

ORIGINAL RESEARCH

Ecomorphological adaptations of owl feet and talonsC. Cameron¹, D. H. Johnson², G. Gauthier³, N. Lecomte¹ & J.-F. Therrien⁴ ¹Canada Research Chair in Polar and Boreal Ecology, Université de Moncton, Moncton, NB, Canada²Global Owl Project, Alexandria, VA, USA³Université Laval, Quebec City, QC, Canada⁴Hawk Mountain Sanctuary, Orwigsburg, PA, USA**Keywords**

hindlimb morphology; diet specialization; hunting technique; *Strigidae*; *Tytonidae*; *Bubonidae*; raptors; owls.

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Abstract

Feet and talons are the most specialized predatory attributes of raptor morphology. As such, the hindlimb morphology of owls should reflect their dietary specialization. Owls' diet varies widely between species with only a subset of owl species preying predominantly on small mammals. We hypothesize that different owl species have varied hindlimb morphology, adapted to their main prey types, and that only dietary specialists will be distinguishable based on talon morphology (e.g. toe length, talon curvature and thickness, etc.). We used a sample of 63 specimens from 15 owl species to obtain a variety of measurements of hindlimb morphology. We then used a discriminant function analysis to investigate the degree of variation between species and diet groups in terms of their morphological measurements. Our results indicate that talon morphology is linked to prey type in the owl species studied. Insect specialists and small mammal specialists were characterized by a low talon curvature, whereas generalists presented a pronounced talon curvature. Fish specialists presented particularly thick and robust talons, and insect specialists showed lower digit strength than other owl species. These findings could help determine the diet of other owl species, particularly endangered species for which data on diet is often scarce. This study will also be very useful in future studies of the ecology of sympatric species, resource partitioning between species, or between sexes of the same species, and more generally to the evolution of owls.

Introduction

Feet and talons are the most specialized predatory attributes of raptor morphology (Brown, 1976; Orr, 1971), and the detailed study of interspecific hindlimb measurements can give valuable insight about some aspects of a species' ecological niche (hunting technique, Fowler et al., 2009; prey size, Tsang et al., 2019; mode of locomotion, Birn-Jeffery et al., 2012; ecological group, Hedrick et al., 2019; behavior, Cobb & Sellers, 2020, Thomson & Motani, 2021). The shape and power of these structures are considered adaptations to the type and size of prey taken (Brown, 1976, Csemery & Gaibani, 1998; Ward et al., 2002), as well as to the specific hunting technique employed by a species (Bouchner, 1977; Grossman & Hamlet, 1964; Lloyd & Lloyd, 1970; Olsen, 1995; Walter, 1979). In a multispecies comparative study, Tsang et al. (2019) concluded that the raptor talon is more likely shaped by feeding adaptations than developmental constraints, such as allometry. Owls and raptors use their feet to catch, kill, restrain, and carry their prey (Hertel, 1995; Olsen, 1995). Therefore, hindlimb functional morphology, that is, the various morphological traits of raptors feet and talons, such as talon robustness, curvature, length, and grip strength and speed, could be the result of the selective pressures associated with the

unique hunting behaviors of raptors. While owl species (*Strigiformes*) are often viewed as predators specializing on relatively small prey subdued mainly through constriction (primarily small mammals; Fowler et al., 2009), many owl species show a much wider range in diet, which can include much larger prey such as hares, young foxes, and birds up to the size of ducks and gamebirds. (König & Weick, 2008). Even for apparent small mammal specialists, alternative prey may be crucial at certain stages of their life cycle and can include a diverse suite of prey species and sizes (König & Weick, 2008; see Table 1). Overall, owls have been underrepresented in hindlimb morphological studies (e.g. Tsang et al., 2019, but see Ward et al., 2002) and a very limited number of species and individuals (Fowler et al., 2009) have been investigated. Such a bias can hamper our ability to further understand the variation in hindlimb morphology in a group of raptors whose diet varies widely between species.

