
Commentary: Defining Raptors and Birds of Prey

Authors: Christopher J. W. McClure, Sarah E. Schulwitz, David L. Bryce W. Robinson, Elizabeth K. Mojica, et. al.

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SHORT COMMUNICATIONS

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COMMENTARY: DEFINING RAPTORS AND BIRDS OF PREY

CHRISTOPHER J. W. MCCLURE,¹ SARAH E. SCHULWITZ, AND DAVID L. ANDERSON
The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709 USA

BRYCE W. ROBINSON
Ornithologi, PO Box 6423, Boise, ID 83707 USA

ELIZABETH K. MOJICA
EDM International, Inc. 4001 Automation Way, Fort Collins, CO 80526 USA

JEAN-FRANCOIS THERRIEN
Hawk Mountain Sanctuary, 410 Summer Valley Road, Orwigsburg, PA 17961 USA

M. DAVID OLEYAR
HawkWatch International, 2240 South 900 East, Salt Lake City, UT 84106 USA

JEFF JOHNSON
University of North Texas, Department of Biological Sciences, 1155 Union Circle #310559, Denton, TX 76203 USA

ABSTRACT.—Species considered raptors are subjects of monitoring programs, textbooks, scientific societies, legislation, and multinational agreements. Yet no standard definition for the synonymous terms “raptor” or “bird of prey” exists. Groups, including owls, vultures, corvids, and shrikes are variably considered raptors based on morphological, ecological, and taxonomic criteria, depending on the authors. We review various criteria previously used to define raptors and we present an updated definition that incorporates current understanding of bird phylogeny. For example, hunting live vertebrates has been largely accepted as an ecological trait of raptorial birds, yet not all species considered raptors are raptorial (e.g., Palm-nut Vulture [*Gypohierax angolensis*]), and not all raptorial birds are considered raptors (e.g., skuas [*Stercorariidae*]). Acute vision, a hooked bill, and sharp talons are the most commonly used morphological characters for delineating raptors; however, using those characters as criteria may cause confusion because they can be vague and exceptions are sometimes made. Old World vultures, for example, are in the family Accipitridae along with hawks and eagles, and thus are usually considered raptors despite their lack of sharp talons. We define raptors as species within orders that evolved from raptorial landbirds (Telluraves) in which most species maintained raptorial lifestyles. Raptors are therefore all species within Accipitriformes, Cathartiformes, Falconiformes, and Strigiformes. Importantly, we believe that seriemas (Cariamiformes) should also be considered raptors. Our definition combines phylogeny with morphology and ecology, and avoids ambiguity associated with owls, vultures, and shrikes. Establishing a common definition of raptors should improve interpretability across studies and lessen ambiguity of research and management recommendations.

KEY WORDS: *bird of prey; morphology; phylogeny; raptor; raptorial; taxonomy; terminology.*

¹ Email address: cmclure@peregrinefund.org

COMENTARIO: DEFINIENDO RAPACES Y AVES DE PRESA

RESUMEN.—Las especies consideradas como rapaces están sujetas a programas de seguimiento, libros de texto, sociedades científicas, legislación y acuerdos multinacionales. Sin embargo, no existe una definición estándar para los términos sinónimos “rapaz” o “ave de presa”. Los grupos que incluyen búhos, buitres, córvidos y alcaudones son a veces considerados como rapaces usando criterios morfológicos, ecológicos y taxonómicos, dependiendo de los autores. Revisamos varios criterios usados previamente para definir rapaces y presentamos una definición actualizada que incorpora el conocimiento actual de la filogenia de las aves. Por ejemplo, el cazar vertebrados vivos ha sido comúnmente aceptado con un rasgo ecológico de las aves “de presa” (i.e., que tienen garras contráctiles para agarrar a la presa mientras la consumen), aunque no todas las aves consideradas rapaces son “de presa” (e.g., *Gypohierax angolensis*), y no todas las aves “de presa” son consideradas como rapaces (e.g., págalos o skúas [Stercorariidae]). La visión aguda, el pico en forma de gancho y las garras afiladas son los caracteres morfológicos más comúnmente usados para delinear a las rapaces; sin embargo, el uso de estos caracteres como criterio podría causar confusión ya que pueden ser imprecisos y a veces se hacen excepciones. Los buitres del Viejo Mundo, por ejemplo, están en la familia Accipitridae junto con halcones y águilas, y por ende son usualmente considerados como rapaces a pesar de no presentar garras afiladas. Nosotros definimos a las rapaces como aquellas especies dentro de los órdenes que evolucionaron a partir de aves terrestres “de presa” (Telluraves) en los cuales la mayoría de las especies mantuvieron sus estilos de vida “de presa”. Las rapaces son por ende todas las especies dentro de Accipitriformes, Cathartiformes, Falconiformes y Strigiformes. Destacamos que creemos que los Cariamiformes también deberían ser considerados como rapaces. Nuestra definición combina filogenia con morfología y ecología, y evita la ambigüedad asociada con los búhos, buitres y alcaudones. El establecimiento de una única definición de rapaces debería mejorar la interpretación de los distintos estudios y disminuir la ambigüedad de las investigaciones y las recomendaciones de manejo.

