jelölések mellett a számok az egyedszámot jelentik

Figure 2. Migration paths (lines) of Spoonbills between the wintering location (w1) and the Carpathian Basin (n1) including stopover sites (s1, s3) during spring migration within one migration season for each individual. The numbers after the letters indicate the number of individuals

2. ábra Kanalasgémek tavaszi vonulási útvonalai (vonal) a telelőhelyek (w1) és a Kárpát-medence (n1) között a megállóhelyekkel (s1, s3), egy vonulási szezonon belüli megfigyelések alapján. A jelölések mellett a számok az egyedszámot jelentik

We classified spring stopovers where birds were observed between February and May for subadults and adults, and autumn stopovers where records came from a period between June and October for juveniles, sub-adults and adults. These periods were used also in the case of immature birds, but only for those that returned to the Carpathian Basin.

Using this approach, we analysed 201 stopover and migration records of 119 colour ringed individuals. We obtained information on (1) both wintering areas and a single stopover site in the case of 34 individuals, or (2) two stopover sites in the case of five specimens, or (3) two distinct wintering sites of one individual in connection with a wintering area shift, which together allowed us to identify 42 migration paths (16 by direct approach and 26 indirectly), as two individuals were seen at stopover sites in two different seasons.

To calculate average coordinates, we treated spring and autumn migrations separately. Observations of the same individuals from one location were considered only once. Data received from the bird with satellite transmitter were not included in this analysis.

When calculating the number of days spent at the stopovers, we treated two localities as one stopover site, if the same individual was observed in both of them, and the distance

Figure 3. Migration paths (lines) of Spoonbills between the Carpathian Basin (n1, n2) and the wintering locations (w1, w2) including stopover sites (s1, s2, s3) during autumn migration with observations from different years. The numbers after the letters indicate the number of individuals

3. ábra Kanalasgémek őszi vonulási útvonalai (vonal) a Kárpát-medence (n1, n2) és a telelőhelyek (w1, w2) között a megállóhelyekkel (s1, s2, s3), különböző évekből származó megfigyelések alapján. A jelölések mellett a számok az egyedszámot jelentik
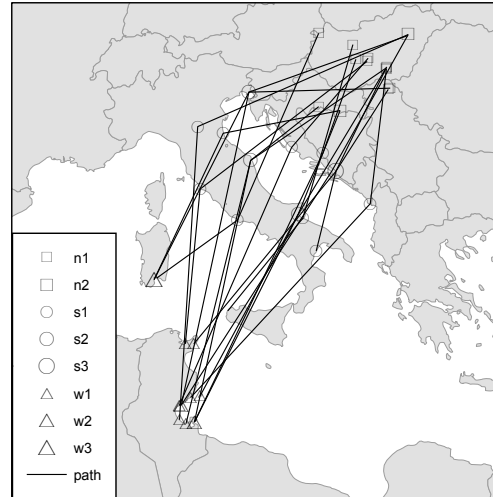
Figure 4. Migration paths (lines) of Spoonbills between the wintering location (w1, w2, w3) and the Carpathian Basin (n1, n2) including stopover sites (s1, s2, s3) during spring migration with observations from different years. The numbers after the letters indicate the number of individuals

4. ábra Kanalasgémek tavaszi vonulási útvonalai (vonal) a telelőhelyek (w1, w2, w3) és a Kárpát-medence (n1, n2) között a megállóhelyekkel (s1, s2, s3), különböző évekből származó megfigyelések alapján. A jelölések mellett a számok az egyedszámot jelentik

between the two localities was not more than 50 km. Spoonbills are rather mobile birds and may cover up to 50 km between feeding sites, or between feeding and roosting sites during their regular daily movements. It is difficult to estimate the real length of stopover duration of colour ringed individuals, as we suppose there was no possibility for the observers to regularly follow the birds in all cases. Probably, in most occasions the observations were casual, and that is why a lot of stopover durations were detected as one-day-long stays. Therefore these data probably do not provide exact values, but may indicate the minimum length of stopover. We calculated the mean values and standard errors (SE) to describe the differences between age groups (juvenile and non-juvenile) and migration seasons (spring and autumn), but the distribution of the data was not normal in any of these cases.

We used only records raising no doubts about the circumstances of the observations.

All statistical analyses were performed using the PAST statistical software (Hammer *et al.* 2001).

Results

Colour-ringed Spoonbills

Our results suggested 16 distinct, direct migration paths of 16 individuals, which were observed within one autumn or one spring migration season *(Figure 1, 2)*. Further, using the indirect approach, from movements of 24 individuals we outlined another 26 paths during the autumn and spring migration *(Figure 3, 4, 5)*.

We identified 59 stopover sites of the Central European Spoonbill population of 118 individuals (this number does not include the observation of wintering area shift in West Africa). 39 stopover sites were used during autumn migration, while 24 on spring migration. Only four of them were used on both spring and autumn migrations *(Figure 6, 7)*.

We analysed the stopover localities of 119 individuals (including the individual which wintered in West Africa). 55 stopover sites were identified along the Adriatic Flyway, used by 114 individuals (95.8% of 119). Four stopover sites were found east of the Adriatic Flyway, used by four individuals (3.4% of 119). We know of only one individual (0.8% of 119) that was seen on the East Atlantic coast of Africa, which started to spend its first winter in Morocco, and was observed later in Mauritania until its 6cy *(Figure 5)*.

Our findings indicate the existence of two main routes in the Adriatic Flyway *(Figure 1, 2, 3, 4)*. One of them starts in the Carpathian Basin and proceeds south of the Alps to the north of Italy, then further to Sardinia, Tunisia and probably also to south Italy, Libya and Algeria, referred to as North-Adriatic Flyway. The other route leads across the Bosnian karst lakes, to the coastal area between the Neretva river mouth and the Bojana/Buna river mouth, and runs further to south Italy, Tunisia and probably also to north African wintering areas in Libya, referred to as South-Adriatic Flyway. Records between the two main routes across the Adriatic Sea indicate lower importance for Spoonbill movements.

Figure 5. Migration route (line) of a Spoonbill (B/W [TN]) from the Carpathian Basin (n) with shift in its wintering locations (w). The individual was seen in Morocco in its first winter (juvenile), but was observed as a wintering individual in Mauritania in its second winter (immature) and 6cy-old adult age

5. ábra A B/W [TN] kódú kanalasgém vonulási útvonala (vonal) a Kárpát-medencéből (n) telelőhely-váltással (w). Első telesként (fiatal) Marokkóban figyelték meg, de második telesként (immatur) és hatodik naptári éves öreg madárként már Mauritániában azonosították mint telelő egyedet

The average coordinates of the spring (43.66°N, 15.10°E) as opposed to their autumn (40.64°N, 13.11°E) stopover sites are different along the Adriatic Flyway *(Figure 6, 7)*. The average spring stopover coordinates are closer to the western coast of Balkan Peninsula, while the average autumn coordinates are located closer to the south-western coast of Italy.

We have records from both the autumn and the spring migration periods for eight

Figure 6. Autumn stopover sites (1, 2, 3, 4, 6, 10, 11) of Spoonbills between the Carpathian Basin and the wintering areas. (×) indicates average coordinates of autumn stopover sites. The numbers after the symbols indicate the number of individuals

6. ábra Kanalasgémek őszi megállóhelyei (1, 2, 3, 4, 6, 10, 11) a Kárpát-medence és a telelőhelyek közt. Az (×) az őszi megállóhelyek átlagkoordinátáit mutatja. A jelölések mellett a számok az egyedszámot jelentik

Figure 7. Spring stopover sites (1, 2, 3, 4, 6, 10, 11) of Spoonbills between the Carpathian Basin and the wintering areas. (×) indicates average coordinates of spring stopover sites. The numbers after the symbols indicate the number of individuals

7. ábra Kanalasgémek tavaszi megállóhelyei (1, 2, 7, 9) a Kárpát-medence és a telelőhelyek közt. Az (×) a tavaszi megállóhelyek átlagkoordinátáit mutatja. A jelölések mellett a számok az egyedszámot jelentik

individuals *(Figure 8)*. Five of these birds used stopovers along the same routes: three birds were reported from the North-Adriatic Flyway, while two from the South-Adriatic Flyway. One bird chose the South-Adriatic Flyway and stopped exactly on the same stopover site in the salinas of Ulcinj during its autumn and spring migration. For the last three individuals, it was not possible to determine whether there was a shift between the spring and the autumn migration paths.

Observations from stopover sites in different years were collected for only four individuals, all of them seen during spring migration *(Figure 9)*. Three of them had stopover sites along the same route, and two of them were seen exactly on the same locations, or nearly at the same sites, where they had been observed previously. In the case of the fourth individual, it was not possible to determine if there was a shift between the two spring migration paths from one year to the next.

We analysed 92 records of autumn and 43 records of spring stopover durations along Adriatic Flyway. During autumn migration (n=92) the average stopover length was 3.6±0.696 (mean±SE) days. The mean length of stay for juveniles (n=70) was 4.0±0.856 (mean±SE) days, whereas it was 2.6±1.023 (mean±SE) days for non-juveniles (1cy <, n=22), but the two age groups are statistically not different with respect to stopover length (Mann-Whitney test, p=0.520). The detected longest stopover duration was 35 days for juveniles, and 23 days for non-juveniles during the autumn migration. The mean length of spring stopover duration was 2.1±0.398 (mean±SE) days among non-juveniles (n=43). The detected
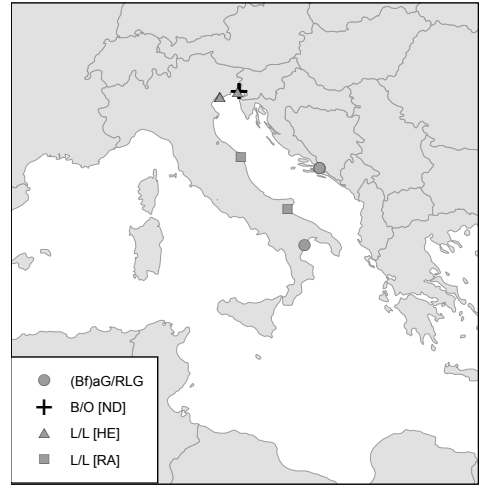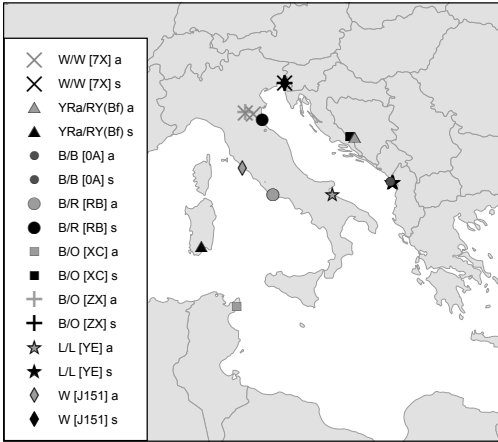
Figure 8. Autumn and spring stopover sites of eight colour marked Spoonbills seen during both autumn and spring migration along the Adriatic Flyway. The letter 'a' after ring code indicates autumn stopover, while the letter 's' indicates spring stopover. The North-Adriatic Flyway was used by W/W[7X], B/O[ZX] and W[J151], while the South-Adriatic Flyway was used by B/B[0A] and L/L[YE] during both spring and autumn migration. It was not possible to determine whether there was a shift between migration paths in the case of YRa/RY(Bf), B/R[RB] and B/O[XC]

8. ábra Nyolc színes gyűrűs kanalasgém őszi és a tavaszi vonulási állomása az adriai vonulási úton. Ezek az egyedek mind az őszi, mind a tavaszi vonulás során megfigyelésre kerültek. Az egyed kódja után az „a" az őszi, míg a „s" a tavaszi megállóhelyet jelöli. A tavaszi és az őszi vonulás során is az észak-adriai vonulási utat használta a W/W[7X], a B/O[ZX] és W[J151] kódú egyed, míg a dél-adriai vonulási úton vonult a B/B[0A] és a L/L[YE] kódú példány. Az YRa/RY(Bf), a B/R[RB] és a B/O[XC] kódú madarak esetén nem dönthető el, hogy tavaszi és őszi vonulásuk alatt az egyik adriai vonulási útról váltottak-e a másikra, vagy ugyanazon vonultak

Figure 9. Spring stopover sites of four individuals along the Adriatic Flyway. These individuals were seen in different years during their spring migration. Three individuals were observed along the same migration route where they had been observed previously; (Bf)aG/RLG stopped in two years along the South-Adriatic Flyway, while B/O[ND] and L/L[HE] stopped along the North-Adriatic Flyway in two and three years, respectively. It was not possible to determine whether there was a shift between migration paths in the case of L/L[RA]

9. ábra Négy színes gyűrűs kanalasgém tavaszi vonulási állomásai az adriai vonulási úton. Ezek az egyedek legalább két tavaszi vonulás során is megfigyelésre kerültek. Három egyed ugyanazt a vonulási útvonalat használta, mint korábban; a (Bf)aG/RLG kódú egyed két évben állt meg a dél-adriai vonulási úton, míg a B/O[ND] két évben, a L/L[HE] pedig három évben került megfigyelésre az észak-adriai vonulási úton. A L/L[RA] esetén nem dönthető el, hogy a madár váltott-e vonulási utat
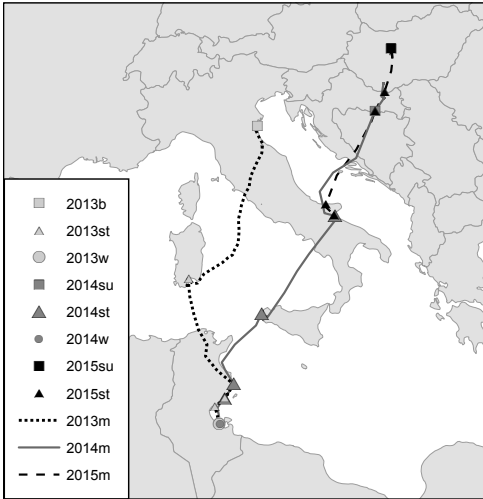
Figure 10. Autumn movements of the GPS tagged individual between the breeding/summering areas and the wintering area. The numbers next to the symbols indicate the year of migration. The meanings of letters after numbers: b – breeding area; st – stopover site; w – wintering area; su – summering area; m – migration path

10. ábra A jeladós kanalasgém őszi vonulásai a költő-/nyaralóhely és a telelőterület között. A számok a szimbólumok mellett a vonulás évét jelentik. A betűk jelentése a számok mellett: b – fészkelőhely; st – megállóhely; w – telelőhely; su – átnyaralóhely; m – vonulási út
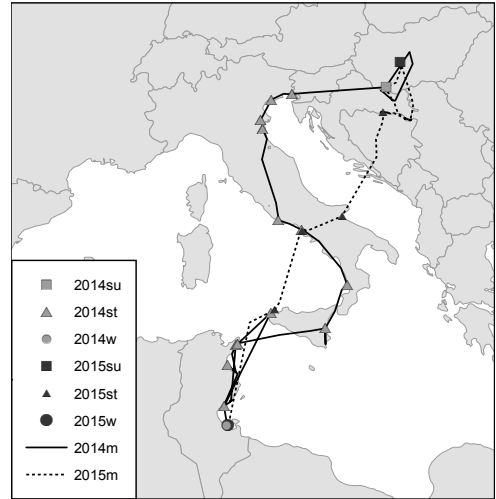
Figure 11. Spring movements of the GPS tagged individual between the wintering area and the breeding/summering areas. The numbers next to the symbols indicate the year of migration. The meanings of letters after numbers: st – stopover site; w – wintering area; su – summering area; m – migration path

11. ábra A jeladós kanalasgém tavaszi vonulásai a telelőhely és a költő-/nyaralóhely között. A számok a szimbólumok mellett a vonulás évét jelentik. A betűk jelentése a számok mellett: st – megállóhely; w – telelőhely; su – átnyaralóhely; m – vonulási út

longest stopover duration during spring migration was 14 days. The difference between the autumn and spring stopover duration is not significant either between non-juveniles (1cy <) (Mann-Whitney test, p=0.993) or between all individuals (Mann-Whitney test, p=0.487).

A few lucky observations allowed us to derive information on the speed of migration. One juvenile individual was observed in the natal area in Hungary on the 2nd of October, and was next observed on the coast of Djerba Island, Tunisia in the wintering area on 9th of October. The distance between the two sites (1698 km) was covered by the Spoonbill within seven days, which indicates a minimum speed of 243 km/day. During spring migration a 5cy individual was observed at a stopover site in Italy on 26th of April, and was resighted in the breeding area in Serbia on 29th of April. That individual moved 651 kilometres within 3 days, with an average speed of 217 km/day.

Our database includes records of four individuals, which used two stopover sites within one migration season. The distance between two stopovers was between 70 and 546 km *(Table 1)*, with no information on any other stops.

Spoonbill with GPS device

The adult Spoonbill equipped with a GPS tag provided detailed information on five journeys: three from breeding/summering areas to wintering grounds and two from the return flights, which occurred between late summer of 2013 and the autumn of 2015 *(Figure 10, 11, Table 2, 3)*.