While breeding success depends on the abundance of small mammal populations in some species (Barn owl *Tyto alba*, Great Gray owl *Strix nebulosa*, and Snowy owl *Bubo scandiacus* König & Weick, 2008), other species such as Bay Owls *Phodilus* spp., and some dense forest species such as the Barred owl (*Strix varia*) also hunt various insects, reptiles, amphibians, and birds (Del Hoyo et al., 1999, Livezey, 2007).

Table 1 Sample size and diet of the 15 owl species used in this study (IS: Invertebrate specialists, SMS: Small mammal specialists, SSMS: Seasonal small mammal specialists, FS: Fish specialists, G: Generalists, with reported % of prey (frequency) when available). We used only specimens where the 4 talons of the foot were fully intact from the collection at the Smithsonian Museum of Natural History in Washington, D.C.

Family	Species	Common name	N	Main prey items (% of the diet)
Strigidae	<i>Strix nebulosa</i>	Great Gray Owl	9	SMS (94–100%) ^a
Strigidae	<i>Asio otus</i>	Long-eared Owl	2	SMS (94%) ^b
Strigidae	<i>Bubo ketupu</i>	Buffy fish owl	4	FS ^c
Strigidae	<i>Strix varia</i>	Barred Owl	9	G (69% small mammals, 3% lagomorphs, 10% birds, 6% amphibians, 2% fish) ^d
Strigidae	<i>Bubo scandiacus</i>	Snowy owl	11	SSMS (from 100% small mammals ^e to 100% birds ^f)
Strigidae	<i>Otus senegalensis</i>	African scops owl	1	G (43% reptiles, 35% small mammals, 22% invertebrates) ^g
Strigidae	<i>Bubo blakistoni</i>	Blakistoni's fish owl	1	FS ^c
Strigidae	<i>Otus scops</i>	Eurasian Scops Owl	3	IS (90–98%) ^h
Strigidae	<i>Bubo bubo</i>	Eurasian Eagle Owl	4	G (highly variable) ⁱ
Strigidae	<i>Bubo virginianus</i>	Great horned owl	11	G (highly variable) ^l
Strigidae	<i>Otus socotranus</i>	Socotra Scops Owl	1	IS ^c
Strigidae	<i>Otus spilocephalus</i>	Mountain Scops Owl	1	IS ^c
Tytonidae	<i>Phodilus badius</i>	Oriental Bay Owl	1	G ^c
Tytonidae	<i>Tyto furcata</i>	American Barn Owl	4	SMS (>80%) ^j
Tytonidae	<i>Tyto alba</i>	Common Barn Owl	1	SMS (90%) ^k

^aSulkava and Huhtala (1997).

^bBirrer (2009).

^cKönig and Weick (2008).

^dLivezey (2007).

^eTherrien *et al.* (2011).

^fWilliams and Frank (1979).

^gDixon (1994).

^hLatková *et al.* (2012).

ⁱDonazar *et al.* (1989).

^jRomano *et al.* (2020).

^kLove *et al.* (2000).

Tiny Scops and Screech owls (*Otus* spp. and *Megascops* spp.) prey mainly on insects, large *Bubo* spp. (e.g. Eurasian Eagle *B. bubo* and Great Horned *B. virginianus*) take large prey-like hares or waterfowl (Donazar *et al.*, 1989), and Asian fish owls (e.g. *B. ketupa*) and the Blakiston's Fish owl (*B. blakistoni*) specialize on fish (König & Weick, 2008). Even within species that prey mainly on small mammals during the breeding season, some, like the Snowy owl, are known to catch prey larger and heavier than themselves in winter (Therrien *et al.*, 2011, Williams & Frank, 1979). We would thus expect the wide variation in owl diet summarized above to be associated with a large diversity in hindlimb morphology.

Fowler *et al.* (2009) rightfully suggested that prey restraint and immobilization strategies should vary as prey vary in type and size. In other words, species feeding on relatively small prey compared to their own body size should exhibit morphological characteristics that maximize grip strength to increase their constriction ability, whereas species hunting larger prey should have talons adapted toward prey retention and immobilization. Einoder and Richardson (2007) studied the relationship between diet and hindlimb morphology in Australian birds of prey, and discovered convergent structures (e.g. toe length, tarsus length, etc.) in species from different raptor families sharing the same prey type. They concluded that the type of prey or killing technique employed affects selection for hindlimb structure more than prey size *per se*.