[Traducción del equipo editorial]

Precise terminology is essential in science and conservation for comparison of findings across studies, communication within and across disciplines, concise drafting of policy instruments, and proper application of management actions. Birds typically classified as raptors, or birds of prey, have received much public and scientific attention over past decades, especially due to critical conservation issues surrounding them (e.g., Ratcliffe 1967, Prakash et al. 2003, Ogada et al. 2016). For these species, there exists discipline-specific infrastructure for research, monitoring, and conservation. Indeed, several textbooks and manuals directly address techniques to study and manage birds considered raptors (e.g., Giron Pendleton et al. 1987, Hardey et al. 2006, Bird and Bildstein 2007, Anderson et al. 2017) and large-scale monitoring programs track populations of birds designated as raptors across entire continents (e.g., Farmer and Hussell 2008, Kovács et al. 2008, African Raptor Databank 2017). In addition, several professional societies (e.g., Asian Raptor Research and Conservation Network, Neotropical Raptor Network, Raptor Research Foundation) and scientific journals (e.g., Journal of Raptor Research, Vulture News) are dedicated specifically to enhancing collaboration between researchers studying birds considered to be raptors and disseminating results of their studies.

Despite attention applied to species classified as raptors, and efforts to define raptor-specific terminology (Postupalsky 1974, Franke et al. 2017, Steenhof et al. 2017), there are no established or reliable criteria by which to

include or exclude any individual taxon from the group “raptors.” Farquhar (2017) recently reviewed how the term “raptor” became synonymous with “bird of prey.” However, ambiguity remains regarding exactly which species we should consider raptors. Cooper (2002), for example, followed what he referred to as the “traditional method” of differentiation of raptors by including birds that were at the time within two Orders, specifically Strigiformes and Falconiformes. This latter order has more recently been subdivided by most taxonomic authorities to also include the Orders Accipitriformes and Cathartiformes based on phylogenetic evidence (Hackett et al. 2008). Many—probably most—publications covering raptors follow this convention (e.g., Bierregaard 1998, Virani and Watson 1998, Bird and Bildstein 2007, Donazar et al. 2016). Tradition thus holds that raptors include hawks, eagles, and allies, as well as Old World vultures (now in Accipitriformes), New World vultures (now in Cathartiformes), falcons, and caracaras (Falconiformes), and owls (Strigiformes). Despite tradition, however, varying groups of birds have been listed as raptors (e.g., Newton 1979, Andersen et al. 1985, Campbell and Lack 1985, Booms et al. 2010, Donazar et al. 2016) with the justification usually involving various combinations of factors such as morphology, now-outdated phylogeny, ecological similarity, or mere simplicity. Consequently, we argue that currently there are no clearly articulated and scientifically supported criteria for determining whether a given taxon is within the groups considered to be raptors.

The issue of correctly defining a raptor is not merely an academic exercise but could also have important implications due to its influence on research priorities, funding decisions, and conservation actions. For example, in the early 1990s, before The Peregrine Fund decided to embark on a captive breeding program for California Condors (*Gymnogyps californianus*), there were internal discussions regarding whether vultures fell under the organization's mission of conserving raptors (R. Watson pers. comm.). Since that discussion, The Peregrine Fund has raised and allocated tens of millions of dollars for vulture conservation across the world (The Peregrine Fund, unpubl. data). Therefore, determining membership within the group "raptors" is especially important for organizations dedicated to research and conservation of birds of prey.

The field of raptor research has produced some of the most successful conservation and monitoring efforts ever undertaken (e.g., Ratcliffe 1967, Jones et al. 1995, Cade and Burnham 2003, Farmer and Hussell 2008, Pain et al. 2008, African Raptor Databank 2017). Yet over half of all species within the four traditional raptor orders have declining global populations and 18% are classified as threatened with extinction (McClure et al. 2018). Buechley et al. (2019) further note that 10 species of traditional raptors account for one-third of raptor research, while one-fifth of traditional raptor species remain virtually unstudied. To meet current and future conservation challenges and address knowledge gaps, raptor researchers must remain innovative, nimble, and adaptive—resisting complacency and constantly challenging the status quo. We thus believe it is time to revisit the criteria that define raptors.