In 2013, southward migration started on 1st of October from the wetlands around Comacchio (Italy), where it bred in that year. After a non-stop flight, it stopped for two weeks in Cagliari in Sardinia, and then continued its journey to Tunisia, to the Gulf of Gabes. The bird spent the winter there, mainly in the coastal, tidal wetlands west of the town of Gourine.

The bird's path at the start of the following spring migration in 2014 was less linear. The Spoonbill flew to Sicily (Trapani saltpans) between 1st and 4th of April but after two days, on 6th of April returned back to the Gulf of Gabes and stayed there for 12.5 days. On 21st of April the Spoonbill moved again and reached wetlands south of Catania in Sicily. It resumed migration on the 3rd of May and the route strictly followed the Tyrrhenian coast to the Lake of Fogliano. After a 40-hour stop the Spoonbill flew to the Comacchio lagoons where it visited the breeding colony, but then moved to rice fields nearby and spent 9.5 days there. The journey continued with a two-day stop at the lagoon of Venice, and a one day long stop in the river mouth of Isonzo and finally finished on the Fishpond Sumony (S Hungary) on 20th of May. It probably did not breed in 2014 because it moved back and forth from wetlands in south and central Hungary to fishponds along the Sava river in Croatia and Bosnia and Herzegovina between its arrival to Hungary and the end of July, never stopping in the same area for more than 10–15 days.

The following autumn, movement towards south started on 13rd of October. The adult Spoonbill departed from Fishpond Jelas (Croatia), and in a single journey crossed the mid-Adriatic Sea south of Split and finally settled in the Gulf of Manfredonia for 11 days. Then it took three more steps with stops in the salinas of Trapani (Sicily) and Chebba (Tunisia) and arrived to the Gulf of Gabes, the same region where it had spent the previous winter.

In the spring 2015, the return migration started on 26th of April, directly from the wintering ground in the Gulf of Gabes. A three-step movement through the wetlands of Campania and Manfredonia (Italy) and across mid-Adriatic Sea finished close to Fishpond Jelas

Individual	Stopover coordinates 1	Stopover coordinates 2	Distance	Elapsed time (day)
W/W [3P]	41.40°N; 12.88°E	42.43°N; 11.20°E	181 km	5
B/L [YP]	44.88°N; 11.07°E	44.57°N; 11.83°E	70 km	26
W [J240]	41.02°N; 13.92°E	40.72°N; 17.80°E	328 km	9
W [J224]	40.57°N; 15.07°E	36.83°N; 10.98°E	546 km	36

Table 1. Coordinates of stopover sites of four individuals found on two stopovers during the same autumn migration and the distance between the stopover sites and the time between the observations. See also *Figure 1.*

1. táblázat Az őszi vonulás során két megállóhelyen is megfigyelt négy példány megállóhelyeinek koordinátái, valamint a megállóhelyek távolsága és a megfigyelések között eltelt idő. Lásd az *1. ábrát* is

Migration season, year	Time and date of departure	Location of departure	Time and date of arrival	Location of arrival	Distance between stops (km)	Time (hour) between stops
A 2013	6:00-6:30, 1 October	Valli di Comacchio (I)	21:30-22:00, 1 October	Cagliari (I)	755	17-18
A 2013	20:00-21:00, 16 October	Cagliari (I)	6:00-7:00, 17 October	Sidi Mansour (To)	536	9-11
A 2013	12:00-18:00, 17 October	Sidi Mansour (To)	<24:00, 17 October	Kneiss Island (To)	78	6-12
A 2013	>0:00, 20 October	Kneiss Island (To)	<12:00, 20 October	Gourine (To)	78	<12
S 2014	1 April	Gourine (To)	1 April	Kneiss Island (To)	78	
S 2014	6:00-12:00, 2 April	Kneiss Island (To)	<18:00, 2 April	Sebkhet Halk el Manzel (To)	212	6-12
S 2014	00:00-12:00, 3 April	Sebkhet Halk el Manzel (To)	12:00-18:00, 3 April	Barrage Lebna (To)	95	6-12
S 2014	>6:00, 4 April	Barrage Lebna (To)	<18:00, 4 April	Trapani saltpans (I)	203	<12
S 2014	>6:00, 6 April	Trapani saltpans (I)	<24:00, 6 April	Kneiss Island (To)	428	<18
S 2014	>6:00, 19 April	Sfax (To)	<18:00, 19 April	Barrage Lebna (To)	240	<12
S 2014	>6:00, 21 April	Sidi Abdel Monaam (To)	<24:00, 21 April	Mouth River Simeto, Catania (I)	370	<18
S 2014	8:00-12:00, 3 May	S of Catania (I)	14:00-16:00, 3 May	Mouth River Savuto (I)	204	2-8
S 2014	2:00-4:00, 4 May	Mouth River Savuto (I)	14:00-16:00, 4 May	Mouth River Volturno (I)	297	10-14
S 2014	4:00-6:00, 5 May	Mouth River Volturno (I)	6:00-14:00, 5 May	Sabaudia (I)	99	<10
S 2014	>6:00, 7 May	Sabaudia (I)	18:00-20:00, 7 May	Comacchio lagoons (I)	368	12-14
S 2014	6:00-10:00, 17 May	Codigoro rice fields (I)	<18:00, 17 May	Lagoon of Venice (I)	85	8-12
S 2014	2:00-4:00, 19 May	Lagoon of Venice (I)	8:00-14:00, 19 May	Mouth of river Isonzo (I)	80	4-12
S 2014	> 6:45-10:00, 20 May	Mouth of river Isonzo (I)	<20:00, 20 May	Fishpond Sumony (H)	340	10-13
A 2014	>8:00, 13 October	Fishpond Jelas (Hr)	<24:00, 13 October	Manfredonia (I)	515	16
A 2014	8:00-12:00, 27 October	Manfredonia (I)	18:00-20:00, 27 October	Trapani (I)	519	6-12
A 2014	18:00-20:00, 2 November	Trapani (I)	6:00-8:00, 3 November	Chebba (To)	372	10-12
A 2014	>22:00, 3 November	Chebba (To)	<24:00, 3 November	Sfax (To)	51	<2
A 2014	>18:00, 8 November	Sfax (To)	20:00-22:00, 8 November	Gourine (To)	108	2-4
S 2015	>6:00, 26 April	Gourine (To)	< 24:00, 26 April	NW Sicily (I)	567	18
S 2015	00:00-6:00, 27 April	NW Sicily (I)	<18:00, 27 April	Mouth river Volturno (I)	342	12-18
S 2015	6:00-8:00, 7 May	Mouth river Volturno (I)	<16:00, 7 May	Manfredonia (I)	162	8-10
S 2015	> 8:00, 9 May	Manfredonia (I)	18:00-20:00, 9 May	Fishpond Jelas (Hr)	435	10-12
A 2015	9:00-12:00, 15 October	Rétszilas (H)	<15:00, 15 October	Donji Miholiac (Hr)	122	3-6
A 2015	> 9:00, 22 October	Donji Miholiac (Hr)	<18:00, 22 October	Fishpond Jelas (Hr)	78	9
A 2015	>6:00, 30 October	Fishpond Jelas (Hr)	<21:00, 30 October	Lakes of Lesina-Varano (I)	408	15
A 2015	>12:00, 31 October	Lakes of Lesina-Varano (I)	<24:00 October 31	Manfredonia	59	<12

Table 2. Migration pattern of the Spoonbill with GPS device. "A" means autumn migration, "S" means spring migration. Distance between two stops was calculated based on the signals of the GPS device

2. táblázat A jeladós kanalasgém vonulási mintázata. Az „A" az őszi, míg a „S" a tavaszi vonulást jelenti. A távolságot két megállás között a jeladó adatai alapján számítottuk

Migartion season, year	Stopover site	Arrival to stopover site	Departure from stopover site	Duration of stay at stopover site (days)
A 2013	Cagliari (I)	21:30-22:00, 1 October	20:00-21:00, 16 October	15
A 2013	Sidi Mansour	6:00-7:00, 17 October	12:00-18:00, 17 October	0.2-0.5
A 2013	Kneiss Island (To)	18:00-24:00, 17 October	00:00-6:00, 20 October	2-2.5
S 2014	Kneiss Island (To)	1 April	2 April	
S 2014	Sebkhet Halk el Manzel (To)	12:00-18:00, 2 April	00:00-6:00, 3 April	0.5-0.75
S 2014	Trapani saltpans (I)	18:00, 4 April	6:00, 6 April	1.5
S 2014	Kneiss Island – Sfax (To)	00:00, 7 April	6:00-12:00, 19 April	12.5
S 2014	Barrage Lebna / Sidi Abdel Monaam	6:00-18:00, 19 April	6:00-12:00, 21 April	2
S 2014	Wetlands S of Catania	18:00-24:00, 21 April	8:00-10:00, 3 May	11.5
S 2014	Mouth river Savuto (I)	15:00-16:00, 3 May	2:00-4:00, 4 May	0.5
S 2014	Mouth river Volturno (I)	12:00-14:00, 4 May	4:00-6:00, 5 May	0.5
S 2014	Sabaudia (I)	6:00-14:00, 5 May	>6:00, 7 May	2
S 2014	Rice fields near Comacchio lagoons and Codigoro (I)	18:00-20:00, 7 May	6:00-10:00, 17 May	9.5
S 2014	Lagoon of Venice (I)	<18:00, 17 May	2:00-4:00, 19 May	1.5
S 2014	Mouth river Isonzo (I)	8:00-14:00, 19 May	> 6:45-10:00, 20 May	0.75
A 2014	Manfredonia (I)	<24:00, 13 October	8:00-12:00, 27 October	13.5
A 2014	Trapani (I)	18:00-20:00, 27 October	18:00-20:00, 2 November	6
A 2014	Chebba(To)	8:00, 3 November	22:00-24:00, 3 November	0.5-0.75
A 2014	Sfax (To)	00:00, 4 November	16:00-18:00, 8 November	4.75
S 2015	NW Sicily (I)	< 24:00, 26 April	00:00-6:00, 27 April	0.25
S 2015	Mouth river Volturno (I)	<18:00, 27 April	6:00-8:00, 7 May	9.5
S 2015	Manfredonia (I)	<16:00, 7 May	> 8:00, 9 May	1.75
A 2015	Donji Miholiac (Hr)	<15:00, 15 October	> 9:00, 22 October	6.75
A 2015	Fishpond Jelas (Hr)	<18:00, 22 October	>6:00, 30 October	7.5
A 2015	Lakes of Lesina-Varano (I)	<21:00, 30 October	>12:00, 31 October	0.63

Table 3. Arrival and departure date and stopover duration of Spoonbill with GPS device during migration. "A" means autumn migration, "S" means spring migration.

3. táblázat A jeladós kanalasgém érkezése és elvonulása az egyes megállóhelyeken, illetve a rajtuk töltött idő. Az „A" az őszi, míg a „S" a tavaszi vonulást jelképezi

(Croatia) on 9th of May. The Spoonbill spent the following summer moving among wetlands located in central Hungary or along the Danube and the Sava rivers and, likely, again skipped breeding.

In 2015, autumn migration started on 15th of October from Fishpond Rétszilas in central Hungary. After a two-step movement to Fishpond Jelas, the Spoonbill made another long flight across mid-Adriatic to coastal lakes of Lesina and Varano and finished its journey on 1st of November in Manfredonia. Data collected in the following days contained a series of points concentrated in an arable field suggesting that the bird died. We suppose it was shot dead by poachers.

The distances of flights between two stopovers were 283.0±67.3 km (SE) during autumn migration, and 255.8±34.3 km (SE) during spring migration. Stopover duration was 5.7±1.0 (SE) days during autumn migration and 3.9±1.2 (SE) days during spring migration. The calculated maximal speed of flight was between 48.7–59.6 km/h.

Discussion

Our resight records indicate that Spoonbills from Central Europe mainly use the Central Mediterranean or the Adriatic part of the Black Sea/Mediterranean Flyway. Waterbirds (including Spoonbills) may fly along the Adriatic coast and they can also cross the Adriatic Sea (Sackl *et al*. 2014). Kralj *et al.* (2012) reported Spoonbills crossing the central part of the Adriatic Sea. Smart *et al.* (2007) supposed that Spoonbills cross the Adriatic Sea at the Straight of Otranto, but we did not find evidence for that. Our results from colour-ringed birds indicate that high number of Spoonbills may cross the Adriatic Sea between Gulf of Manfredonia (Italy) and (1) Ulcinj (Montenegro), or (2) the coastline among Split and Metković (Croatia). GPS tracks of the adult Spoonbill also support this hypothesis. Resights also confirm that individuals breeding/summering in the Carpathian basin or NE Italy may fly along the west Adriatic coast before crossing the Appenines, stop in coastal wetlands of central Italy before flying to the wintering grounds in Tunisia. Alternatively, North Africa can be reached both via Sicily or Sardinia. The same routes can be used during spring migration. A few Spoonbills were reported from the East Mediterranean area, where West Asian/East African and Black Sea/Mediterranean Flyways overlap while a few birds were detected along East Atlantic coast, where the East Atlantic and Black Sea/Mediterranean Flyways overlap.

We have identified two routes used by Spoonbills within the Adriatic Flyway, the North-Adriatic and the South-Adriatic Flyways. We suppose that these routes are defined by suitable wetlands, as the North Adriatic Flyway includes wetlands in north-eastern Italy and follows mainly the north Adriatic coast and as far as we know does not cross the Adriatic Sea. In contrast, the South-Adriatic Flyway involves wetlands across the western Balkan Peninsula (the karst lakes of Bosnia and Herzegovina and coastal wetlands between Split and northern Albania) and crosses the Adriatic Sea. Between those two routes there are few or no wetlands suitable for Spoonbills as resting or refuelling sites both along the Adriatic coasts of the Balkans and Italy. This is also confirmed by field observations that report

only small number of Spoonbills from the intermediate coastal Croatian areas (Stumberger *et al.* 2013), as there are only a few wetlands appropriate for this species. Similarly, the Italian coast between Cervia and Lesina is hilly and highly anthropized without wetlands suitable for waterbirds. GPS tracks suggest that the two Adriatic routes may overlap in S Italy and join between W Sicily and Cape Bon where birds chose to address towards the wintering grounds located along the West or South coast of Tunisia. Our results imply that most individuals may use stopover sites along the same migration route (North- or South-Adriatic Flyway) during both spring and autumn migrations. Furthermore, most Spoonbills showed high fidelity to the same stopover sites or areas in their vicinity in following years, although we also detected in a single occasion (in the case of adult fitted with GPS) where Spoonbill shifted from the North-Adriatic Flyway to the South-Adriatic one. The bulk of our observations indicate fidelity to stopover sites during both migrations, but further studies are needed because of the small available sample size.

We have identified 59 stopover sites in the Balkan Peninsula, Italy, the Middle East and North Africa by the resights of colour ringed Spoonbills ringed in Central Europe and another four by the signal of the GPS device. We believe that we were able to delineate the most important stopovers along the Adriatic Flyway using these methods. However, there could be further important stopover sites in Albania and western Greece, from where observations are lacking, and probably we were not able to recognise several stopovers in North-Africa after birds left Cape Bon or Lake Tunis in Tunisia. The GPS-tagged Spoonbill's track revealed that birds may stop at additional sites along the northern and eastern coast of Tunisia but preferably move to the more suitable tidal areas located in the Gulf of Gabes which are largely used in winter (Smart *et al.* 2007). Interestingly, two stopover sites were also found in the Carpathian Basin by tracking the Spoonbill with the GPS tag. Stopover sites of Spoonbills from Central Europe were previously identified only in the west Balkan Peninsula (Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, northwest Albania) (Stumberger *et al.* 2013). As most of the Central European Spoonbills migrate to Tunisia and Italy (Smart *et al.* 2007, Pigniczki 2009, 2010, Kralj *et al.* 2012, Pigniczki & Karcza 2013), this study covered large part of the most important stopover sites for this population along the Adriatic Flyway. The estimated number of wintering individuals in Tunisia is high; between 3447 and 4033 individuals were counted by January IWC between 2008 and 2014 (Azafzaf *et al.* 2015). In Italy, the number of wintering Spoonbills recorded by mid-January IWC, increased from less than 100 individuals distributed across eight sites in 1991–1995, to almost 800 individuals spread over 44 sites in 2006–2010 (Zenatello *et al.* 2014).

We have only few records of stopovers from the central and eastern part of the Balkan Peninsula, and we have only limited numbers of records from the Middle East. These sites seems to belong to another route used by Spoonbills, with known wintering areas in Turkey and mainly old winter recoveries along the Egyptian and Sudanese part of the Nile (Pigniczki 2009, 2010, Pigniczki & Karcza 2013). However, the East-Mediterranean area is not the main migratory and wintering area for the Central European population: those sites are mainly used by Eastern European Spoonbills as a large proportion of individuals ringed in the Danube Delta (Romania) were observed in Israel and also in Turkey, Cyprus and Oman

(Kiss *et al.* 2007). Israel is an important area both during autumn migration, with up to 900 individuals observed, and as a wintering site hosting around 800–1500 individuals in north of the country (Shirihai *et al.* 1996). Furthermore, flocks of up to 70 individuals were seen in Egypt during migration in the 1980s, with no wintering records from the Nile Delta from the same period (Goodman & Meininger 1989); however, no recent records are available in the literature from this location. Wintering Spoonbills (including a Serbian ringed individual) were observed in 2008–2015 along the Nile at Abu Simbel (maximum of 11 individuals) and at Aswan (maximum of 40 individuals) (D. Hoek & H. Ibrahim *pers. comm.*). As there is only a small overlap between the flyways of Central European and East European Spoonbills (Kiss *et al.* 2007, Kralj *et al.* 2012, Pigniczki 2015) our results support the proposal of splitting the Central and the East European Spoonbill populations, which have been considered to belong to the same population in the recent international action plan of the species (Triplet *et al.* 2008). This would help to best address future conservation actions (Pigniczki *et al.* in press).