In species specializing in prey retention (e.g. generalists) rather than constriction (e.g. small mammal specialists), highly curved talons may be more effective in securing prey to the ground (Tsang *et al.*, 2019), although it lowers the reach for the same arc length (Fowler *et al.*, 2009). Lower curvature is expected in species for which the prey is encircled by the grip, and for which reach might be more important (Fowler *et al.*, 2009). In birds hunting aerial prey such as birds and insects, the greatest challenge is often making contact with the prey. For these predators, a greater reach allows the predator to spread its foot wider and maximize the chances of success (Einoder & Richardson, 2007). Although these types of prey may be hard to catch, they are usually easy to subdue and kill. In species specializing in capturing aerial prey, robust talons might not be necessary, and thinner, lighter talons may increase both rapidity and agility (Einoder & Richardson, 2007). Robust talons are more likely to be needed in generalist birds relying at times on hunting relatively strong prey (e.g. hares, young foxes, fish; König & Weick, 2008). The trade-off between the need for speed or strength can also be important in hindlimb morphology (Fowler *et al.*, 2009). Indeed, birds preying on prey entirely encircled by the talon, and therefore relying on prey constriction (e.g. small mammal specialists) might need more grip strength to achieve prey suffocation, whereas birds catching rapid prey (e.g. insect specialists) are likely to have

evolved toward more speed in grip closure (Fowler *et al.*, 2009).

We hypothesize that different owl species have hindlimb morphology adapted to their prey types. We predict that the species specializing on specific prey types (e.g. insects or small mammals) are distinguishable based on talon morphology whereas diet generalists are not assignable to a specific group, due to higher shape variance. We predict that talon robustness, as measured by talon thickness and width, should increase with the size of their prey relative to their own body size, especially in the case of strong prey such as medium-sized mammals and fish. Owls catching larger and/or stronger prey should also present more curved talons, to maximize prey retention. Owls that use their talons to constrict their prey, such as small mammal specialists, are expected to have the strongest grip, whereas insect specialists, which lack the need for strength, are expected to have weaker talons that maximize speed to catch small and fast-moving prey. Lastly, we predict that species specializing in catching aerial prey, such as insect specialists and some generalists, would show a relatively high reach.

Materials and methods

Talon measurements

We used a sample of 63 specimens belonging to 15 owl species from the avian osteological collection at the Smithsonian Museum of Natural History in Washington, D.C. (Table 1). For each specimen, on all four digits of one foot, toe length (Toe) as well as talon width (BW; letter codes follow Fowler *et al.*, 2009) and height (BH) at the base of talon were measured directly on the specimen to the nearest 0.1 mm on all digits, using electronic calipers. All measurements were performed by a single observer (JFT). We assessed the precision of measurements by measuring the same 10 digits five times and found high repeatability (all SDs < 0.1 mm representing less than 0.1% of the measurements themselves). Toe length was measured from the proximal extremity of the first phalanx to the distal extremity of the outer phalanx, whereas talon width and height were taken at the base of each talon, as close as possible to the proximal extremity of the first phalanx. Feathers were moved to ensure a good view when necessary. We recorded sex of individuals when available.

For each bird, we also took a close-up photograph of the four talons of one foot against a flat surface and over a standard ruler for reference. We derived a variety of measurements from the talon photographs. On all pictures, each length was measured in pixels, using Microsoft Paint pixel calculator tool. Pixel count was then compared to the standard ruler reference in each picture, and converted to the nearest millimeter. In a comparative study of methods for assessing the shape of vertebrate claws, Tinius and Russell (2017) concluded that the dorsal claw arc provides a more generalized estimate of claw curvature compared to the ventral claw arc. Therefore, in this study, all talon measurements were made using the outer curvature of the talon. We measured the radius of the outer talon curvature using the intersecting chord theorem to find the center of each talon arc (Fig. 1), as well as chord length of the

outer curvature from base to tip of the talon. We then calculated the angle of curvature (Oo) using radius and chord length (Ao). We subsequently used the radius and angle of talon curvature (Oo) to calculate the outer arc length of the talon (Alo), giving a measure of talon size. We also measured the height of talon (Hmo) at midpoint of chord (see Fig. 1 for all measurements). We used only specimens where the 4 talons of the foot were fully intact.