We posit that to study and conserve any group of animals, it is best to operate under a precise and scientifically justified definition of the group; ambiguity, uncertainty, and even adherence to tradition can hamper progress. To bring awareness to this issue and improve clarity of communication, we review the various groups identified as raptors and the criteria previously used to classify them as such. We further discuss recent phylogenetic work that elucidates the evolutionary history of raptors and aids in their more precise definition. We do not present an exhaustive literature review, but instead concentrate on classic or influential work, and instances that stray from the "traditional" definition of raptors. We then propose our own criteria for classifying a species as a "raptor" or "bird of prey"—terms used interchangeably in this manuscript and throughout the popular and scientific literature (Campbell and Lack 1985, Fowler et al. 2009, Farquhar 2017). Our intent is not to criticize past definitions, lists, criteria, or authors; we simply highlight where differences have occurred and suggest a path forward.

RAPTORIAL BIRDS

Raptors have frequently been defined on the basis of diet or predatory ecology. In fact, the term "raptor" has

been applied to a fairly broad spectrum of animals including extinct feathered theropod dinosaurs in the Family Dromaeosauridae, which includes recognizable genera such as *Velociraptor* (Farquhar 2017). Here, we focus on use of the term "raptor" within extant birds (Class: Aves). Although the term "bird of prey" denotes a bird that preys on other living animals (Brown 1971, 1976a), Brown (1971) concluded such a definition would encompass most groups of birds including warblers and gulls, and thus a more precise definition is required. Another term, "raptorial," can refer to bird species that feed on vertebrates (Jarvis et al. 2014).

Most species within groups commonly considered raptors are raptorial. Yet other groups including shrikes (Order Passeriformes, Family Laniidae; Rimmer and Darmstadt 1996, Pérez and Hobson 2007, Sustaita and Rubega 2014) and some seabirds (Charadriiformes; Newton 1979, Catry et al. 1999, Trathan et al. 2008, 2011) have also been described as raptorial. Designation as a raptor is traditionally restricted to landbirds, thus separating them from raptorial seabirds. Therefore, a raptorial lifestyle alone is not an exclusive or precise criterion for defining birds of prey (Bildstein 2017). Perhaps, a further complication is that many predatory birds—from shrikes and small falcons, to hawks and eagles—often have remarkably similar diets that, at times, consist of small vertebrate and insect prey (del Hoyo et al. 1994). One would not be considered more predatory than the other and all could be considered raptors based solely on diet (Brown 1971). Further, vultures are often considered raptors, but—withstanding occasional observations of hunting (Buckley 1999, Murn 2014)—would be excluded if obligatory hunting of live prey were the primary basis for defining a raptor. In fact, nearly all carnivorous vertebrates are facultative scavengers (DeVault et al. 2003) and many iconic raptors such as large eagles (e.g., Bateleurs [*Terathopius ecaudatus*] and fish eagles [*Haliaeetus* spp.]) often scavenge (Ferguson-Lees and Christie 2001). Conversely, the Palm-nut Vulture (*Gypohierax angolensis*) is highly frugivorous (Ferguson-Lees and Christie 2001). Perhaps the main source of confusion in defining birds of prey is that not all raptor species are fully raptorial, and not all raptorial birds are raptors.

MORPHOLOGY

Certain morphological features are often used to describe raptors and thus warrant discussion in any effort to separate raptors from other birds. For example, Brown (1976a; also see Brown 1976b) stated, "True birds of prey are those which have powerful, taloned feet for grasping and killing, and hooked beaks for tearing flesh." But often the morphological criteria used to describe raptors are merely adaptations to a raptorial lifestyle that fail to distinguish raptors from other raptorial species. Thus, any effort to define raptors as a subset of species possessing an

undefined and shifting (depending on the author) suite of some raptorial traits would fail to consistently separate raptors from other birds. Many authors have ascribed such characteristics to raptors as keen eyes for detecting prey, feet with sharp talons that can seize or grip, and hooked beaks for killing and consuming prey (e.g., Brown 1971, Newton 1979, Bildstein 2017); thus, we explore each of these morphological criteria individually.

Eyes. Birds of prey have been said to possess “acute vision” (Newton 1979), “intense, forward-looking eyes” (Boal and Dykstra 2018), and “keen eyesight” (Bildstein 2017), as an adaptation for hunting. These characteristics fail to exclude other groups of birds. Gill (2007) lumped both songbirds and raptors as being believed to have “the keenest eyesight of all birds.” Further, visual acuity is highly dependent on light levels, with certain species performing better than others under low-light conditions, and vice versa (Martin 2018). The famed visual acuity of some raptor species only occurs under ideal lighting conditions and is reduced drastically as natural light levels decline (Martin 2017). Acuity is thus relative, and is not the same across raptor species. For example, the visual acuity of Wedge-tailed Eagles (*Aquila audax*) is roughly 2.5× that of humans and, along with some Old World vultures, among the highest recorded for vertebrates to date (Martin 2017). Conversely, visual acuity of some Strigiformes, Cathartiformes, and Falconiformes is substantially below that of humans (Gaffney and Hodos 2003, Potier et al. 2016, Martin 2017, Mitkus et al. 2018). Differences in visual acuity across birds traditionally considered to be raptors therefore limit broad generalizations (Mitkus et al. 2018). Indeed, the stereotype of raptors having especially acute vision might best apply to Accipitriformes, but even within this order there is a great deal of variation (Martin 2017).