Staging areas of trans-Saharan migrants remained completely unknown. Spoonbills from the Carpathian Basin and NE Italy reach wetlands in Niger, Nigeria and Mali (Spina & Volponi 2008, Volponi *et al.* 2008, Pigniczki 2009, 2010, Kralj *et al.* 2012, Pigniczki & Karcza 2013). We suppose that trans-Saharan migrants may have staging areas in the coastal wetlands of Gulf of Gabes and stopover sites in desert wetlands of Tunisia and Algeria. Trans-Saharan migration is a risky journey, as several individuals with Carpathian Basin origin were found dead in the middle of the desert in Algeria (Pigniczki & Karcza 2013). Recent observations indicate that only small numbers of Spoonbills are found in the wetlands of the Sahel (Triplet *et al.* 2008, Zwarts *et al.* 2009, J. Broower *pers. comm.*).

Some colour-ringed individuals reached the Atlantic coast of Africa and spent the winter in Morocco and Mauritania (Pigniczki & Karcza 2013). However, we have only limited numbers of observations of Central European individuals from this route, thus this wintering area seems to be only marginally important for this population. However, West African sites are essential wintering areas of the Spanish and Dutch populations (de le Court & Aguilera 1997, Lok *et al.* 2011). Central European Spoonbills may reach the east Atlantic coast after flying along the coast of the Mediterranean Sea.

From earlier recoveries of metal-ringed individuals we know that Spoonbills used stopover sites along the coasts of Italy and Montenegro, the karst lakes of Bosnia and Herzegovina, wetlands along the River Danube in southern Romania, and further away in Camargue (France) and the European part of Turkey (Pigniczki 2010). These data complement recent records of colour-ringed birds, in the sense that Spoonbills also used the eastern part of the Balkans in the past, and reached the coastal Mediterranean Sea west of Italy. Spoonbills probably still use these sites in low numbers, but we suspect the observation effort is low in the Balkan Peninsula, and this resulted in few records from these sites (Pigniczki & Végvári 2015).

Certain stopover sites were used more often in spring while others were preferred in autumn along the Adriatic Flyway: for example, wetlands in the Po Delta, Margherita di Savoia saltpans and water reservoirs of Cape Bon were used dominantly during autumn, while the delta of Neretva River and the mouth of the River Isonzo (NE Italy) were used mainly

during spring migration. Different autumn and spring migration strategies may result in differential preferences for stopover sites in autumn and spring. This pattern could be also a result of observational bias, as it could be difficult to detect Spoonbills during the short time of spring stopovers in Tunisia or in southern Italy, where also transient and wintering birds may mix. The track of the Spoonbill with the GPS tag indicates that birds may also use the water reservoirs of Cape Bon during spring migration. Further, the Delta of Neretva River is not used during autumn migration because human disturbance is heavier that time than in spring (Stumberger *et al.* 2013, Pigniczki *et al.* in press).

We also found that: (1) stopover duration may last longer for juveniles than for non-juveniles (< 1cy), and (2) Spoonbills may have longer stopover duration during autumn than spring migration. However, we did not find statistical support for these results. Juveniles generally stay longer on stopover sites than adults, as it could be expected because 1cy are unexperienced individuals (Nilsson *et al.* 2013). Furthermore, adults during spring migration have generally shorter stopover duration than on autumn migration, as they try to arrive back to the breeding areas as fast as it is possible to occupy the best territories to breed (Nilsson *et al.* 2013).

Interestingly, the average autumn stopover duration of Spoonbills seems to be longer along the Adriatic Flyway than in the north Iberian stopover site on the East Atlantic Flyway, which site is mostly used by long-distance migrants (Navedo *et al.* 2010, Kralj *et al.* 2012). Those individuals of the East Atlantic population which cross the Sahara spend on average 2.7 days at stopovers, while Spoonbills wintering in South-Iberia spend 1.5 days there (Navedo *et al.* 2010). These stopover durations seem to be different from that of Spoonbills from the Central European population, which indicate that the two populations may have different migration and stopover strategies. However, further studies are needed to confirm our result of longer stopovers along the Adriatic Flyway.

Distances between stopover sites used by the same individual within one season were between 70 and 546 km, and the bird with GPS device showed similar distances (between 78 and 755 km). This indicates that Spoonbills that use the Adriatic Flyway may employ hopping or skipping migration strategy (Warnock 2010), but our sample size is very small. As several stopover sites are found halfway between the natal or breeding area located in the Carpathian Basin and the wintering area in southern Italy or northern Africa, this also supports the assumption that most of the Central European Spoonbills belong to hoppers or skippers. However, a small number of Central European Spoonbills that cross the Sahara (Smart *et al.* 2007, Kralj *et al.* 2012, Pigniczki & Karcza 2013), may belong to jumpers during their trans-Saharan migration (Warnock 2010).

Data provided by the Spoonbill fitted with the GPS device showed that migration could be both diurnal and nocturnal. Cramp and Simmons (1977) described the migration of Spoonbills as a mainly diurnal activity. Our focal individual spent up to 17-18 hours in the air between two stops with active flights. The bird retreated after departing during its spring migration in 2014 and returned to the Gulf of Gabes. After a long stay in the wintering area, it eventually reached its previous breeding site in Italy, then later moved to the Carpathian Basin. The reason of the unusual spring retreat to the wintering site remained unknown. On those days no extreme weather conditions were recorded, but on the 5th and 6th of April

winds turned from W to NW blowing with speed of 7.6 to 44.6 km/h (data source: https://weatherspark.com). Similarly, that individual arrived to the Carpathian Basin also very late in 2015. Birds may reverse their heading and retreat during migration if encounter harsh or extreme weather events (Strandberg *et al.* 2009). If migrants start their spring migration too late or retreat during the course of the journey, they are likely arrive later at their breeding area, and either skip breeding or if they breed, generally have low breeding success (carry over effect) (Strandberg *et al.* 2009, Zwarts *et al.* 2009, Lok 2013). The state of wetlands in the breeding area may also have a significant influence on the decision to whether or not start to breed. For instance, adult Spoonbills in the Carpathian Basin may skip breeding under dry conditions (Pigniczki 2015, Pigniczki & Végvári 2015). We suspect the adult bird with GPS device was shot dead in Italy, as the same happened to two out of three young that started to winter in this area. Poaching pressure is high along Adriatic Flyway, especially on the Balkans (Schneider-Jacoby 2008).

Our results highlight the importance of the Adriatic Flyway for Spoonbills. Similarly, most waterbird species breeding in Central Europe also use the Adriatic Flyway (Schneider-Jacoby 2008). The wintering areas of waterbird species using the Adriatic Flyway are mostly located in North Africa, with large concentrations of wintering individuals in the Gulf of Gabes (Tunisia and Libya) and in the Niger Basin (Schneider-Jacoby 2008). Migratory bird censuses indicate the special importance of the Adriatic Flyway for ducks at Bojana-Buna river delta, as thousands of Garganeys *(Anas querquedula)*, Northern Shovelers *(Anas clypeata)* and Eurasian Wigeons *(Anas penelope)* were seen during their migration over the Adriatic Sea (Sackl *et al.* 2014). Furthermore, the Adriatic Flyway has special importance for the Common Crane *(Grus grus)* as well. Large numbers of Cranes use the two main routes of the Adriatic Flyway (North and South), similarly to what we described here for Spoonbills (Stumberger & Schneider-Jacoby 2010).

Stopover sites have key importance during migration (Navedo *et al.* 2010b, Warnock 2010), so we believe that our results are useful for Spoonbill and wetland conservation projects along the Adriatic Flyway. The AEWA Single Species Action Plan for the Eurasian Spoonbill provides limited information on migration routes and has no description of stopover sites for the Central European population (Triplet *et al.* 2008). Our study aims to fill this gap. Assuring habitat and bird protection at stopover sites is of crucial importance, especially in the Balkan Peninsula, where several wetlands have been destroyed or exposed to unsustainable levels of hunting or poaching pressure (Schneider-Jacoby 2008, Stumberger *et al.* 2013, Pigniczki *et al.* in press). Furthermore, it is important to identify major migration routes to prevent the establishment of wind farms along the important routes and in the vicinity of key sites, as collision with wind turbines is often fatal for birds (Desholm & Kahlert 2005, Kirby *et al.* 2008).

Combining regular surveys of Spoonbills with colour ring readings is an important method to determine which stopovers are used, and which migration routes connect these stopovers among the Central European breeders. As we have only limited numbers of recoveries and there are no continuous data on individual movements, new technologies such as GPS-GSM or GPS-GSM-UHF trackers could greatly help to understand movements of birds and integrate that information with traditional survey data (Pigniczki *et al.* in press). As shown

by the information gathered by one of the adult Spoonbills equipped with GPS-GSM device in Italy, the use of GPS trackers would allow us to answer open questions, such as the existence of a proposed link between the Balkans and east Libya across the Mediterranean Sea for Spoonbills, which connection has been found for the Montagu's Harrier *(Circus pygargus)*, the Saker Falcon *(Falco cherrug)* and the Red-footed Falcon *(Falco vespertinus)* (Palatitz *et al.* 2009, Zwarts *et al.* 2009, Prommer *et al.* 2012, Pigniczki 2015). Furthermore, the connections between colonies of Spoonbills in the Carpathian Basin and wintering sites through the trans-Saharan and the East Mediterranean routes are not known well enough. The need to deploy GPS-trackers on Spoonbills, particularly on individuals breeding in the Carpathian Basin is thus high as the species has a large conservation importance along the Adriatic Flyway (Schneider-Jacoby 2008, Pigniczki *et al.* in press).

Acknowledgements

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Can we explain vagrancy in Europe with the autumn migration phenology of Siberian warbler species in East Russia?

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László Bozó, Wieland Heim, Andrea Harnos & Tibor Csörgő 2016. Can we explain vagrancy in Europe with the autumn migration phenology of Siberian warbler species in East Russia? – Ornis Hungarica 24(1): 150–171.

Abstract We examined the autumn migration phenology of nine Siberian breeding songbirds: Thick-billed Warbler *(Iduna aedon),* Black-browed Reed Warbler *(Acrocephalus bistrigiceps),* Pallas's Grasshopper Warbler *(Locustella certhiola)*, Lanceolated Warbler *(L. lanceolata),* Yellow-browed Warbler *(Phylloscopus inornatus)*, Arctic Warbler *(Ph. borealis),* Dusky Warbler *(Ph. fuscatus),* Radde's Warbler *(Ph. schwarzi),* Two-barred *Warbler (Ph. plumbeitarsus)* and compared the migration dynamic characteristics with their European occurrence time. The study was carried out within the Amur Bird Project in the Russian Far East along the river Amur at Muraviovka Park between 2011 and 2014. The birds were caught with mistnets and ringed with individually numbered rings. For the characterization of the migration, we used timing, the intervals and the peaks of the migration, the percentage of the recaptures and the average time between the first and the last captures. The timing of migration in the studied species differed in the timing, the intervals (30–67 days) and the migration peaks (14 August – 17 September).

Considering the size and location of the distribution area, the timing and annual patterns of European occurrences, it is likely that most individuals of Thick-billed Warbler, Pallas's Grasshopper Warbler, Dusky Warbler, Radde's Warbler and Two-barred Warbler get to Europe due to the impact of Siberian cyclones. In case of Yellow-browed Warblers, other factors (reverse migration, weather conditions, dispersal movements) may also play a role. Because of their Scandinavian breeding populations, dispersion movement is the most likely reason for vagrants of Arctic Warbler and Lanceolated Warbler. The distribution of the Black-browed Reed Warbler is limited to the eastern edge of the continent, and therefore this species has no European record to date.

Keywords: reverse migration, weather anomalies, dispersion, Muraviovka Park, Siberian Passerines

Összefoglalás Szibériában fészkelő kilenc énekesmadár – vastagcsőrű nádirigó *(Iduna aedon),* keleti foltos nádiposzáta *(Acrocephalus bistrigiceps),* csíkos tücsökmadár *(Locustella certhiola),* foltos tücsökmadár (*L. lanceolata),* vándorfüzike *(Phylloscopus inornatus),* északi füzike *(Ph. borealis),* barna füzike *(Ph. fuscatus),* vastagcsőrű füzike *(Ph. schwarzi),* szalagos füzike *(Ph. plumbeitarsus)* – őszi vonulási fenológiáját vizsgáltuk és összehasonlítottuk őszi vonulásdinamikai jellemzőiket az európai megkerülésük idejével. A vizsgálatokat az Oroszország Amur menti részén elhelyezkedő Muraviovka Parkban végeztük 2011–2014-ben, az őszi vonulás során. A madarakat japán típusú függönyhálókkal fogtuk, és egyedileg számozott gyűrűvel jelöltük. A vonulás jellemzésére a vonulás időzítését, intervallumát, csúcsát, a visszafogott madarak százalékát, a befogás és visszafogás közötti átlagos időtartamot használtuk. A vizsgált fajok vonulása különbözött mind az időzítés, mind az intervallum (30–67 nap), mind a vonulási csúcs (augusztus 14. – szeptember 17.) vonatkozásában.

Az elterjedési terület méretét és elhelyezkedését, az európai megkerülések idejét és évi mintázatát figyelembe véve a legtöbb vastagcsőrű nádirigó, csíkos tücsökmadár, barna füzike, vastagcsőrű füzike, szalagos füzike példány a szibériai ciklonok hatása miatt juthat el Európába. A vándorfüzike esetében minden egyéb tényező (reverz vonulás, időjárási tényezők, nagy diszperziós elmozdulások) szerepet játszhatnak. Az északi füzike és a foltos tücsökmadár skandináviai fészkelőállománya miatt a diszperziós mozgásból eredő megkerülés a legvalószínűbb. A keleti foltos nádiposzáta költési areája kicsi és a legkeletebbi előfordulású, valószínűleg ezért nincs európai megkerülése.

Kulcsszavak: reverz vonulás, időjárási anomáliák, diszperzió, Muraviovka Park, szibériai énekesmadarak

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Introduction

In the last decades, a significant number of Siberian species appeared in many European countries, and both the number of species and the observations are increasing (Gilroy & Lees 2003). Possibly the increase in the number of observers in the past decades plays a considerable role. Nevertheless, the question arises, how and why the otherwise mostly in Southeast Asia wintering individuals occur in the opposite or at least very different direction? Answers could include weather anomalies, migration defects (reverse or mirror migration), dispersal movements and changes in the wintering areas (Rabøl 1969, Baker 1977, Folvik 1992, Berthold 1996, Thorup 1998, 2004, Phillips 2000, Elkins 2002, Gilroy & Lees 2003, Krüger & Dierschke 2004, Harrup 2007, De Juana 2008, Jiguet & Barbet-Massin 2013).

The migration of Siberian species which winter in South-South East Asia is less known, we have information only on the autumn migration of some species (Nisbet 1967, Cramp 1992, Marchetti *et al.* 1995, Halmos *et al.* 2000, Katti & Price 2003, Duckworth 2007, Raess 2008). To understand the causes of the European vagrancies, information on migration phenology of this species is needed.

This study aims to describe the migration phenology of nine species: Thick-billed Warbler *(Iduna aedon)*, Black-browed Reed Warbler *(Acrocephalus bistrigiceps)*, Lanceolated Warbler *(Locustella lanceolate)*, Pallas's Grasshopper Warbler *(L. certhiola)*, Yellow-browed Warbler *(Phylloscopus inornatus)*, Arctic Warbler *(Ph. borealis)*, Dusky Warbler *(Ph. fuscatus)*, Radde's Warbler *(Ph. schwarzi)*, Two-barred Warbler *(Ph. plumbeitarsus)*, which migrate in relatively large numbers at Muraviovka Park, and assess the validity of the different vagrancy theories.

The Thick-billed Warbler is a common breeder and abundant migrant in the Muraviovka Park (Heim 2014). Separation of the migratory birds and dispersion of breeding individuals is therefore not possible. The species migrate in one wave within a relatively narrow interval and rather fast. The migration peak is in mid-August. Of the studied species, this one spent the shortest time at the study site. The last individuals were captured in mid-September, by which time the first individuals can arrive to Central China (Williams 2000, Carey *et al.* 2001). In Beidaihe, which lies nearly halfway on the migration route, app. 800 km southwest of the Muraviovka Park, this species migrates through from August to mid-October with a peak in mid-September (Williams 2000, Harrop 2007). They reach the northern part of their wintering area between the end of September and end of October (Harrop 2007).