A subsample ($N = 10$) of these photograph measurements was also taken directly on the specimen using the same method as for the Toe measurements, and the two sets compared to check the accuracy of photographic measurements. Either right foot or left foot was used for measurements, depending on availability and condition. We photographed a subset of the sample specimens ($N = 10$) on both feet to verify that foot laterality (right or left) did not affect talon morphology.

Dimensionality reduction

The direct measurements of hindlimb structures can be used to represent functional morphological characteristics (Hedrick *et al.*, 2019). However, direct measurements are likely to be highly correlated between digits of the same foot. Moreover, some measurements are likely correlated to the same overall morphological feature (e.g. height at midpoint and height at base of talon). Collinearity is a major problem for classification analyses such as LDAs (Næs & Mevik, 2001). For this reason, we first applied a Principle Component Analysis (PCA) on all measurements to obtain functional morphological variables that

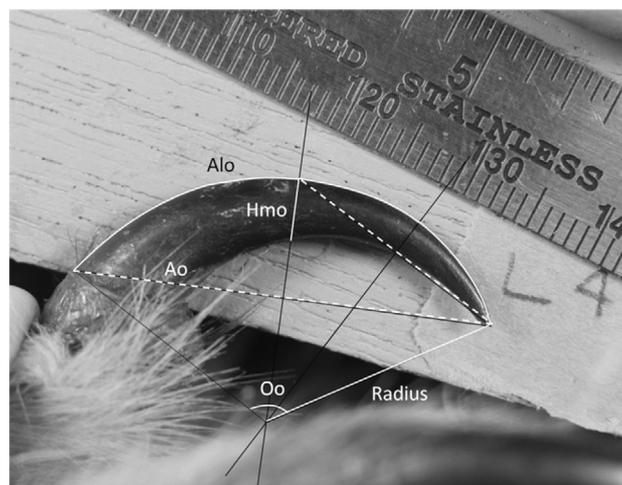


Figure 1 Morphological measurements taken from each talon. Center of outer curvature was determined by finding the intersection point of the perpendicular bisectors of two chords drawn using the outer talon curvature (from base tip of talon, and from midpoint to tip of talon, dashed lines in above picture). Angle of outer curvature (Oo), height of talon at midpoint (Hmo), chord length from base to tip of talon (Ao), and arc length of outer curvature (Alo) were used in subsequent analyses.

would present minimal collinearity (summarized in Table 2). This method of using a PCA for dimension reduction before classification analyses has proven successful in retaining important discriminatory information (Verma & Sahu, 2013; Yang & Yang, 2003). A separate PCA was applied on each set of correlated measurements to ensure retention of a maximum of discriminatory information and to obtain readily interpretable functional morphological variables. Talon height on the four digits (at midpoint, Hmo, and at base of talon, BH) and width (at base of talon, BW) were used to describe talon robustness, whereas total digit length for the four talons (toe length, Toe + chord of talon, Ao) was used as an estimate of reach (Einoder & Richardson, 2007). One way to evaluate the trade-off between speed and strength in hindlimb morphology is to look at the ratio between talon length and toe length. In owls, the flexor tendons attach to the tubercle at the proximal end of the ungual, with the toe acting as an outlever and the metatarsus as the inlever. In such lever systems, a short outlever will increase the potential strength of the system, whereas a long outlever will increase its potential velocity (speed; Fowler et al., 2009). This means that short toes combined with long talons will increase grip force production while maintaining the reach of the digit (Fowler et al., 2009). On the other hand, increased toe length compared to talon length would maximize speed by increasing the length of the outlever. The ratio between talon length and toe length for the four digits (Alo/Toe) was therefore used as an estimate the speed/strength variable. The overall curvature of the talons was also estimated using the curvature (Oo) on the four digits. For each morphological variable (Table 2; curvature, robustness, reach, and strength), we retained the minimum number of principal components that allowed us to represent at least 80% of the variance of the original variables. We then used the PCA scores as the new variables in subsequent analyses.