The problem further rests in undefined and relative qualifiers of visual acuity. For example, what threshold of acuity, and under what lighting conditions, defines a visual system as “acute” or “keen”? We are unaware of any accepted thresholds or criteria to separate raptors from other birds based on visual acuity. The visual system of a given species has evolved tradeoffs between acuity (spatial resolution), sensitivity (light detection), motion detection, and color vision that suit its environment (Martin 2017, 2018, Mitkus et al. 2018). Thus many bird species have vision superior to other taxa in at least some aspects or situations (Martin 2017, 2018). Because visual acuity is unquantified for a majority of bird species and most could be considered to have relatively “keen” eyes in some situations (Table 1), visual acuity as a criterion for being a raptor, or even as a broad descriptor, is unhelpful.

Feet. The term “raptor” is derived from the Latin combining form “rapt” (Bildstein 2017) or the verb *rapio* (Farquhar 2017), meaning “to seize or plunder,” in reference to the stereotypical raptor hunting strategy of seizing prey (Bildstein 2017, Farquhar 2017). Therefore, foot morphology is often used to characterize raptors. For example, Newton (1979) stated raptors have “strong legs

and feet equipped with sharp, curved claws...” Boal and Dykstra (2018) also mention talons—defined as claws, particularly on birds of prey (Campbell and Lack 1985)—as a characteristic of raptors, and Brown and Mindell (2009) stated the strong feet of owls were an adaptation to a raptorial lifestyle. Brown (1971) further stated all raptors except vultures have “powerful grasping feet equipped with long sharp talons.” Qualitative descriptions including “sharp,” “curved,” and “strong” are ambiguous and thus of limited use in classifying species as raptors. Moreover, foot morphology is highly variable among birds of prey (Einoder and Richardson 2007, Fowler et al. 2009), to the degree that several species commonly accepted as being raptors (e.g., vultures and caracaras) have appreciably duller talons and weaker feet than many other raptor species. The feet of vultures and caracaras are also poorly suited for grasping compared to other raptors, whereas species not considered raptors may possess feet capable of grasping (e.g., parrots, Psittaciformes). Indeed, Brown (1976b) noted that “...shrikes can even carry quite large prey in their claws.” And Panov (2011) stated that shrikes have strong feet “equipped with curved, sharp claws” as an adaptation to a predatory lifestyle. The criterion of possession of strong or sharp-taloned feet is thus ambiguous and unevenly applied when defining, or describing, raptors.

Beak. Many authorities have considered raptors to have “hooked” beaks (Brown 1976a, Newton 1979, Boal and Dykstra 2018) that function in tearing flesh. Indeed, species considered raptors often have characteristic beaks with an upper mandible that curves over and past the lower mandible. Recent evidence suggests that raptor beak morphology is constrained by similar genetic mechanisms (Bright et al. 2016); however, the difficulty in using hooked beaks as a defining feature of raptors is that hooked beaks are also possessed by several groups of birds that are not considered raptors (Table 1). The beaks of shrikes are raptorial (Sustaita and Rubega 2014), yet Brown (1971) highlighted that even though shrikes and cormorants (Phalacrocoracidae) have “something of a hook on the beak” they are not considered birds of prey. Parrots similarly have beaks that might be considered hooked, but parrots are not regarded as raptors. Like keen eyes and sharp-taloned feet, a hooked beak is an ambiguous criterion when defining raptors, given that many hook-beaked birds are not considered raptors (Table 1).

TAXONOMY

Similar morphological traits shared among raptorial species have obscured the taxonomy of raptors for centuries largely due to difficulty of distinguishing convergence from true evolutionary relationships. For example, Linnaeus (1758) grouped many species as congeneric that we now recognize as belonging to different orders. Vultures and some eagles were identified as *Vultur*, falcons and some

Table 1. Groups of birds that have been considered, or compared to, raptors by past authors and some characteristics that those groups possess that have been attributed to raptors. An “X” designates a group as generally possessing a given characteristic. “Ecological Equivalency” indicates that a taxon has been included in lists or studies of raptors because of a raptorial lifestyle or ecological interactions with raptors (e.g., competition for nests sites). Note that these designations are rough generalizations and there are some exceptions per group, which highlights the difficulty in using solely morphology or ecology to classify groups of birds as raptors. The “Raptor” column indicates groups that fit our proposed definition of raptors.

