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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

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[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)		Massachusetts	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

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[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 as 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.

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