Effect of body size and phylogeny

To remove the potential effect of body size variations between species on morphological variables (Pike & Maitland, 2004) and to ensure that the results obtained were not merely due to the close phylogenetic relatedness of the species studied, we performed a PGLS regression of the PC scores for each variable on body length. Due to incomplete carcasses and poor condition of specimens, we were unable to obtain body length

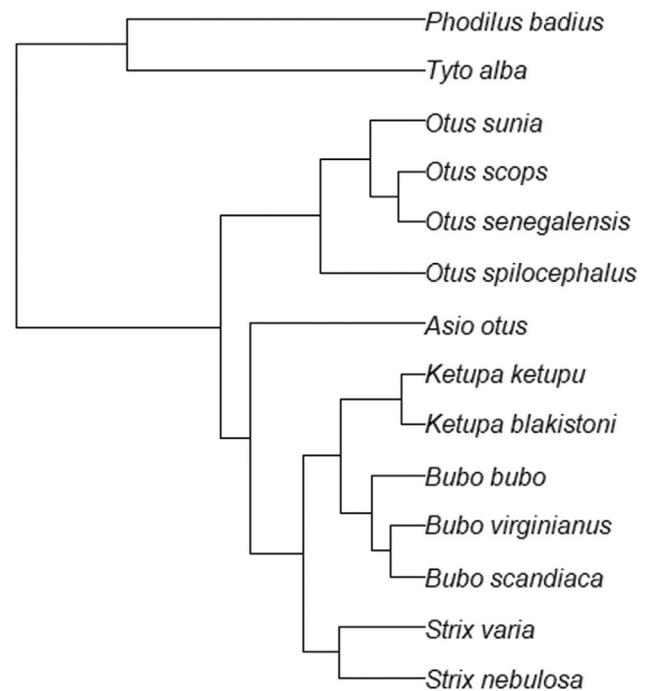


Figure 2 Consensus phylogenetic tree of 13 of the 15 owl species used in this study + *Otus sunia*. Data from *Otus sunia* were used for *Otus socotranus* and data for *Tyto alba* and *Tyto furcata* were pooled.

measurements from the samples. We therefore used each species average body length, using data from König and Weick (2008) in the PGLS regression. This physical characteristic has been used in previous studies as a mean of body measurements standardization. It is assumed to be an accurate representation of overall body size (Peters, 1983; Wiklund, 1996), especially when comparing species of the same basic body shape (Einoder & Richardson, 2007), such as in the present case. When known, we used sex specific body length averages for standardization purpose, as sexual dimorphism is present in some species. A consensus tree (Fig. 2) was obtained using the phytools package in R (Revell, 2012) with the branch distance score criterion from a set of 100 trees downloaded from BirdTree.org (Jetz et al., 2012). When phylogeny was unavailable for a species (2 species: *Tyto alba* and

Table 2 Prey capture functions, owl hindlimb morphological characteristics, measured variables (on all digits) and associated PCA variables generated from each set of measurements

Function	Dietary group ^a	Morphological characteristics	Measured variables ^b	PCA variables
Large prey restraint	G, SSMS	Talon curvature	Oo	Curvature (PC1)
Capture of strong prey	G, FS	Talon robustness	Hmo, BH, BW	Robustness (PC1)
Capture of aerial prey	IS, G	Digit reach	Ao + Toe	Reach (PC1)
Prey constriction	SMS, SSMS	Hindlimb strength	Ratio Alo/Toe	Overall strength (PC1) Strength digit 1 (PC2)

^aAcronyms for dietary groups defined in Table 1.

^bAlo, arc length from base to tip of talon; Ao, chord length from base to tip of talon; BH, height at base of talon; BW, width at base of talon; Oo, Angle of outer curvature; Hmo, height at mid-point of talon; Toe: Toe length.