GROUP	ORDER	CHARACTERISTIC					ECOLOGICAL EQUIVALENCY	RAPTOR
		KEEN EYES	RAPTORIAL TALONS	HOOKE D BEAK	PREDATORY	DIURNAL		
Hawks and Eagles	Accipitriformes	X	X	X	X	X	X	X
Falcons	Falconiformes	X	X	X	X	X	X	X
Caracaras	Falconiformes	X	X	X		X	X	X
Owls	Strigiformes	X	X	X	X		X	X
Old World Vultures	Accipitriformes	X		X		X	X	X
New World Vultures	Cathartiformes	X		X		X	X	X
Seriemas	Cariamiformes	X	X	X	X	X	X	X
Shrikes	Passeriformes	X		X	X	X	X	
Ravens	Passeriformes	X			X	X	X	
Cormorants	Suliformes	X		X	X	X		
Warblers	Passeriformes	X			X	X		

hawks and eagles as *Falco*, and shrikes and some flycatchers as *Lanius*, all of which were in the now obsolete Order Accipitres. Since Linnaeus (1758), taxonomy of raptors has changed as new species concepts emerged and gained popularity and new technologies were implemented.

Disagreement Over Certain Taxa. Some taxa, such as shrikes, owls, vultures, and even ravens (Order Passeriformes, Family Corvidae, Genus *Corvus*) have been particularly lively sources of professional disagreement regarding what constitutes a raptor. Shrikes, for example, are generally no longer considered raptors, despite their raptorial behavior and morphology (Brown 1971). Nonetheless, many studies or lists of raptors include shrikes (e.g., Grant et al. 1991, Vrezec 2014, Duerr et al. 2015, Jankowiak et al. 2015a, 2015b). In fact, several studies of shrikes have been published within the Journal of Raptor Research (Andersen and Rongstad 1989, Poulin et al. 2001, Collister and Wilson 2007), though their inclusion has been dependent on editorial preferences. Shrikes are usually included in studies of raptors because of their predatory ecology, or raptorial lifestyle, and thus their ecological equivalency to raptors (Duerr et al. 2015, Jankowiak et al. 2015a, 2015b).

Although not traditionally considered birds of prey, ravens (e.g., *Corvus corax*, *C. cryptoleucus*) are also sometimes included in studies of raptors (Craighead and Mindell 1981, Brubaker et al. 2003, Steenhof et al. 2007). Indeed, Hardey et al. (2006) included ravens in their guide for surveying and monitoring raptors. As with shrikes, inclusion of ravens is usually because of ecological equivalency, as Bednarz et al. (1990) stated, “We include Chihuahuan

Raven (*Corvus cryptoleucus*) in this paper because they function ecologically as raptors....” Booms et al. (2010) further stated, “For simplicity, we considered the Common Raven a cliff-nesting raptor because of its similarity in breeding biology to raptors and the important role they play in creating and occupying cliff nests.” These authors thus included ravens within studies of raptors because of similarities in ecology. Ravens and shrikes have also been subjects of thesis research within Boise State University’s Master of Science in Raptor Biology Program (Atkinson 1991, Woods 1994, Valutis 1997). Further, during the 1980s and 1990s there were informal discussions within the Raptor Research Foundation regarding whether ravens should fall under their purview (J. Bednarz pers comm.). Ecological similarities between shrikes, ravens, and raptors have thus prompted serious consideration regarding whether life history, niche, and species interactions should define the taxa considered under raptor research.

Owls are often absent from lists of raptors (e.g., Brown 1976a, Bildstein et al. 1998, Ferguson-Lees and Christie 2001, Bildstein 2017). For example, Newton (1979) did not include owls with raptors, but instead stated owls were “the nocturnal equivalent of raptors,” and was later echoed by Bildstein (2017). Santoro et al. (2012) contrasted parasites of European owls with those of what they considered birds of prey (Accipitriformes and Falconiformes). And, Geen et al. (2019) considered owls separate from raptors when examining the negative effects of transmitting devices on birds. However, other authors do include owls in lists of raptors (e.g., Hardey et al. 2006, Bird and Bildstein 2007, Boal and Dykstra 2018, Buechley et al. 2019) presumably

because, as a group, owls are monophyletic raptorial landbirds (e.g., Hackett et al. 2008, Jarvis et al. 2014). Indeed, the *Dictionary of Birds* defines “Bird-of-prey” as members of Accipitriformes, Cathartiformes, and Falconiformes, while noting the definition is sometimes expanded to include Strigiformes (Campbell and Lack 1985).