It is a very rare vagrant in Europe, with only six records from Western and Northern Europe (Norway, Great-Britain) since 2001 (www.tarsiger.com), typically between mid-September

species	distributional range (km²)	migratory distance (km)	distance beetwen breedind range and West Europe (km)	distance beetwen Muraviovka Park and northern border of breeding range (km)
Thick-billed Warbler	2,670,000	2000	5000	800
Black-browed Reed Warbler	2,320,000	1500	5000	600
Pallas's Grasshopper Warbler	1,620,000	2000	5000	1500
Lanceolated Warbler	2,960,000	2500	breeding population in Skandinavia	2000
Yellow-browed Warbler	11,000,000	3000	2500	2000
Artic Warbler	3,360,000	2500	breeding population in Skandinavia	2000
Dusky Warbler	3,830,000	2000	2000	1500
Radde's Warbler	1,170,000	2500	4000	500
Two-barred Warbler	4,640,000	2500	6000	1000

Table 1. The size of the breeding area, the avarage migration distance and the distance between the breeding area and W-Europe, as well as the distance between breeding area and wintering sites (BirdLife International 2013)

1. táblázat Az egyes fajok fészkelőterületének mérete, átlagos vonulási távolsága, az area távolsága Nyugat-Európa és a telelőterületek közt (BirdLife International 2013)

and mid-October (Harrop 2007). This covers approximately the second half / end of the migration period of the species. The western border of its distribution area lies 5000 km from Western Europe, which is much more than the average migration distance *(Table 1)*. Thus, it seems likely that Thick-billed Warblers could appear in Europe mainly because of weather anomalies.

The Black-browed Reed Warbler is one of the most abundant breeding birds at Muraviovka Park, and a common migrant as well (Heim 2014). It has only some long-term recaptures from the first part of the study period. These individuals should be local breeders. The western border of the breeding area is app. 5000 km away from Western Europe. The length of the migration route is the shortest of the studied species *(Table 1)*. There is no European record.

The Pallas's Grasshopper Warbler is an abundant breeder and a common migrant in Muraviovka Park (Heim 2014). The species migrate in a month and a half interval. The migration peak is in mid-August. The migration is fast, with only few and short-term recaptures, despite the fact that the study site is on the southern part of the breeding area, so the northern birds have to migrate 1500 km to reach this site. The last individuals were captured in mid-September. By this time, the first individuals can arrive to the wintering area in Malaysia (Nisbet 1967). In Europe, this species appears in small numbers between the beginning of September and the end of October (www.tarsiger.com, www.netfugl.dk), which coincides with the arrival to the wintering area. These individuals can thus be reverse migrants,

however, the distance between the breeding and wintering areas (2000 km) is much less than the distance between the breeding area and Europe (5000 km) *(Table 1)*. This reduces the possibility of reverse migration and predicts that Pallas´s Grasshopper Warblers reach Europe due to weather anomalies.

The Lanceolated Warbler is a common breeder and regular migrant at Muraviovka Park (Heim 2014), although only few individuals were captured. Birds captured at the beginning of the study period most likely belong to the local population. Migration begins between mid-August and the beginning of October and peaks at the beginning of September. Only few individuals were trapped at the study site, which spent only a short time here, despite the distance between the northern border of the breeding area and Muraviovka Park being around 2000 km. At Beidaihe, this species can be observed from August to mid-October with a peak in the end of September (Williams 2000, Harrop 2007). Here, only migrants and no local breeders occur, which could explain the narrower interval of observation than at the Park. They arrive to Hong Kong in the northern part of their wintering area in October (Harrop 2007). The first individuals arrive to the Malay Penninsula during the beginning of October (Nisbet 1967). In Europe, it is a rare vagrant between the beginning of September and the end of October (Hudson & the Rarities Committee 2007, 2008, 2009, 2010, 2011, Rogers & the Rarities Committee 2001, 2002, 2003, 2004, www.tarsiger.com).

The northwestern edge of its distribution area extends into Europe (BirdLife International 2013). In Finland, 20 singing males were observed in 2000 and in the same year, one week before its earliest occurrence ever, the species appeared on 1st of September in Shetland (Rogers & the Rarities Committee 2000). Concidering the species´ distribution area and migration dynamics, some individuals could get to Europe from Siberia by reverse migration and weather anomalies, but some most likely originate from the European population.

The Yellow-browed Warbler is not a breeder, but an abundant migrant at Muraviovka Park (Heim *et al.* 2012, Heim & Smirenski 2013). It migrates in a broad interval, covering almost two months. Only few individulas stay for a short time at the study site, despite the northern border of the breeding area being 2000 km from Muraviovka Park. It has the largest distribution area among the studied species: 2.4 times higher than the second largest and 9.4 times higher than the smallest *(Table 1)*. The migration peak is at the beginning of September.

In Beidaihe it occurs between mid-September and the end of October (Williams 2000, Harrop 2007), while in Hong Kong, which is the northern part of the wintering area, it arrives during mid-September (Harrop 2007). The first half of its migration to Hongkong and Beidaihe overlaps with its occurence in Europe.

Of the Siberian species, the Yellow-browed Warbler is the most commonly recorded in Europe. Some authors explain this with weather factors (Williamson 1959, Baker 1977, Howey & Bell 1985, Baker & Catley 1987, Elkins 1988), whereas others with genetic defects (birds are misorientated, defective ones, mirror migration) (Rabøl 1969, 1986, De Sante 1983, Thorup 1998, 2004), or with the establishment of a new wintering area (De Juana 2008).

Furthermore, it has the largest distribution area of the studied species (BirdLife International 2013). The distance between the wintering and breeding areas (3000 km) is only a little more than the distance to Western Europe (2500 km). In some years, there are mass migrations not only in Western and Northern Europe, but also even further south, for example

in the Carpathian Basin (Hadarics & Zalai 2008, www.birding.hu, www. rombird.ro) and in the Mediterranean (De Juana 2008). The westernmost record comes from Senegal (De Juana 2008).

In Northern and Western Europe, this species occurrs typically between mid-September and mid-November, with a peak in mid-October (Harrop 2007). The number of spring records is much lower – for example, in Germany, this rate is 40:1 (Krüger & Dierschke 2004). These individuals must be successful wintering survivors (Dymond *et al.* 1989). It appears earliest in Finland, Sweden and Denmark, then two weeks later in the Netherlands and the United Kingdom. In the latter country, there is a difference between the Northeastern Scottish and southern English areas, and the north of Sweden experiences their arrival one week earlier than the south of the country (Baker & Catly 1987, Marchant 2002). The number of observed individuals grows in time southward (De Juana 2008).

The temporal pattern of European observations render reverse migration probable, however, the large differences in the number of individuals can be explained by annual weather anomalies (for example in Finland, it had only 79 records in 2010, while in 2011, it had 230 records) (www.tarsiger.com). Individuals might reach Europe from the north-western part of their breeding area during dispersal movements, but it could also reflect different success on the breeding areas: if the species has a good breeding success in a given year, it can occur in larger numbers in Europe.

The Arctic Warbler is a common migrant at Muraviovka Park (Heim 2014). It migrates in a narrow, one month interval between the beginning of August and mid-September. The migration peak is in the second half of August. The northern border of the breeding area is 2000 km north of the Park *(Table 1),* but only a few individulas spend a short time in the study site.

It occurs in Western Europe primarily in September (www.tarsiger.com). There is a significant breeding population in Scandinavia, so some of the European occurrences could originate from dispersion movements. The European occurrences do not show large annual differences (Rogers & the Rarities Committee 2000, 2001, 2002, 2003, 2004, Fraser *et al.* 2005, 2006, Hudson & the Rarities Committee 2007, 2008, 2009, 2010, 2011), so they are probably not the consequences of weather anomalies, but of stable dispersal movements.

The Dusky Warbler is a common breeder and migrant at Muraviovka Park (Heim & Smirenski 2013, Heim 2014). It shows a protracted migration from July to the first part of October, however, breeding birds and migrants cannot be separated. This might explain the long interval, which is three times longer than that of the Two-barred Warbler. The migration peaks in the second half of September. The birds spent longer time at the study site than the other studied species, and their migration is the slowest.

In Beidaihe, it occurs in October (Williams 2000, Harrop 2007). Since there are not local breeders there, the observation interval is narrower than at the Muraviovka Park. Hong Kong, which is the northern part of the wintering area, is reached by migrating birds by the second half of October (Harrop 2007).

In the British Islands, this species is most common from mid-October to mid-November (Harrop 2007). Records from Central and Eastern Europe are between September and February. Most of the European records are from the migration peak, but in some cases,

individuals were also trapped after this period (Rogers & the Rarities Committee 2001, 2002, 2003, 2004, www.tarsiger.com). The specific European observation times overlap with the arrival times to the wintering sites. The distance between the wintering sites and the breeding area is comparable to the distance between the western border of the area and Europe (app. 2000 km) *(Table 1),* which makes reverse migration a possible explanation for the occurrences of vagrants. However, the role of weather factors is more probable, since there is a high variation in the annual number of records in Europe (Rogers & the Rarities Committee 2000, 2001, 2002, 2003, 2004, Fraser *et al.* 2005, 2006, Hudson & the Rarities Committee 2007, 2008, 2009, 2010, 2011, www.tarsiger.com).

The Radde's Warbler is a regular migrant and rare breeder at Muraviovka Park (Heim *et al.* 2012, Heim 2014). It migrates in a reatively narrow interval from the second part of August to the second part of September. The migration peak is in mid-September. The northern border of the breeding area is the closest to the Park among the studied species *(Table 3).* In Beidaihe, it occured from the end of September to mid-October (Williams 2000, Harrop 2007). Hong Kong, which is the northern part of the wintering area, is reached from the last week of October to the third week of November (Harrop 2007). In Europe, it occurs typically in October (Harrop 2007) as a rare vagrant, primarily in the northern and western countries (Rogers & the Rarities Committee 2001, 2002, 2003, 2004, www.tarsiger.com). The low number of records might be explained by the long distance between the breeding area and Europe. The number of observed birds shows annual variability in Great Britain (Rogers & the Rarities Committee 2000, 2001, 2002, 2003, 2004, Fraser *et al.* 2005, 2006, Hudson & the Rarities Committee 2007, 2008, 2009, 2010, 2011), which strengthens the weather hypothesis.

The Two-barred Warbler is a regular migrant at Murviovka Park (Heim 2014). It migrates in a narrow interval from mid-August to the beginning of September. The migration peak is in the end of August. The migration is fast, the individuals spent only a short time at the study site.

In Beidaihe, it migrates from September to October, the peak is in mid-October (Williams 2000, Harrop 2007). It arrives to the northern part of the wintering area in the end of September, the peak is in the end of October (Harrop 2007).

In Europe it is a very rare vagrant from mid-September to the end of October (Harrop 2007). It is one of the rarest vagrants, until 2013 it had only 14 European records between the end of September to the end of November in the western and northern countries (www.tarsiger.com). It has the largest distribution area of all studied species, however, the distance between the breeding area and Europe is the longest *(Table 1).* The low numbers of records might be explained by weather anomalies.

Methods

The study was carried out during the autumn migrations in 2011–2014 at Muraviovka Park along the middle stream of the Amur River in the Russian Far East. The study site is located 60 km southeast of the city of Blagoveshchensk *(Map 1).*
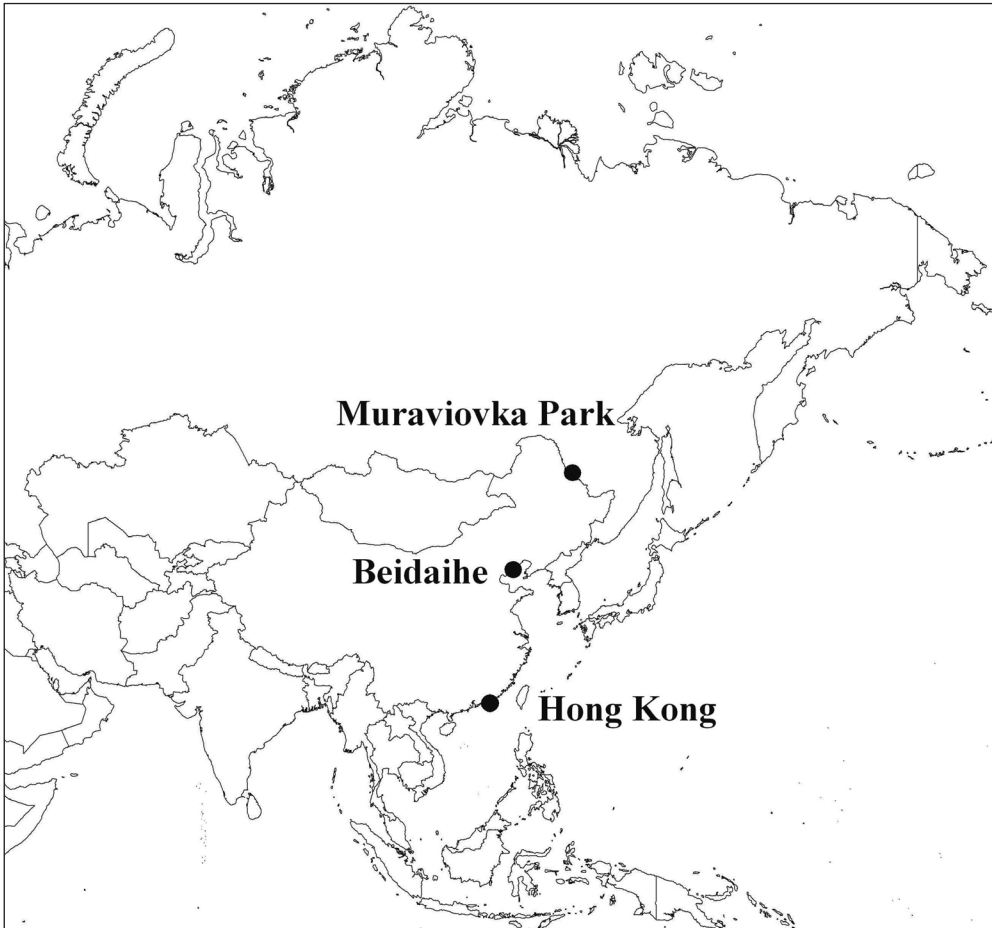
Map 1.   The ringing places of the studied species in East-Asia
1. térkép A vizsgált fajok gyűrűzési helyei Kelet-Ázsiában

Up to 34 mist nets (12 and 6 meters in length with 5 packets) were set up in a variety of habitats: homogeneous reed beds, sedges and grassy swamps interspersed with willows and raspberries, rich shrub-layered mixed forest, very dense scrub and stubble. The work was carried out from sunrise to sunset and the nets were checked every hour. The nets were controlled also during the night in 2014.

The study periods were the following: in 2011, from 7th September to 24th October; in 2012, from 29th August to 16th November; in 2013, from 25th July to 23rd October, while in 2014, from 25th July to 29th September. In 2011 and 2012, the work began later due to financial reasons, while in 2013, the Amur flooded, which had a strong impact on the work.

For the calculations, we used the earliest common starting date of all years (25th July).

The data analysis was carried out based on 5256 individuals of the nine species. Rings were supplied by the Moscow Ringing Centre. Identification of the species was based on Svensson (1992) and Brazil (2009).

species	captures (n)	recaptures (n)
Thick-billed Warbler	628	82
Black-browed Reed Warbler	353	25
Pallas's Grasshopper Warbler	341	56
Lanceolated Warbler	100	13
Yellow-browed Warbler	1580	123
Artic Warbler	122	14
Dusky Warbler	1107	347
Radde's Warbler	217	30
Two-barred Warbler	98	20

Table 2.　　Number of studied species
2. táblázat　A vizsgált fajok egyedszáma

We pooled the daily trapping data of the four years and fittedkernel smoothed arrival distribution curves. Subsequently we determined the migration period for each species (the first and last day when the species was captured) and the location of the maximum value as the peak of the smoothed migration curve. We also calculated the percentage of recaptures and the stop-over timing.

All statistical analyses and graphs were made by the R 3.2.2 program (R Development Core Team 2015) and the smoothed curves were fitted by the ''mgcv'' package (Wood 2006).

Results

Thick-billed Warbler

Of all the studied species, this one was the third most abundant with 628 ringed individuals *(Table 2)*. The migration took place between the 1st and the 55th day. The peak of the migration wave was on the 21st day. Of the ringed birds, 13.1% have been recaptured, 65.9% within two days. An average of 2.7 days elapsed between the first and last capture, only one bird was re-trapped after one week *(Figure 1, Table 3)*.

species	interval	length (day)	peak
Thick-billed Warbler	25 July – 17 Sept.	55	14 Aug.
Black-browed Reed Warbler	25 July – 29 Sept.	67	15 Aug.
Pallas's Grasshopper Warbler	25 July – 21 Sept.	59	15 Aug.
Lanceolated Warbler	27 July – 5 Oct.	71	3 Sept.
Yellow-browed Warbler	26 July – 13 Oct.	80	3 Sept.
Artic Warbler	1 Aug. – 17 Sept.	48	22 Aug.
Dusky Warbler	25 July – 11 Oct.	79	17 Sept.
Radde's Warbler	5 Aug. – 26 Sept.	49	11 Sept.
Two-barred Warbler	4 Aug. – 29 Sept.	57	23 Aug.