Otus socotranus), phylogeny of the closest relative was used. We used residuals from the PGLS regression in subsequent analyses when there was a significant relationship between body size and the morphological variable (PC scores were used otherwise). We used results on Pagel's lambda (λ) obtained in the PGLS regression to assess the presence of a phylogenetic signal. λ varies between 0 and 1, and indicates the level of phylogenetic signal in the data, where 0 represents no phylogenetic signal and 1 a trait that has evolved as expected under a Brownian motion model of evolution. We used residuals with correction for phylogeny in subsequent analyses when $p(\lambda) = 0$ was <0.95 .

Determination of diet classes

To investigate whether the selective pressures associated with prey capture and feeding habits may be responsible for any variation in hindlimb morphology, we grouped species according to their main prey type (see Table 1 for references). We assigned species as being either specialists, when predominantly taking a certain type of prey ($>80\%$ of the diet), or generalists (G), when commonly preying on a range of different animals. Among specialists, we distinguished fish specialist (FS), small mammal specialists (SMS), and insect specialists (IS). These constitute broad categories, as even diet specialists present some degree of spatial and temporal variation in diet, which can often extend beyond their specialized diet. The snowy owl represents a special case, as it has been described as a small mammal specialist during the breeding season (up to 99% of their diet) but has also been reported to rely heavily on a large spectrum of prey during the non-breeding season or in the absence of small mammals to the point of even excluding small mammals from their diet (Campbell & MacColl, 1978, König & Weick, 2008, Therrien *et al.*, 2011, Williams & Frank, 1979). We hypothesized that if the capture of larger prey is crucial in their annual cycle, the selective pressure on talon morphology might have been different on them than on other small mammal specialists. We therefore treated them in a separate diet class, which we called seasonal small mammal specialists (SSMS), as their talon morphology might not align with that of other SMS.

Discriminant function analysis

We used residuals from the PGLS regression (or average PC scores when no body size correlation and no phylogenetic signal were present) for each species for each morphological characteristic as the input variables in a linear discriminant analysis (LDA) to investigate the degree of variation among species and diet groups in terms of their talon morphology. The LDA allowed us to distinguish two or more groups of individuals based on the morphological variables. We produced canonical discriminant functions, which are linear combinations of the original morphological variables, each describing a proportion of the total group differences. We then visualized the variation between groups in a bivariate plot using the first two discriminant functions, which allowed us to interpret clustering and

separation in terms of the original variables contributing to the new canonical variables. We normalized and centered the variables used in the LDA, so that the weight of each variable in each discriminant function could be directly compared. We also performed a classification matrix test to evaluate the success of the LDA in separating groups. The classification matrix shows the percentage of samples that were correctly classified. As the snowy owls are the sole species belonging to SSMS, we excluded them from the discriminant analysis and used the value obtained for their morphological variables to predict its loadings on the LDA axis a posteriori to assess how they compare to other dietary groups.

To assess which key morphological variables statistically distinguished members of a given dietary groups from other owls, we performed Welch two sample t-tests with Bonferroni corrections for multiple tests, using species either average PCA scores or PGLS residuals for the main discriminant on each axis of the LDA. Normality was tested for each variable. All statistical analyses were performed using R v.4.0.3 (R Core Team, 2020).

Results

PCA analysis

The principal component analyses (PCA) for the 4 morphological characteristics (curvature, robustness, reach, and strength) showed positive and very similar scores on the PC1 for all four digits and, in the case of robustness, for the three measurements (Table 3). This means the PC1 scores represent the overall variance across all digits and measurements for each characteristic. The first component of the PCA for curvature, robustness, and reach represented $>80\%$ of the variance, and were therefore used alone in subsequent analyses. For strength, 2 PCs were necessary to reach a percentage of variance $>80\%$. The second PC was mostly driven by a positive effect of digit 1, meaning that PC2 is representative of strength in digit 1, whereas PC1 is representative of overall strength in all digits.