The classification of vultures as raptors has also been a source of disagreement. The obligate scavenging behavior of many vultures and their lack of especially sharp talons differentiate them ecologically and morphologically from other birds of prey such as hawks, eagles, and owls. Brown (1971) included vultures in his book, *African Birds of Prey*, but did not consider them to belong “properly” to raptors. Bildstein (2017), asserted that members of Accipitridae, Pandionidae, and Sagittariidae are “core” raptors because they share a common ancestor, but noted that most biologists, including himself, consider vultures to be raptors. Similarly, during the debate over whether New World vultures (Cathartiformes) were more closely related to storks (Ciconiiformes) or raptors, several authors questioned whether cathartids were birds of prey (Piper 1994, Seibold and Helbig 1995, Tagliarini et al. 2011). That said, most references listing species of diurnal raptors include Old and New World vultures (e.g., Brown and Amadon 1968, Brown 1976a, Ferguson-Lees and Christie 2001). Increasingly more researchers acknowledge that New World vultures should be recognized as their own order, Cathartiformes (Chesser et al. 2016, Mindell et al. 2018). This order is sister to Accipitriformes, and fossil calibrated phylogenetic analyses suggest that their common ancestor is as old or older than other recognized avian orders (Jarvis et al. 2014, Prum et al. 2015, Johnson et al. 2016). Lerner and Mindell (2005) established that Old World vultures are not monophyletic within Accipitridae; Palm-nut, Egyptian (*Neophron percnopterus*), and Bearded (*Gypaetus barbatus*) Vultures are separated from all other Old World vultures based on molecular phylogenetic analyses.

Seriemas (Cariamiformes) are another group of raptorial landbirds that pose a challenge for defining raptors. The two extant species of seriemas inhabit South America and superficially resemble Secretarybirds (*Sagittarius serripentarius*, Order Accipitriformes, Family Sagittariidae) in diet, behavior, and appearance (del Hoyo et al. 1996, Winkler et al. 2015) so much that seriemas and Secretarybirds were once placed in the same order (Cariamiformes; see Stresemann 1959). The beak of seriemas is somewhat hooked, they have claws that might be considered sharp, and they prey on small vertebrates (Redford and Peters 1986, del Hoyo et al. 1996, Winkler et al. 2015). However, seriemas occasionally eat fruit and other vegetable matter (Redford and Peters 1986, del Hoyo et al. 1996). Although they were previously thought to be most closely related to cranes and rails (Gruiformes), recent phylogenetic work places this lineage as sister to the clade including falcons, parrots, and songbirds (Fig. 1; Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015). In fact, Jarvis et al. (2014) listed

seriemas as “birds of prey” stating, “Seriema at the deepest branch of Australaves could be considered to belong to a raptorial taxon because they kill vertebrate prey (Redford and Peters 1986) and are the sole living relatives of the extinct giant “terror birds,” apex predators during the Paleogene (Alvarenga and Höfling 2005, Mayr 2009).

An Evolving Phylogeny. Many authors assert that shared characters between raptorial birds, even groups commonly considered raptors, are likely due to convergent evolution (e.g., Brown and Amadon 1968, Newton 1979, Boal and Dykstra 2018). Indeed, Bildstein (2017) affirms that such is the case due to biological similarities among raptor groups, and not due to shared evolutionary history. Until roughly a decade ago, however, diurnal raptors were considered monophyletic within the Order Falconiformes (families Falconidae, Accipitridae, Cathartidae, Sagittariidae, and Pandionidae; Peters 1931, American Ornithologists’ Union 1957, Brown and Amadon 1968, Cade 1982, Dickinson 2003), thus justifying the separation of Strigiformes (owls) and Falconiformes into two monophyletic groups and sometimes leaving the distinction of “raptors” solely to Falconiformes (e.g., Brown 1971, Newton 1979, Gill 2007). More recent research, however, reveals falcons are more closely related to parrots and songbirds than to most other raptors such as hawks, eagles, and vultures (Fig. 1; Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015). Monophyly among diurnal raptors, therefore, is no longer supported based on molecular phylogenetic results, and the distinction of being a “diurnal” raptor cannot be one that is based on common ancestry alone, but should also consider generalized life history.

Recent phylogenetic studies using comprehensive taxonomic sampling agree that, of the core landbirds (Telluraves), two primary clades exist—the Australaves and Afroaves (Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015). Both of these clades include a basal distribution of raptorial orders, suggesting that the common ancestor of core landbirds was raptorial (Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015). Consequently, such evidence then supports the hypothesis that the raptorial lifestyle *per se* is a derived trait shared by both clades based on common ancestry (Fig. 1). The Afroaves (Ericson 2012), includes the sister Orders Accipitriformes and Cathartiformes, which together as a clade, are in turn sister to owls (Strigiformes) and all other Coraciimorphae (Fig. 1). The Australaves (Ericson 2012), includes the seriemas which are sister to falcons, which in turn are sister to the clade including parrots (Psittaciformes) and songbirds (Passeriformes; Fig. 1). The concept of an evolutionary grade (i.e., a group defined by conservative traits; Huxley 1959)—as opposed to a clade—might therefore best describe the ancestral condition of core landbirds. Jarvis et al. (2014) and Prum et al. (2015) support the hypothesis that a raptorial grade gave rise to non-raptorial groups resulting in a paraphyletic grouping (a grade) based on the raptorial lifestyle (Fig. 1; Jarvis et al. 2014, Prum et al. 2015). Indeed, the raptorial beak shape may be a function of a basal morphological state