Table 3.　　Characteristics of the migration of the studied species
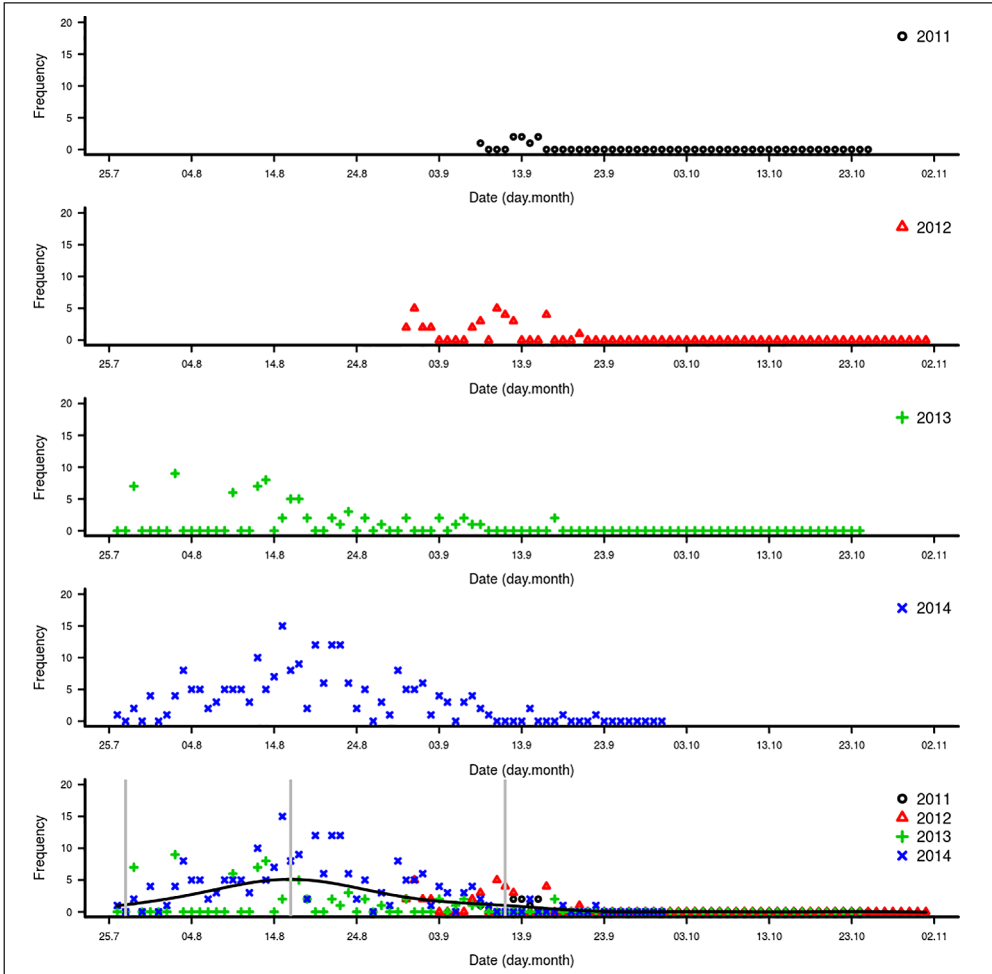*3. táblázat*　A vizsgált fajok vonulásának jellemzői
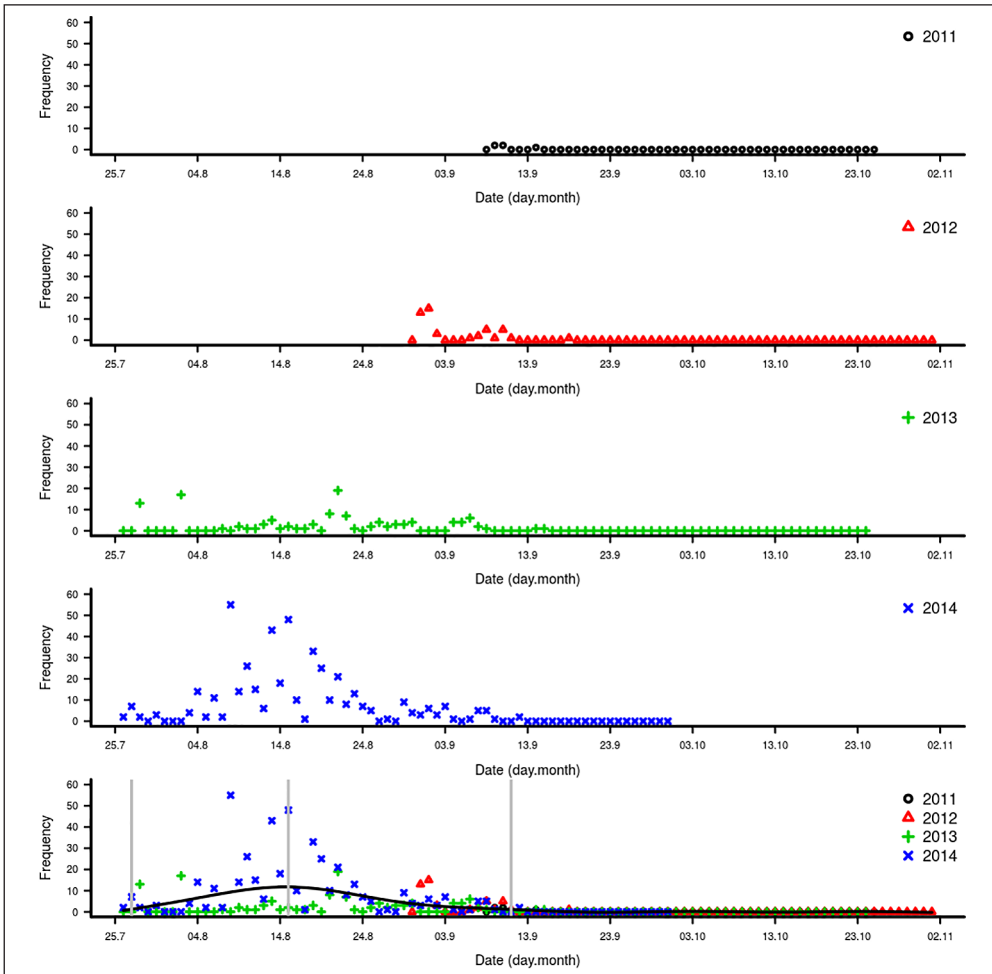
Figure 1. Daily number of ringed Thick-billed Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures

1. ábra A gyűrűzött vastagcsőrű nádirigó napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Black-browed Reed Warbler

The fifth most abundant species with 353 ringed individuals *(Table 2)*. The migration took place between the 1st and the 67th day. The peak of the migration wave was on the 22nd day. Of the ringed birds, 7.1% have been recaptured, 48% within two days. An average of 4.5 days elapsed between the first and last capture, only five birds were re-trapped after one week *(Figure 2, Table 3)*.
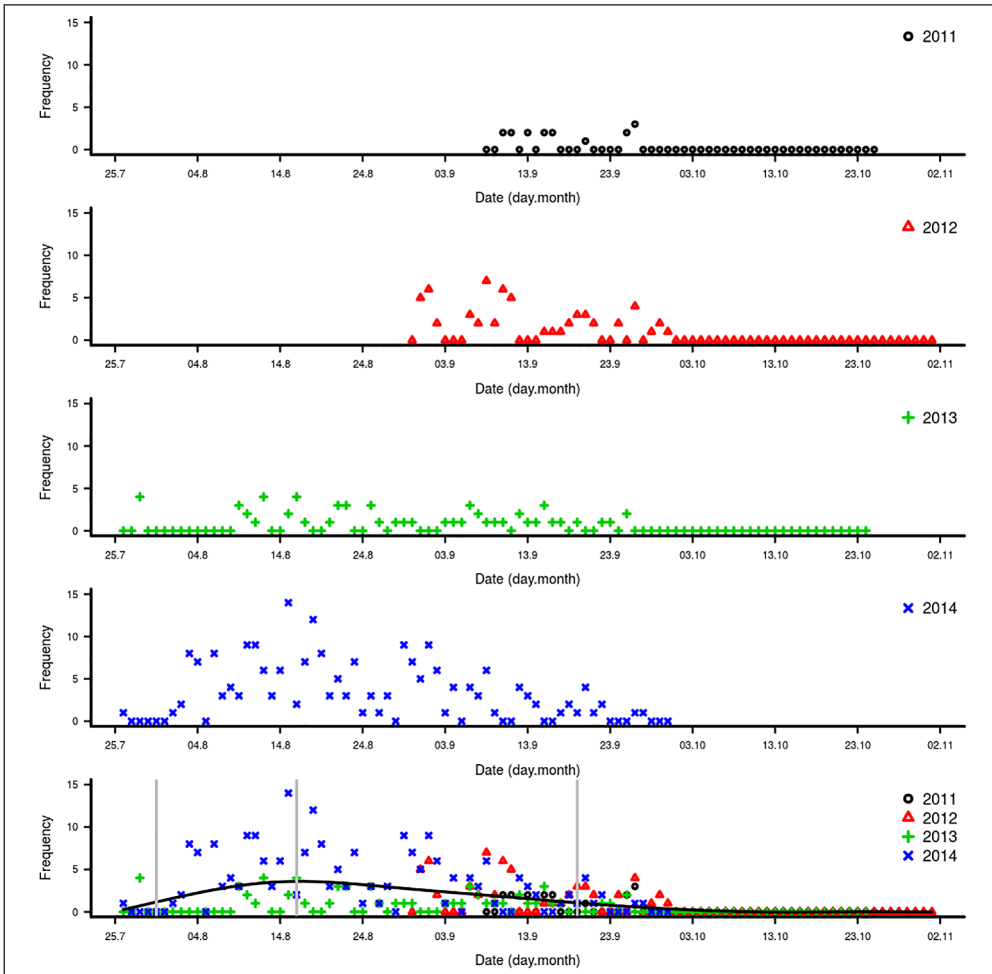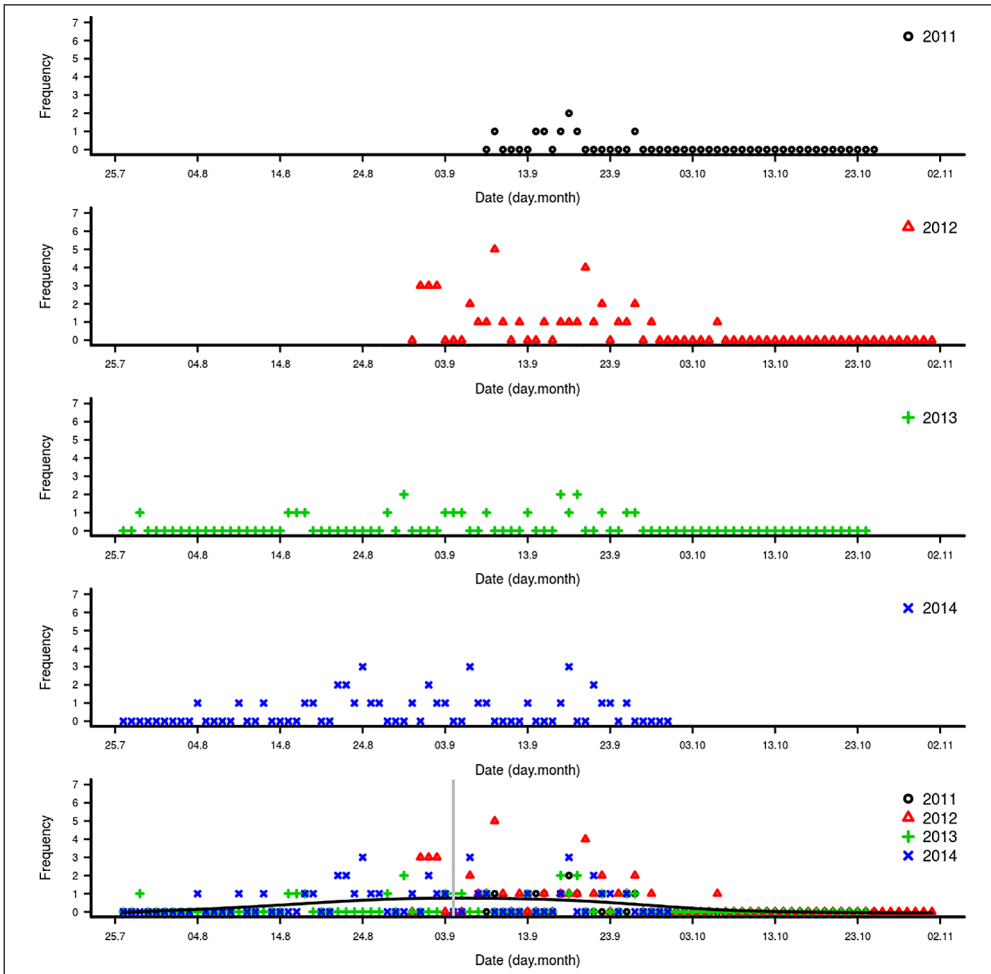
Figure 2. Daily number of ringed Black-browed Reed Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures

2. ábra A gyűrűzött keleti foltos nádiposzáta napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Pallas's Grasshopper Warbler

The fourth most abundant species with 341 ringed individuals *(Table 2)*. The migration took place between the 1st and the 59th day. The peak of the migration wave was on the 22nd day. Of the ringed birds, 16.4% have been recaptured, 39% within two days. An average of 5.4 days elapsed between the first and last capture, 17 birds were retrapped after one week *(Figure 3, Table 3)*.

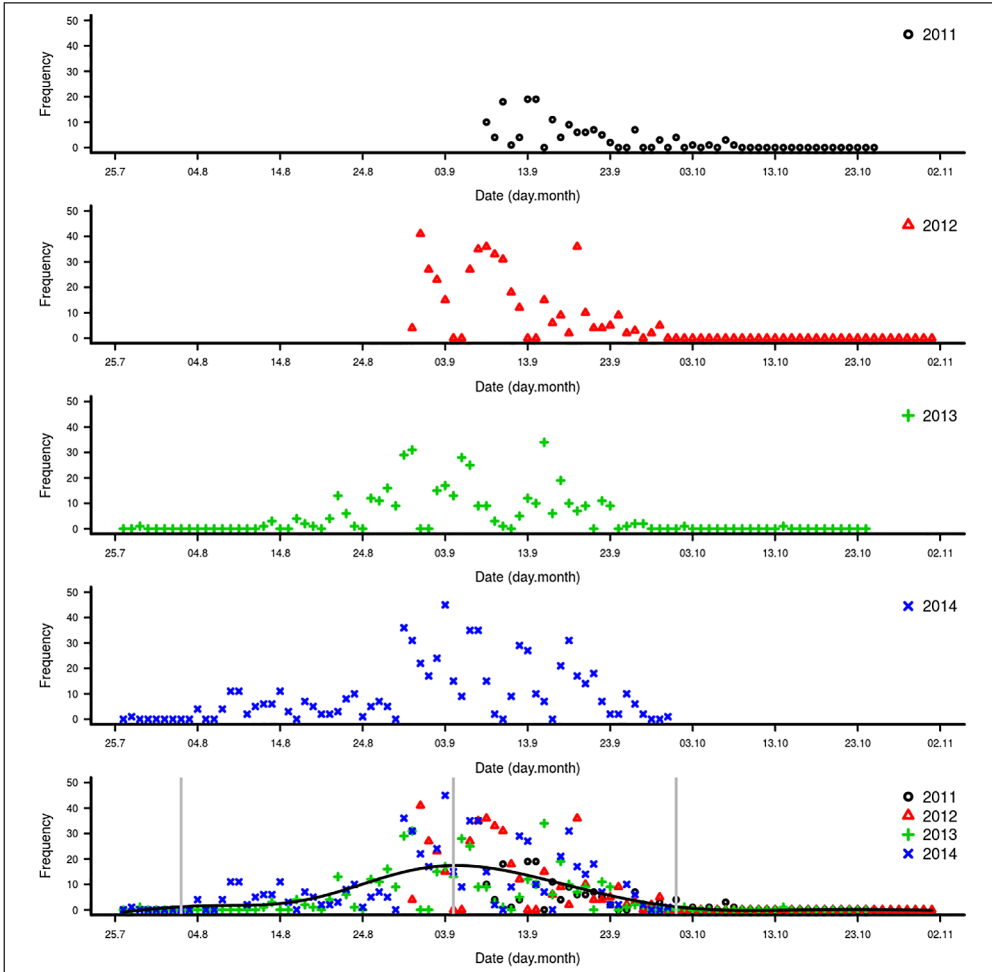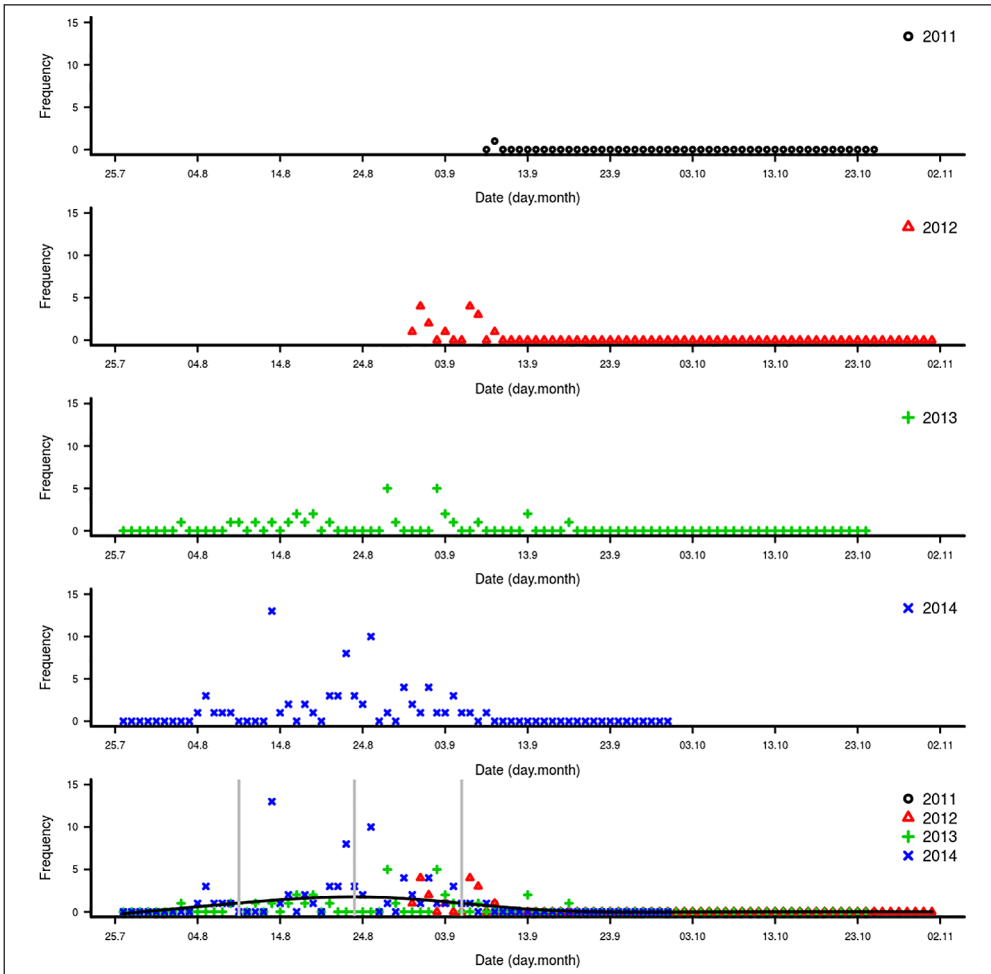*Figure 3.* Daily number of ringed Pallas's Grasshopper Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures

3. ábra A gyűrűzött csíkos tücsökmadár napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Lanceolated Warbler

The eighth most abundant species with 100 ringed individuals *(Table 2)*. The migration took place between the 3rd and the 73th day. The peak of the migration wave was on the 41st day. Of the ringed birds, 13% have been recaptured, 23% within two days. An average of 8.5 days elapsed between the first and last capture, only seven birds were re-trapped after one week. One bird was recaptured one year and five days after the first capture *(Figure 4, Table 3)*.

Figure 4. Daily number of ringed Lanceolated Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last capture.

4. ábra A gyűrűzött foltos tücsökmadár napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Yellow-browed Warbler

Of all the studied species, this one was caught in the highest numbers with 1580 ringed individuals *(Table 2)*. The migration took place between the 2nd and 81st days. The peak of the migration wave was on the 41nd day. Of the ringed birds, 7.8% have been recaptured, 67.5% within two days. An average of 2.8 days elapsed between the first and last capture, only seven birds were retrapped after one week *(Figure 5, Table 3)*.

Figure 5. Daily number of ringed Yellow-browed Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures
5. ábra A gyűrűzött vándorfüzike napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Arctic Warbler

The seventh most abundant species with 122 ringed individuals *(Table 2)*. The migration took place between the 8th and 55th days. The peak of the migration wave was on the 29th day. Of the ringed birds, 11.5% have been recaptured, 78.5% within two days. An average of 2.8 days elapsed between the first and last capture, only two birds were retrapped after one week *(Figure 6, Table 3)*.
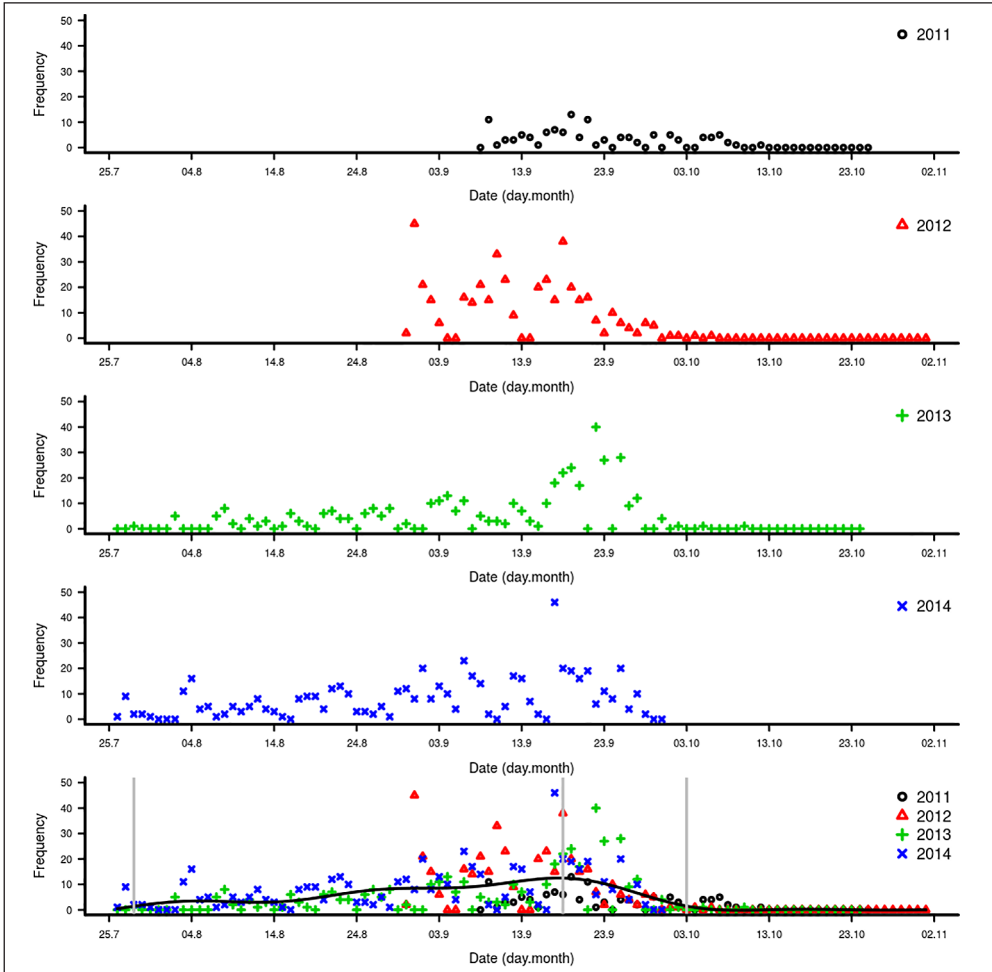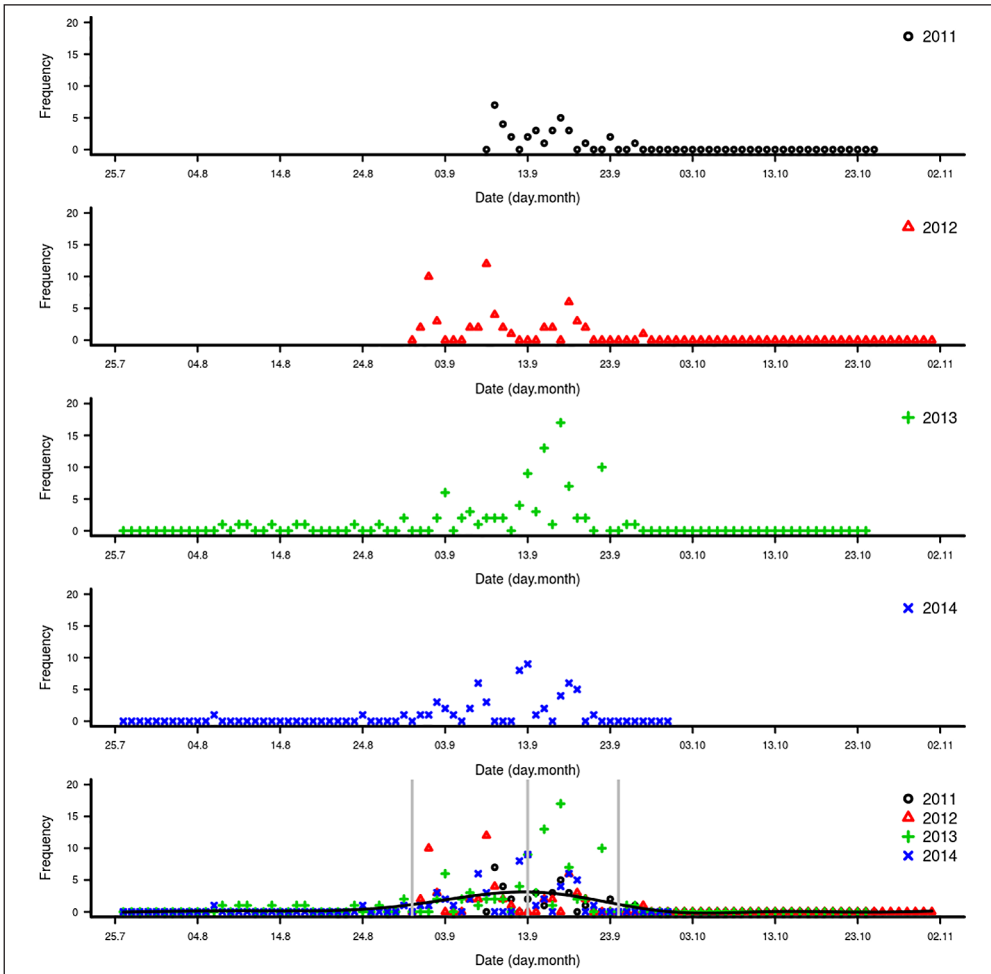
Figure 6. Daily number of ringed Artic Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures

6. ábra A gyűrűzött északi füzike napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Dusky Warbler

The second most abundant species with 1107 ringed individuals *(Table 2)*. The migration took place between the 1st and 79th days. The peak of the migration wave was on the 55th day. Of the ringed birds, 31.3% have been recaptured, 35.2% within two days. An average of 6.4 days elapsed between the first and last capture, 96 birds were retrapped after one week and have three one year and one two years recaptures *(Figure 7, Table 3)*.

Figure 7. Daily number of ringed Dusky Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures

7. ábra A gyűrűzött barna füzike napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Radde's Warbler

The sixth most abundant species with 217 ringed individuals *(Table 2)*. The migration took place between the 12th and 64th days. The peak of the migration wave was on the 49th day. Of the ringed birds 13.8% have been recaptured, 58.3% within two days. An average of three days elapsed between the first and last capture, only two birds were retrapped after one week *(Figure 8, Table 3)*.
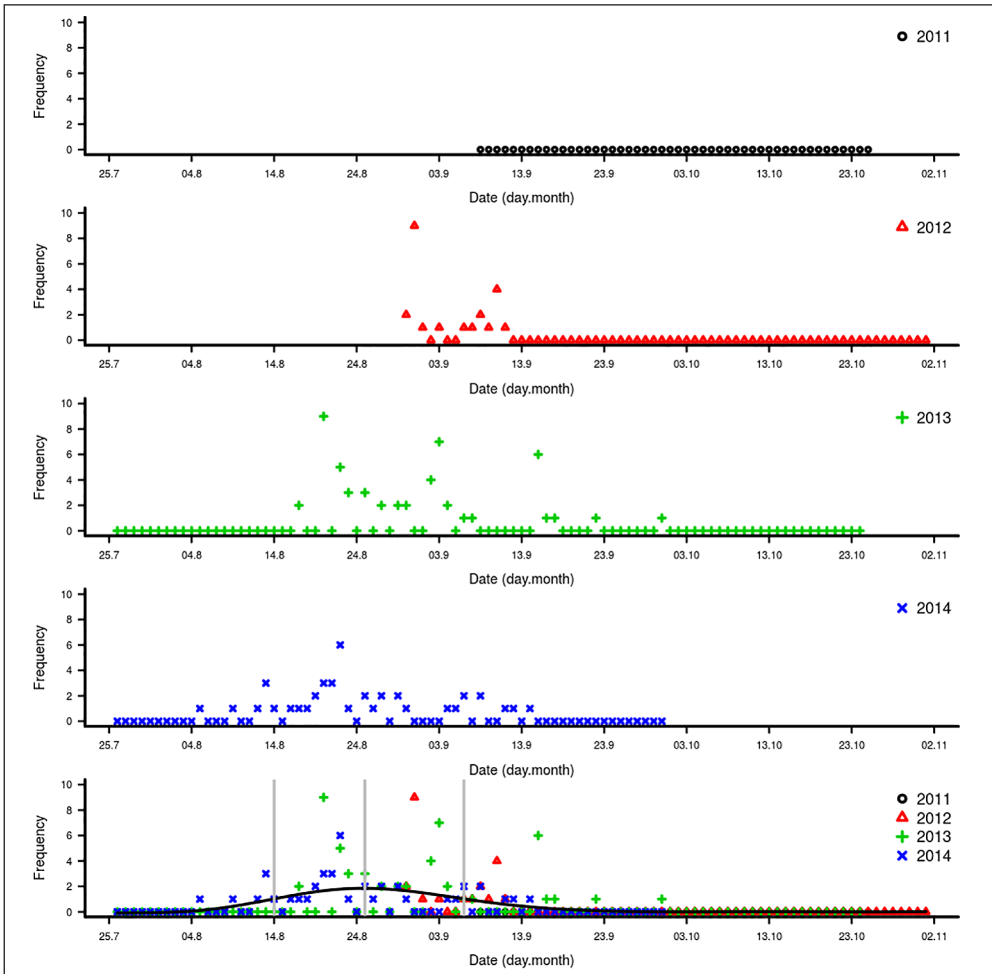
Figure 8. Daily number of ringed Radde's Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures

8. ábra A gyűrűzött vastagcsőrű füzike napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Two-barred Warbler

Of all the studied species, this one was caught in the lowest numbers with 98 ringed individuals *(Table 2)*. The migration took place between the 11th and 67th days. The peak of the migration wave was on the 30th day. Of the ringed birds, 20.4% have been recaptured, 61.1% within two days. An average of 2.8 days elapsed between the first and last capture, only one bird was retrapped after one week *(Figure 9, Table 3)*.

Figure 9. Daily number of ringed Two-barred Warbler annually and pooled with the fitted smoothed curve. The vertical grey lines show the first, peak and last captures

9. ábra A gyűrűzött szalagos füzike napi gyakorisága éves bontásban és egyesítve a simított görbével. A függőleges szürke vonalak az első, a maximális és az utolsó megfogást mutatják

Discussion

Most of the Siberian Passerines use the traditional autumn migration routes for the wintering sites in SE-Asia. However, many species have european, american and african occurrence data, far away from the usual migration routes and wintering sites, even in the opposite direction (Alerstam 1990). There have been many explanations developed for this in the last decades.

Based on the weather hypothesis, these species appear in Europe due to the Siberian anticyclones (Baker 1977, Howey & Bell 1985, Baker & Catley 1987, Elkins 1988). In favor of the hypothesis is the fact that the birds cannot compensate the effect of strong easterly winds (Liechti 2006), which can sweep them far away from their traditional distribution area

by hundreds or thousands of kilometers (Elkins 1988). This hypothesis is confirmed by the captures of several individuals of different species. For example, 58 individuals of 13 species were detected in autumn 1975 in Britain, most of them on the Eastern coast (Baker 1977). There was a similar 'megadrift' in October 1982, when Pallas's, Dusky and Radde's Warbler (which have partially overlapped breeding areas) were observed in high numbers, in contrast with the Yellow-browed Warbler, which has more northerly breeding area, and the Artic and Greenish Warbler, which migrate earlier. These species occurred in lower numbers than the previous ones (Howey & Bell 1985).

The number of observations about a given species shows large variation between the years (Rogers & the Rarities Committee 2000, 2001, 2002, 2003, 2004, www.tarsiger.com, Fraser *et al.* 2005, 2006, Hudson & the Rarities Committee 2007, 2008, 2009, 2010, 2011). For example, in 2013, 420, while in 2004, only 31 Yellow-browed Warbler individuals were observed in Finnland (www.tarsiger.com), due to the different intensity of cyclones (Baker 1977). An indirect confirmation of this hypothesis is that the number of yearly observations of species with different distribution areas and migration timing do not show correlation (Howey & Bell 1985).

The argument against this hypothesis is that the effect of wind velocity should be different on animals of different sizes, although this could not be proven (Pfeifer *et al.* 2007). Also, European occurrence data of certain Siberian species overlap with their migration peaks, which indicates regularity (Harrop 2007). The number of Yellow-browed Warbler in Britain increased sharply from 1984. The annual average was 81 (27–182) between 1968–1983, and it was 382 (211–739) between 1984–1998 (Fraser *et al.* 2000). The Siberian vagrants caught in North Ronaldsay (Great-Britain) were in better condition on arrival than the general run of commoner migrants. The reason for this might be that their build-up of fat reserves must have occurred during their migration (Woodbridge & Duncan 1998).