Phylogenetic generalized least-squares analyses

Our phylogenetic generalized least-squares (PGLS) analyses showed a significant relationship between body height and robustness, reach and overall strength, a near significant relationship with strength of digit 1. As expected, both reach and talon robustness were positively related to body height (reach: linear relationship $P < 0.001$, $\text{adj}R^2 = 0.707$, robustness: logarithmic relationship, $P < 0.001$, $\text{adj}R^2 = 0.784$, respectively). Interestingly, overall strength was also positively related to body height (linear relationship, $P < 0.001$, $\text{adj}R^2:0.690$), i.e. larger birds are a higher talon/toe ratio. This pattern seemed to also be reflected to a smaller extent on strength of digit 1 (linear relationship, $P=0.06$, $\text{adj}R^2: 0.202$) However, no significant relationship between body height and curvature was detected ($P = 0.139$, $\text{adj}R^2: 0.104$). Phylogenetic signal inferred using Pagel's λ was not significantly different from 0 for talon

Table 3 Loadings of each individual measurements and percentage of variance explained by the first two axes (PC1 and PC2) of principal component analyses of hindlimb morphological characteristics of owls ($N = 63$)

Characteristic	Measurement	Digit	PC1	PC2
Curvature	Oo	1	0.589	0.691
		2	0.418	-0.157
		3	0.448	-0.704
		4	0.527	-0.049
	Cumulative proportion of variance		0.878	0.936
Robustness	Hmo	1	0.249	0.404
		2	0.226	0.466
		3	0.214	0.216
		4	0.217	0.411
	BH	1	0.372	0.028
		2	0.368	0.107
		3	0.342	-0.150
		4	0.338	-0.051
	BW	1	0.230	-0.22
		2	0.282	-0.298
		3	0.317	-0.345
		4	0.238	-0.337
Cumulative proportion of variance		0.941	0.964	
Reach	Ao + Toe	1	0.386	-0.608
		2	0.539	-0.113
		3	0.594	-0.101
		4	0.457	0.779
	Cumulative proportion of variance		0.957	0.978
Strength	Ratio Alo/Toe	1	0.645	0.760
		2	0.444	-0.399
		3	0.277	-0.308
		4	0.557	-0.410
	Cumulative proportion of variance		0.781	0.930

Bold values are those with the highest loadings on each PC axis for the first axes that account for >80% of the cumulative variance explained.

curvature, robustness, and overall strength ($\lambda(0): P = 1$), which suggests that variability on these traits is not due to phylogenetic relatedness. However, a phylogenetic signal was detected for reach ($\lambda(0): P = 0.121$), and strength of digit 1 ($\lambda(0): P = 0.129$). We therefore used residuals obtained from the PGLS with correction for phylogeny for reach, and strength of digit 1 and without correction for phylogeny for robustness and overall strength.

Discriminant analysis according to prey type

Our results indicate that talon morphology is linked to prey type in the owl species studied (Fig. 3). The position of each species along the two canonical axes of the LDA revealed that species belonging to the same dietary groups clustered close to each other and were distinguishable. Dietary groupings revealed consistencies in talon morphology, with 100%

replacement accuracy by the classification matrix in all groups based on the individual canonical scores of the LDA ($N = 14$). Loadings on Axis 1 of the LDA, which accounted for 90% of the variance, were driven negatively by talon curvature in most part (Table 4, Fig. 3). Small mammal specialists and insect specialists scored equally high on that axis, generalists scored very low and fish specialists scored about halfway between the other groups. Axis 2 accounted for only 7% of the variance with positive loadings mostly associated negatively with talon robustness. This axis was mostly useful for distinguishing small mammal, which scored positively on this axis, from insect specialists, which scored low on that axis. Loadings for the snowy owl were most similar to that of generalists, and completely opposite those of small mammal specialists on Axis 1.

Dietary group comparisons

Of the two key discriminant variables found in the LDA (curvature and robustness), dietary group were only significantly for curvature (Table 5, Figs. 4 and 5). Both insect specialists and small mammal specialists had significantly lower curvature than species from other dietary groups.