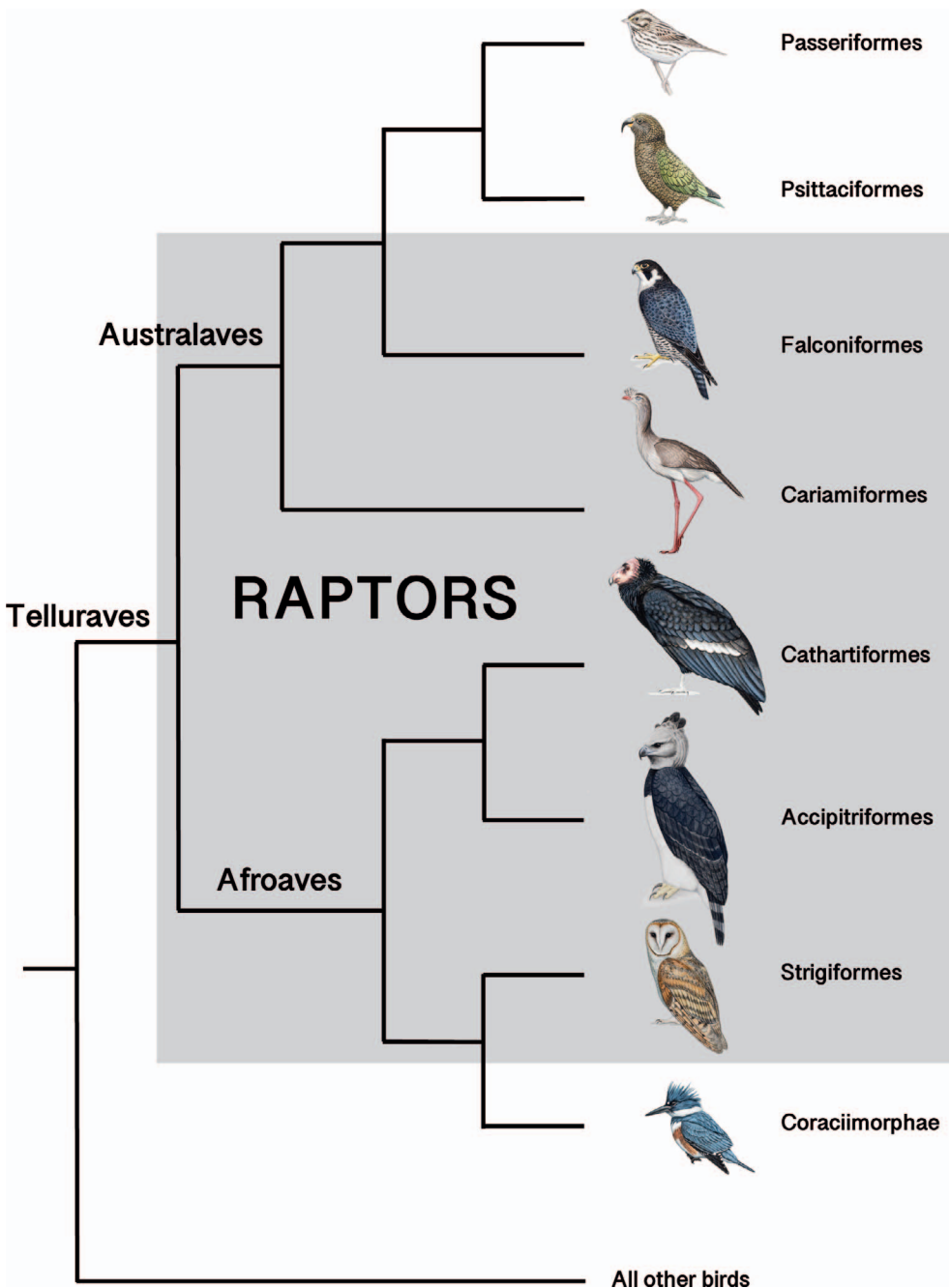


Figure 1. Phylogeny of core landbirds modified from Mindell et al. (2018). The shaded box encompasses the raptorial grade (see text), within which we propose that all orders are considered raptors. Raptors as a group is paraphyletic and mostly share the raptorial lifestyle passed down from their single common ancestor. Such grouping assumes then that the raptorial lifestyle was lost twice independently with the ancestors of both the Coraciimorphae and Passeriformes/Psittaciformes clades. Note that the superorder Coraciimorphae contains six Orders: Coliiformes (mousebirds), Trogoniformes (trogons), Coraciiformes (bee-eaters), Piciformes (woodpeckers), Leptosomiformes (cuckoo-rollers), and Bucerotiformes (hoopoes and hornbills).

that was maintained in taxa considered to be raptors today but later lost in their more recently evolved relatives (e.g., Coraciimorphae among Afroaves and Passeriformes among Australaves; Bright et al. 2016).