On the basis of the reverse migration hypothesis, some individuals could occur in Europe due to genetic defect. In many cases, the migration direction of the observed birds differ by 180 degrees from the generally assumed direction (Rabøl 1969, 1976, Cottridge & Vinicombe 1996, Thorup 1998). The distribution pattern of the occurrences falls in the shadow of the area covered by the correct migration route (vagrancy shadow) (Cottridge & Vinicombe 1996). According to this hypothesis, in these birds, the inherited navigation mechanism is incorrect and the north – south pole or the spring – autumn programme is reversed (Gilroy & Lees 2003, Pfeifer *et al*. 2007). In favor of the hypothesis is that the most of the European data of Siberian species overlap with their migration peaks and the flight distance correlates with the traditional migration distance (Harrop 2007). In addition, the Yellow-browed and Arctic Warbler with more northerly breeding areas occur in northern areas of Great Britain, compared to the Pallas's Leaf Warbler and Two-barred Warbler with more southerly breeding areas (Rabøl 1969).

In principle, the individuals that choose the wrong direction are supposed to be under strong selection, as they can get to areas, where the weather is unfavourable and the food supplies are scarce. However, it seems that some individuals that choose the wrong direction can survive the winter. Orientation experiments show that the migration direction of the survivors in spring is easterly, so they can get back with good chance to the original breeding area, and the wrong direction factor can also be inherited (Thorup 1998). The Yellow-browed Warbler has a stabile wintering population in Great Britain (Thorup 1998, Marchant 2002).

This species had only a few observations before 1958, but between 1958–1985 it had already 2648 occurrences, and between 1986–2003 there were 9093 observations. The record was 853 observation data in one year. Similarly, the Pallas's Warbler had only a few observations before 1951 in Great Britain (Baker 1977), but between 1986–2003 it had already 1783 observation data with a 303 individuals year record (Dymond *et al.* 1989, Gilroy & Lees 2003, Fraser & Rogers 2006).

The argument against this hypothesis is that the yearly occurrences of most species show a big variability both in the British Isles and Scandinavia, despite the fact that the monitoring network is relatively stable, so the observations well approximate the actual numbers, or at least are proportionate (Rogers & the Rarities Committee 2000, 2001, 2002, 2003, 2004, www.tarsiger.com, Fraser *et al.* 2005, 2006, Hudson & the Rarities Committee 2007, 2008, 2009, 2010, 2011). Genetically, the only likely explanation is that in some years, many mutations arise, whereas in other years only a few, and these mutations are rare and their probability is constant (Freeman & Herron 2001, Gilroy & Lees 2003). In case of reverse migration, it could be expexted that the observations fall more-or-less at the same time within the distance from the breeding area. However, the data show that the birds appear earlier in the northern regions than in the southern ones, and the date of observations shifts to later towards the south. This time pattern is observable both in the Scandinavian countries and Great Britain and also in continental scale (September – Scandinavia, December – Canary Islands) (De Juana 2008).

The long-range dispersal hypotesis says that the occurrences not typical for the species may be in any direction (Philips 2000, Gilroy & Lees 2003). With the analysis of capture-recapture data, observations on captive birds and radio telemetry, it can be detectable in some species that in the beginning of the migration, the birds can depart to any – even opposite – direction. These individuals migrate in the right direction only later (Berthold 1996). Dispersional movements have a main role in the discovery of new breeding areas and in the modification of the breeding area.

In favor of the hypothesis is that the Yellow-browed Warbler, the Olive-backed Pipit *(Anthus hodgsoni)*, the Rustic Bunting *(Emberiza rustica)*, the Little Bunting *(E. pusilla)* are regular visitors in Israel (Shirihai *et al.* 1996), while the Red-throated Thrush *(Turdus ruficollis)* has data from Northern-Europe, Israel, Egypt, Greece, France, Spain, Taiwan, Japan and Alaska (Gilroy & Lees 2003).

One Yellow-browed Warbler was observed in 1999 in an Alaskan Island (Lehman 2000), it has been found in Senegal (De Juana 2008) and appeared from Iceland to Morocco, and from the Canary Islands to Kuwait (Snow & Perrins 1998). One Lanceolated Warbler landed on a ship 110 km north of Bjørnøya in the Arctic Ocean (Lewington *et al.* 1991). These observations fall very far from the 'revers migration shadow'. The argument against this hypothesis is that the Yellow-browed and Arctic Warbler with more northerly breeding areas show different pattern in Great Britain than the Pallas's Leaf Warbler and Two-barred Warbler with more southerly breeding areas (Rabøl 1969). Maybe it is more important that the length of dispersal movements of long-distance migratory species is much shorter than the migratory distance itself (Berthold 1996).

Nowadays it is seems, that these birds are not really vagrants, but also regular migrants, which have Western-European or Western-African wintering sites. The high survival rate would explain that why increased the numnber of observed individuals of some species on the last decads (Gilroy & Lees 2003, De Juana 2008), because of the 'west-orientating' genotypes are inherited.

In favor of the hypothesis that going to south the number of spring observations are significantly increased. This also means that the birds use different migrations journays in spring and autumn (loop migration) (De Juana 2008).

A positive impact of climate change on range and population size could promote vagrancy, while the increasing use of such alternative migration flyways could provide adaptive advantages in a changing environment (Jiguet & Barbet-Massin 2013).

From the foregoing it seems to be very difficult – may be impossible – generalize, coherent explanation for this phenomenon. For explanation several other parameters have to be tested for influence to the probability of the occurrences. For example, the number of individuals (unfortunately there are no good estimates of the Siberian species), the size of distribution area, the distance between the breeding and wintering sites, the migratory distance, the timing of migration, the length of the migration intervals, the variability of the European occurrences, the characteristics of the yearly autumn Siberian weather etc. The possibility of the detection is greater, if the distribution area and the number of individuals are larger, the distance is shorter between the breeding and wintering sites (Pfeifer *et al.* 2007). There is lesser probability of the effects of the weather anomalies, if the migration of the individuals is faster and in species-level is narrow interval than a species with slower migration and broader interval.

The studies species have large distribution area, expect the Yellow-browed Warbler and Two-barred Warbler which have very large distribution area (BirdLife International 2013), but in the previous category there are big differences. The average migration length is 1500–3000 km, while the distance between the breeding area and Western-Europe is 2000–6000 km. The average distance between the studied site and the northern border of the breeding area is 800–2000 km *(Table 1)*.

As mentioned above, the occurrence of Siberian species in Europe cannot be explained by any of the hypothesis alone, since the distribution area, timing of migration and intervals of the species differ. The observations of species which have breeding populations in Europe are most likely explained by dispersal movements. In case of the other species, it cannot be excluded that reverse migration takes place. This suits the occurrence data of the Yellow-browed Warbler, whereas the large annual differences might be explained by differences in the intensity of weather conditions.

Climate change will surely have an impact on the distribution areas of the species, but at present, weather anomalies might be a better explanation for the occurrence of Siberian vagrants in Europe.

The expected increase in the number of records, a comparison of the results of studies along the migration routes and the examination of the orientation capabilities of vagrants in Europe will help to understand the observed patterns.

Acknowledgements

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Hitchhikers' guide to analysing bird ringing data

Part 2: distributions, summary statistics and outliers

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Abstract This paper is the second part of our bird ringing data analyses series (Harnos *et al.* 2015a) in which we continue to focus on exploring data using the R software. We give a short description of data distributions and the measures of data spread and explain how to obtain basic descriptive statistics. We show how to detect and select one and two dimensional outliers and explain how to treat these in case of avian ringing data.

Keywords: distribution types, outlier, standard deviation, coefficient of variation, descriptive statistics

Összefoglalás A sorozat második részében folytatjuk a madárgyűrűzési adatok kezelését, elemzését az R statisztikai program használatával (Harnos *et al.* 2015a). A különböző eloszlás típusok ismertetése, a szórás fogamának bevezetése után bemutatjuk, hogyan számolhatunk egyszerű módon leíró statisztikákat az adattáblázatunkra. Módszereket mutatunk a lehetséges egy- és kétdimenziós kiugró értékek felimerésére, és tanácsokat adunk a kezelésükre. Megmutatjuk, hogyan lehet egyszerűen leválogatni az olyan eseteket, amelyeknél gyanús értéket találunk valamely változóban.

Kulcsszavak: eloszlás típusok, kiugró érték, szórás, relatív szórás, leíró statisztika

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Introduction

This paper is the second part of our bird ringing data analyses series (Harnos *et al.* 2015a) in which we continue to focus on exploring data. We will give a short description of data distributions, and explain how to obtain basic descriptive statistics. In general our template dataset is of Pied Flycatchers trapped and ringed at the Ócsa Bird Ringing Station (Central Hungary) between 1984–2014 (for details see Harnos *et al*. 2015b). The dataset is available through our `ringR` package or from the online appendix of this paper along with the code used in this part (OH_2016_24(1)_172-181_appendix.zip). We used R 3.3.0 for the analysis (R Core Team 2016) on the Ubuntu 14.04 platform. The codes were written with RStudio 0.98.1103.

Distribution types

Under a given variable's distribution we mean the pattern of observed values on the number line (Reiczigel *et al.* 2014). We can distinguish uniform, unimodal, multimodal and skewed distribution patterns *(Figure 1)*. In case of uniform distributions the values are spread more or less evenly, without observable clutter or aggregation along the number line. In practice, this pattern occurs rarely and typically is a product of artificial data generation. The other pattern types all show that the frequency of observed values is higher at given locations. If this aggregation occurs around a single value, the pattern is unimodal, as opposed to multiple clutters along the number line in which case, we classify the shape as multimodal (bimodal for two modality centres). Distribution shape and symmetry are also to be considered; distributions can be right-skewed (i.e. more extreme observations are present at larger values) or left-skewed (i.e. more extreme observations are present at smaller values) and can be symmetrical. Distributions can be typically illustrated with histograms and smoothed histograms (see Harnos *et al.* 2015a for details), however boxplots may also show symmetry and give a hint on the shape of distribution. We illustrate distribution types by plotting observed values *(Figure 1)* and we show, how these values shape distributions and how they are represented by boxplots and histograms *(Figure 2a-e)*.

One of the most common and most frequently referred unimodal, bell-shaped, symmetric distribution is the normal or Gaussian distribution. In avian ringing datasets, most of the variables that are measured on a continuous scale (typically biometric measurements) can be expected to have normal distributions (McDonald 2014). This often makes data analyses convenient as most of the commonly used statistical procedures rely on normally distributed
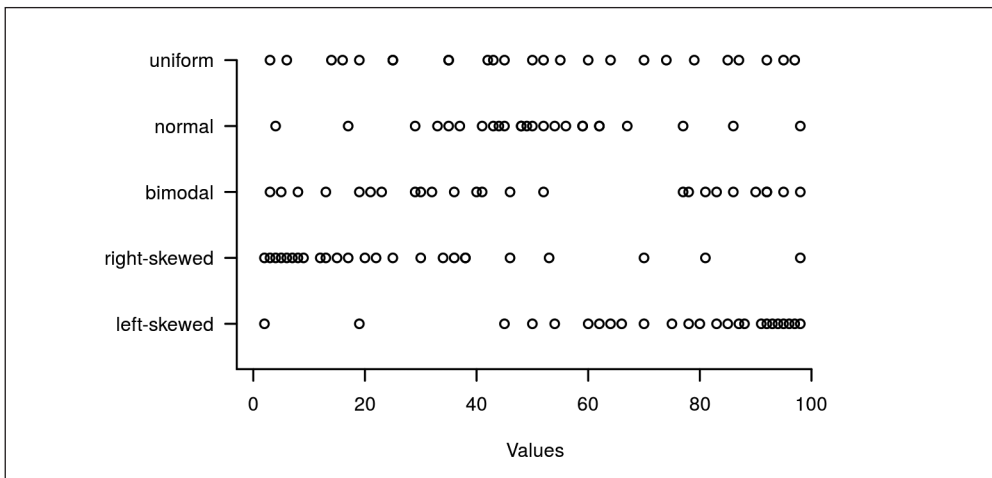

Figure 1. Different distribution patterns described with 25-25 points: evenly distributed on the whole data range (a), symetrically aggregating in the middle (b), aggregating around two values(c), right-skewed (d) and left-skewed (e)

1. ábra Különböző eloszlás-mintázatok 25-25 ponttal ábrázolva: az egész tartományon egyenletesen sűrű (a), középen szimmetrikusan sűrűsödő (b), két értéknél sűrűsödő (c), jobbra ferde (d), balra ferde (e)
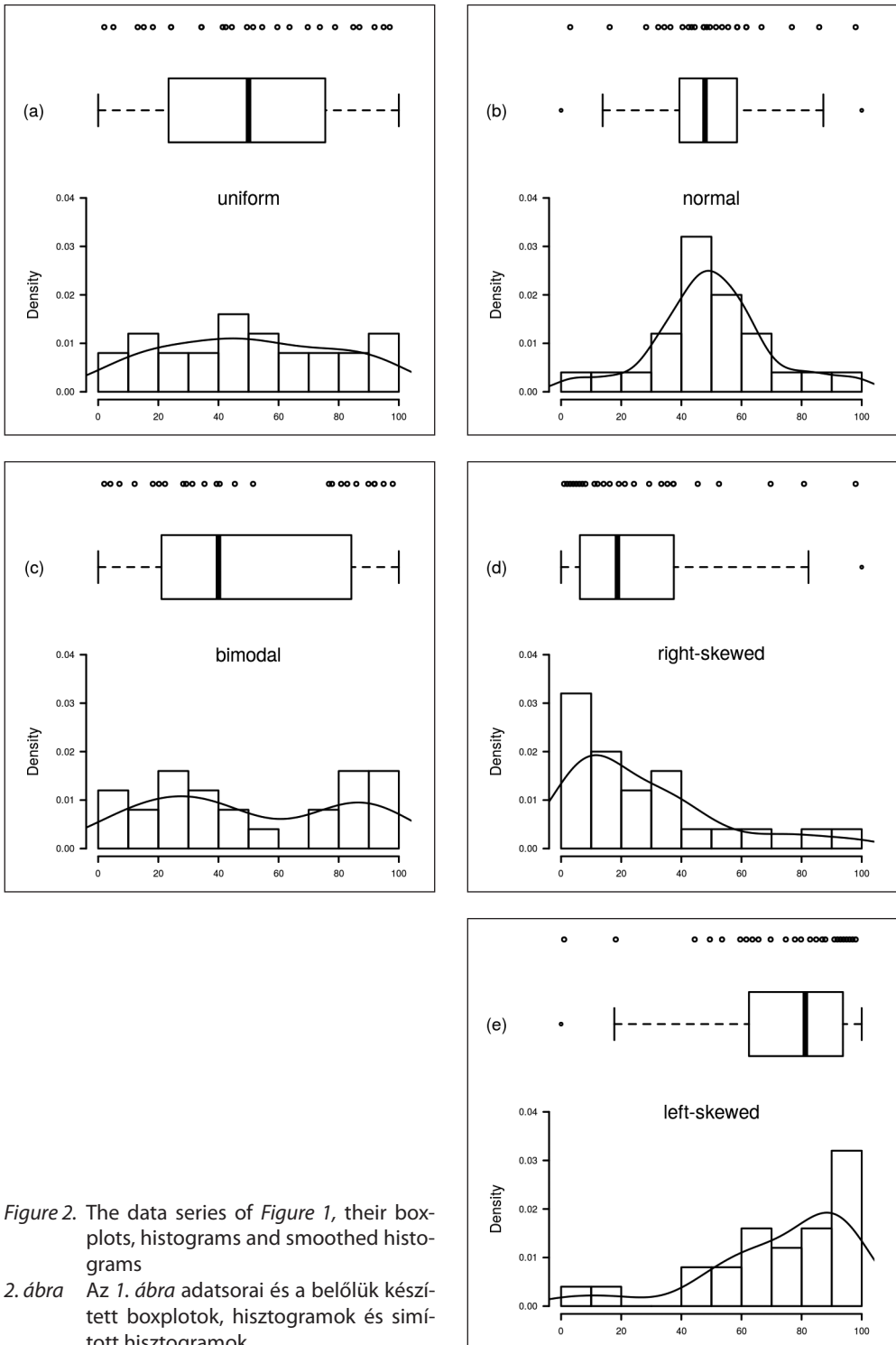
Figure 2. The data series of *Figure 1*, their box-plots, histograms and smoothed histograms

2. ábra Az *1. ábra* adatsorai és a belőlük készí-tett boxplotok, hisztogramok és simí-tott hisztogramok

data. However, in cases when this does not apply, quite often analysts utilise data transformation to artificially create a normal distribution. While transforming data may produce distributions that fulfil the requirements of statistical procedures, one may loose the biological meaning of the data (Ieno & Zuur 2015) making inference on obtained results difficult. Therefore we advise to use common sense and utmost care when applying transformations.

The spread of the data

The distribution of values of a variable can be summarized by two essential statistics, one depicting the central tendency of the data, the other the spread of the data. While central tendency is usually represented with the mean or the median, occasionally with the mode, the spread of the data with the sample variance and sample standard deviation. The variance and the standard deviation measure the average deviation of observed values from the mean as the centre of the distribution. More precisely, the variance is the sum of the squared deviations over all observations divided by n-1, where n is the number of observations. The standard deviation is the square root of the variance, and it is measured on the same scale as the variable. It may be useful to keep in mind, that in case of normally distributed data, approximately 68% values are within one standard deviation away from the mean; about 95% of the values lie within two standard deviations; and about 99.7% are within three standard deviations. This quality of normal distributions is often referred to as the 1-2-3 standard deviation rule *(Figure 3)*.