A DEFINITION OF RAPTORS AND BIRDS OF PREY

Despite many authors considering raptors to include the current orders of Accipitriformes, Cathartiformes, Falconiformes, and Strigiformes, vultures and owls have received the most scrutiny and other groups have variably been included (e.g., Linnaeus 1758, Brown and Amadon 1968, Newton 1979, Bednarz et al. 1990). Definitions of raptors have been confounded by what was understood to be convergent morphology across raptorial species and by phylogenies that have since been revised, yet there was a degree of consilience among the species chosen. For instance, raptorial seabirds were never considered raptors. When considering recent phylogenetic analyses based on DNA sequence data that include raptorial landbirds (Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015), and not solely similarities in raptorial morphology or behavior, one gains a clearer understanding of the evolutionary relationships between groups of raptors.

We therefore propose a definition of raptors, or birds of prey, as all species within orders that evolved from a raptorial landbird lineage and in which most species maintained their raptorial lifestyle as derived from their common ancestor. Based on current taxonomy (Fig. 1; Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015), this definition includes species in the orders Accipitriformes, Cathartiformes, Strigiformes, Cariamiformes, and Falconiformes. These orders share many ecological and morphological similarities, but those similarities do not define their status as raptors. Thus, our definition is not based on the morphology of individual species, but on the evidence that the ancestral raptorial condition of each order generally has been maintained in all of the extant lineages that we identify as raptorial. Our definition therefore combines phylogeny, morphology, and ecology, but places more emphasis on the importance of using evolutionary history to describe patterns of shared common ancestry. Such an approach provides a more scientific basis for grouping species as raptors, and we avoid the ambiguity that often results when using morphology or raptorial behavior as characters for identifying raptors such as with the oft-contested groups including owls and vultures.

Interpretation of our definition hinges on credence placed in the currently supported hypothesis that core landbirds evolved from a raptorial common ancestor (Fig. 1; Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015). If future work continues to support this hypothesis, our definition of raptors should be interpreted as all species belonging to the ancestral raptorial core landbird grade (Fig. 1). Thus, the most parsimonious explanation for morphological similarities among raptor groups would be

the maintenance of the ancestral condition rather than a result of convergence (Bright et al. 2016). If future work reveals the raptorial lifestyle is not ancestral, then raptors as a group are indeed products of convergence. However, our definition would still assign the same groups to “raptors” because they are landbird orders in which most species maintained an ancestral raptorial condition.

Our definition excludes shrikes as birds of prey because their raptorial traits are presumably not ancestral but rather an example of homoplasy (Cade 1967, Panov 2011), and the vast majority of species in their order (Passeriformes) are not raptorial. We do acknowledge that it may be logical to include shrikes, ravens, or other similar species that may possess “raptor-like lifestyles” in studies or monitoring programs for raptors due to simplicity, convenience, or study-specific goals. In these cases, however, we encourage authors to explicitly state the reasons for inclusion of non-raptor taxa with other raptors as defined here (see Bednarz et al. 1990, Booms et al. 2010, Duerr et al. 2015, Jankowiak et al. 2015a, 2015b for examples). Old and New World vultures are included as birds of prey because of broad agreement the two groups are within and sister to Accipitriformes, respectively. The definition posited here thus includes all groups traditionally considered raptors while also settling the status of oft-contested groups. Seriemas have not broadly been considered raptors, yet their raptorial lifestyle and recent evidence that they are closely related to falcons suggest seriemas should be considered raptors. Stated differently, there is currently no morphological, ecological, or evolutionary reason to exclude seriemas from birds of prey.

We strongly argue that ornithologists must operate from as precise a definition of raptors, or birds of prey, as possible because this group forms the basis of specialized scientific societies (e.g., Raptor Research Foundation), textbooks and manuals (Giron Pendleton et al. 1987, Hardey et al. 2006, Bird and Bildstein 2007, Anderson et al. 2017), scientific journals (e.g., Journal of Raptor Research), conservation areas (e.g., Marti 1992, Snyder and Snyder 2000, Watson et al. 2007), and multinational agreements (Coordinating Unit of the Raptors MOU 2015). Importantly, raptors generally occupy higher trophic levels, have larger bodies, home ranges, and territories, and have longer life spans than many other terrestrial birds. These similarities among raptors make them especially vulnerable to common threats including habitat destruction, accumulation of contaminants, persecution by humans, and electrocution, thus contributing to their current status as being more threatened with extinction than other birds in general (McClure et al. 2018). We emphasize that a clear definition of the term “raptor” should aid in the conservation and study of these birds.

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