Using variance (or standard deviation) to describe the spread of data has its limits. For instance, we are interested to know whether Sparrowhawks *(Accipiter nisus)* or Goshawks *(Accipiter gentilis)* have more variable wing length measurements. In our hypothetical
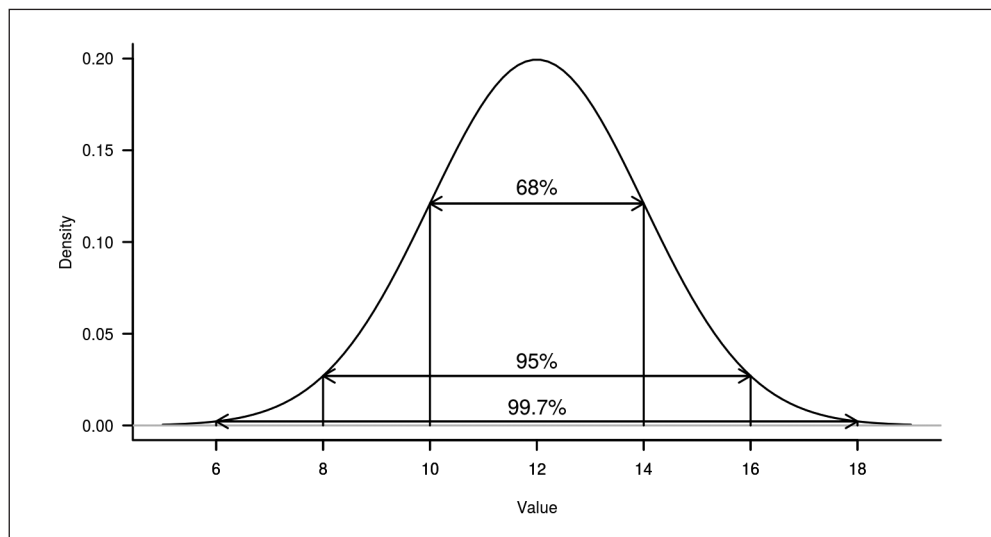

Figure 3. Illustrating the 1-2-3 standard deviation rule in case of a normal distribution if the mean is 12 and the standard deviation is 2

3. ábra Az 1-2-3 szórás szabály bemutatása 12 átlagú és 2 szórású normális eloszlás esetén

example mean Sparrowhawk wing length is 249 mm with a standard deviation of 51 mm while for Goshawks the same statistics are 533 mm and 51 mm. One might intuitively think that both species have similar variation in wing length, as the standard deviations are equal. However, we have to consider the value of the mean when accounting for spread. In order to do this we can calculate the coefficient of variation (CV) as the standard deviation divided by the mean. It can be given in percentages (CV%). This statistics gives a mean-independent assessment of data spread, and as such can be used to evaluate our example, the CV% for Sparrowhawks is 20.5% while for Goshawks it is 9.6%.

Table of the basic descriptive statistics

Let us observe the basic descriptive statistics *(Table 1)* of the distributions shown in *Figure 1*. The table was created with the `RcmdrMisc` package's `numSummary()` command (Fox 2014). The parameters we used were the name of the dataframe and the descriptive statistics to be printed (see. `?numSummary`). Notice that for the first three symmetrical distributions the mean is close to the centre of the value range, while for the left-skewed distribution the mean shifted towards larger, for right-skewed distribution towards smaller values. For symmetrical distributions the median (50% quantile) is similar to the mean, however for skewed distributions it is larger (left-skewed) or smaller (right-skewed) than the mean. The bimodal distribution has the largest standard deviation (`sd`) while the unimodal distribution has the smallest, but the difference is not substantial. However, the coefficients of variation (`cv`) show a marked difference among distributions. Probably the best approach for skewed distributions is to examine the different quantiles.

```
>options(digits = 3)    # setting the number of digits
>library(RcmdrMisc)
>distr_data = read.table("distr_data.csv", sep=";",header=T)
>numSummary(distr_data, statistics = c("mean", "sd", "cv", "quantiles"))
```

Type of distribution	mean	sd	cv	0%	25%	50%	75%	100%
uniform	54.1	27.9	0.516	3	42	52	74	97
normal	50.2	20.1	0.399	4	41	49	59	98
bimodal	50.8	32.8	0.645	3	23	41	83	98
right-skewed	27.7	25.6	0.924	2	8	20	38	98
left-skewed	73.0	24.6	0.337	2	62	80	92	98

Table 1.   Basic descriptive statistics of the data used for *Figure 1* and *2*
1. táblázat Az *1.* és *2. ábrák*hoz használt adatok leíró statisztikái

Summary statistics for groups of data

With the `numSummary()` function we can calculate the basic numerical summaries for groups defined by factors or factor combinations of numeric variables. For example, if we are interested in the basic descriptive statistics of the wing length in the age and sex groups of Pied Flycatchers, we should type (note that we use the data cleaned as shown in Part 1. of this series):

```
>setwd("D:/mydirectory")
>mydata = read.table("FICHYP1.csv", sep=";",header=T)
>numSummary(mydata$WING, statistics = c("mean", "sd", "cv", quantiles"),
groups = mydata$age:mydata$SEX)

        Statistic
  Group     mean     sd      cv     0%    25%   50%   75%  100%
  adult:F   79.5    1.96   0.0246   76   78.0   79    81    85
  adult:M   80.8    1.87   0.0232   77   79.5   81    82    85
  juv:F     79.3    1.77   0.0224   70   78.0   79    80    85
  juv:M     80.3    1.92   0.0239   73   79.0   80    81    87
```

Outliers

In some cases observed values may be out of bounds, or simply impossible (we have already handled the latter in Harnos *et al.* 2015a). These odd values or outliers are values that are somehow out of proportion, too small or too large yet not small or large enough to be able to a priori exclude from the observations. It is important to avoid subjectivity when identifying and treating outliers and here we demonstrate a few methods that may help the evaluation. For normally distributed variables, values that are 3 standard deviations larger or smaller than the mean are considered outliers. For non-normally distributed variables a frequently used rule of thumb is to consider values below or above 1.5 (`const`) interquartile range (`IQR`) from the lower (`Q1`) or upper quartile (`Q3`) to be outliers, and this latter rule is used also by R. These observations can be retrieved using the `boxplot.stats()` command. In the example below we show the outliers of juvenile female Pied Flycatcher wing lengths stored in the `WING` variable. Note that it is important to calculate these values only within homogeneous subgroups of the observations. Calculating the outliers for all ringed Pied Flycatchers regardless of age and sex would produce erroneous results, hence the necessity of subsetting the data. It is useful to evaluate outliers together with the other variables of the individual. To retrieve all observations related to the individuals (i) we can use the `subset()` command as shown below.

```
>mydata_1 = subset(mydata,(mydata$age == "juv" & mydata$SEX == "F" &
>mydata$season == "autumn"))

>boxplot.stats(mydata_1$WING)$out

$out
[1] 70 84 85 84

>Q1 = quantile(mydata_1$WING, na.rm = T)[2]
>Q3 = quantile(mydata_1$WING, na.rm = T)[4]
>IQR = IQR(mydata_1$WING, na.rm = T)
>const = 1.5
>outliers = subset(mydata_1, (mydata_1$WING < (Q1 - const * IQR) |
mydata_1$WING > (Q3 + const * IQR)))

>outliers
           ID        DATE  RECAP      RING AGE  SEX FAT  MUSCLE  MASS WING  THIRD
 258    71051  9/9/1990       0   L52435  1Y     F   4    <NA>  11.7   70     53
 1436  429635  9/2/2006       1  T468844  1Y     F   2       2  13.7   84     60
 1585  503787  9/21/2007     NA   8E3738  1Y     F   0       2  11.5   85     65
 1616  534644  8/26/2008      0   W55664  1Y     F   0       3  11.7   84     64

      TAIL   year  yearday  period.recap   season   age
 258    43   1990      251             0   autumn   juv
 1436   56   2006      244             1   autumn   juv
 1585   56   2007      263             0   autumn   juv
 1616   58   2008      238             0   autumn   juv
```

The code stores the observations in the `outliers` object. Our output shows an interesting pattern; all four outliers in the `WING` variable have correspondingly small or large other measurements indicating that probably the observations are valid and not artefacts due to erroneous data entry. This example demonstrates that outliers are not values that are to be excluded automatically. In fact if we automatically exclude outliers, we alter the distribution pattern, thus new outliers may appear. In extreme cases we may exclude the whole dataset before we realize that there is something wrong. Bear in mind that having outliers may be an indication of skewed distribution and instead of leaving the values out of the analyses we may be more successful in using methods that are applicable to skewed distributions. Quite often we only notice the potential outliers in later phases of the analysis. For example, the outlier indicated with an arrow on *Figure 4* (see *Box 1* for scatterplot) can only be noticed when we examine the two variables together, but separately it is impossible. Such bivariate outliers are useful for checking data entry, e.g. we expect that flycatchers with longer wings have longer tarsi. Such an outlier may help finding misspelled data.

   To explore the relationship of two numerical variables and the outliers, we can use a more advanced scatterplot function from the `car` package. We show its usage with the `WING` and `THIRD` variables in the case of juvenile female birds measured during the autumn migration season *(Figure 5)*. The variables for the plot are given in a so called formula, as $y \sim x$, where y is the dependent and x is the independent variable. Since the variables are measured
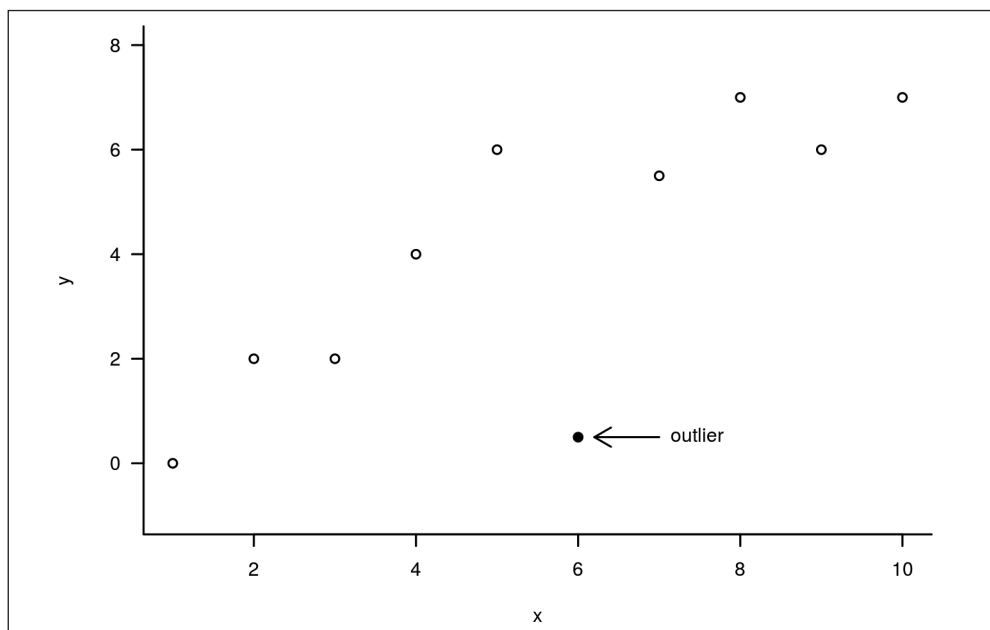
Figure 4. A scatterplot with an outlier
4. ábra Szórásdiagram kiugró értékkel

Scatterplot

To describe the two dimensional distribution of two variables we use the scatterplots, where data is displayed as a set of points. One variable determines the position of the points on the horizontal axis, while the other variable determines the position on the vertical axis. We can inspect the plot visually and notice if there are points that lie distant from the main data distribution. These points are potential outliers in a two dimensional sense.

Box 1. Scatterplot
1. doboz Szórásdiagram

with 1 mm precision, both of them are discrete, therefore, the scatterplot is typically uninformative because the data points are overplotted. Jittering the data (i.e. adding a small random quantity to each coordinate (Cleveland 1994)) can be useful in these cases. We used the `jitter()` function in the formula.

The `scatterplot()` function of the `car` package (Fox & Weisberg 2011) makes a usual scatterplot with several additional options (see `?scatterplot`).

```
>library(car)
>scatterplot(jitter(WING) ~ jitter(THIRD), data = mydata, smooth = F,
subset = (season == "autumn" & SEX == "M" & age == "juv"), reg.line = F,
ellipse = T, levels = c(0.95, 0.99), id.method = "identify")
```
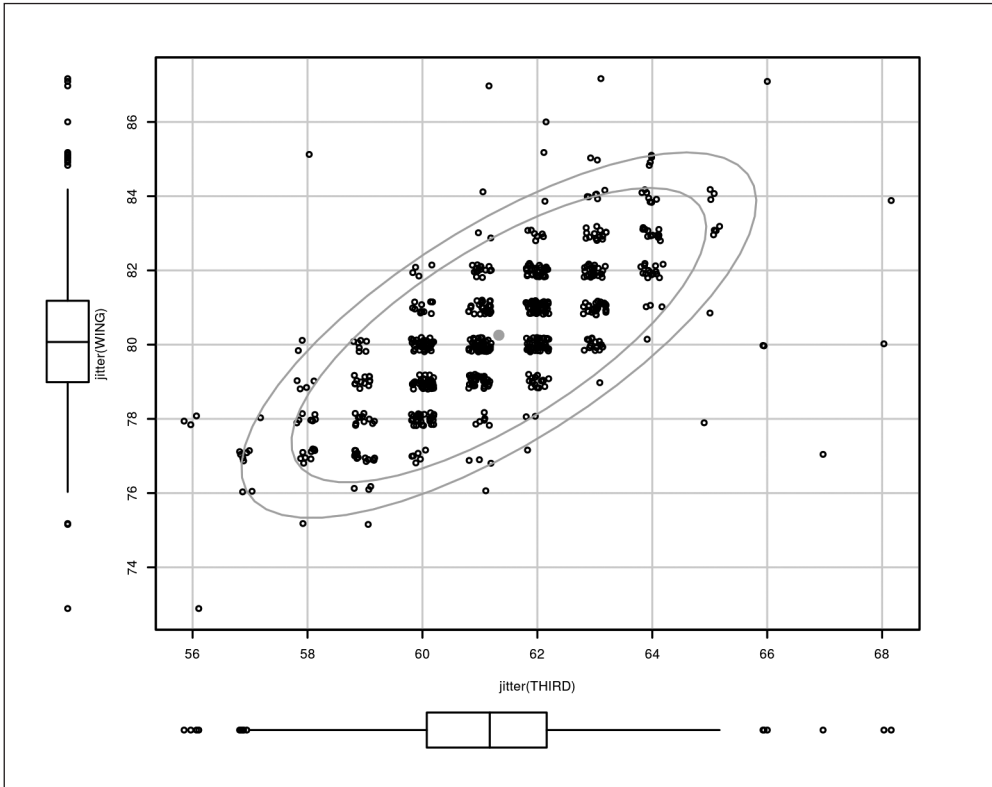
Figure 5. Scatterplot of the jittered `WING` and `THIRD` variables with boxplots on the sides and 95% and 99% concentration ellipses

5. ábra   A `WING` és `THIRD` változók szórásdiagramja boxplotokkal a tengelyek mellett, valamint az adatok 95 és 99%-át tartalmazó ellipszisekkel. Az átfedések miatt a pontokhoz hozzáadtunk egy kis véletlen értéket (jitter) a jobb áttekinthetőség kedvéért

This adds marginal boxplots for both variables *(Figure 5)* and plots a nonparametric-regression curve (`smooth`) and a regression line (`reg.line`) to the plot by default. Since we do not need the regression line now, we set the `reg.line = F`. We call this function with a subset of the data as specified using a logical expression. If we can assume, that the two variables are linearly related and their two dimensional distribution is normal, than the `ellipse` parameter is also useful to find possible outliers (Fox & Weisberg 2011). If it is set to `TRUE`, dataconcentration ellipses are plotted. With the `levels` parameter, the levels of concentration ellipses can be set, which means that in case of a two dimensional distribution, we expect that a specified proportion (set by this parameter) of the data fall inside the ellipses. In this case we used two levels: 95 and 99%. With the parameter `id.method = "identify"`, we can get the position of the graphics pointer when the (first) mouse button is pressed. It then searches the coordinates given in x and y for the point closest to the pointer. If this point is close enough to the pointer, it's index will be returned as part of the value of the call (Becker *et al.* 1988). Usually the identification process can be terminated by pressing the `ESC` key or by closing the graphics device (for more details see `?identify`).

Two dimensional outliers can be caused by erroneous data entry, thus the evaluation procedure should be similar to outliers of a single variable. If we decided that the value is implausible we may exclude the observation. However, if we are unsure, the best approach is to run the statistical analyses with and without the observation in question and evaluate the results. If we plan to publish our results, it is necessary to mention and advisable to report analyses with and without the outliers. Maybe the outliers are our most interesting observations that may help further our knowledge in our field.

Acknowledgments

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