When compared to other dietary groups, the snowy owls showed average talon robustness, average reach, high strength, and pronounced talon curvature, the highest of all studied species in the present study (Fig. 4). Overall, owl species could be divided in two groups according to talon curvature alone (Fig. 4 and 5): insect specialists and small mammal specialists with low talon curvature on one side (mean Oo across all digits: $97^\circ \pm 7.09$ and $101^\circ \pm 6.45$, respectively) and fish specialists, generalists, and seasonal small mammals specialists with higher curvature on the other (mean Oo across all digits: $118^\circ \pm 6.95$; $123^\circ \pm 9.13$; $140^\circ \pm 8.91$, respectively).

Discussion

Our results indicate that hindlimb morphology is highly variable among owl species and can be clearly associated with diet and prey type. The fact that the four studied groups were distinguishable in terms of hindlimb morphology and related diet suggests that strong selective pressures have modulated their prey capture and retention strategies as well as adaptations in their talon morphology. Interestingly, generalists, despite being a heterogeneous group composed of owls with varied diets, were fully distinguishable from any other group.

Talon curvature was one of the more remarkable features associated with prey type. Small mammal and insect specialists showed particularly straight talons, and this morphological characteristic did not appear to be linked to phylogeny or body size. This poor correlation between talon curvature and body size is in line with what has been found in other bird taxa (Birn-Jeffery *et al.*, 2012). As suggested by Tsang *et al.* (2019), the apparent lack of allometric constraint in bird talons could mean that, for these taxa, the evolutionary plasticity of the talon provides the opportunity to exploit ecological niches that could not be accessed through changing of other, more constrained, morphological traits, such as skull shape (Bright *et al.*, 2016). In small

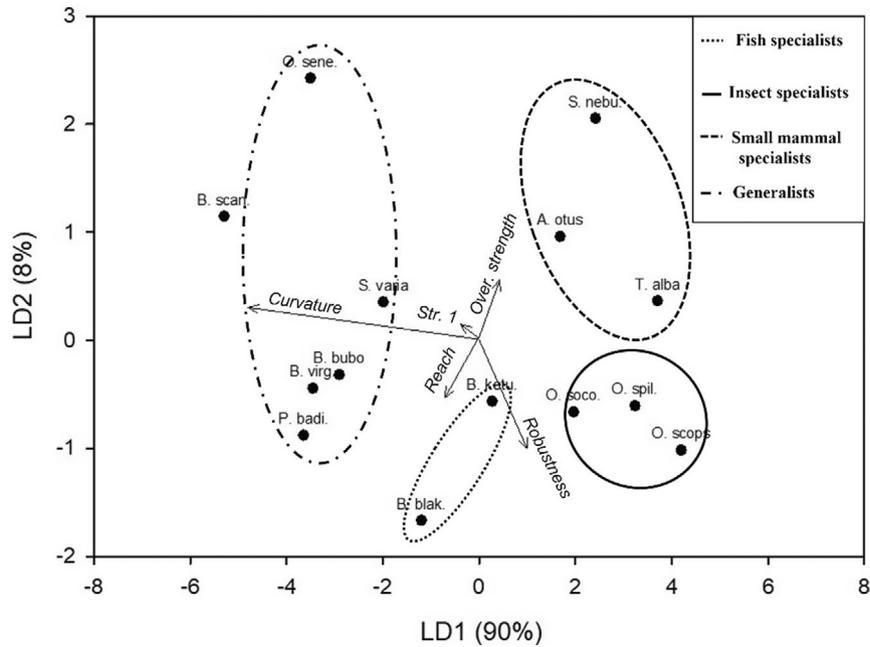


Figure 3 Canonical axes 1 and 2 of a discriminant analysis of hindlimb morphology of owls based on variables issued from a PCA with species grouped by main prey type ($N = 14$). Axes are labeled according to the proportion of variance explained, which is provided in parentheses. Arrows indicate the LDA score for each PC variables and dots are the scores for each species. Score for *Bubo scandiacus* was added a posteriori.

Table 4 Canonical scores along the first two axes of a discriminant function analysis based on morphological variables describing hindlimb morphological characteristics of owls

Morphological variable	LD1	LD2
Curvature	-3.541	0.290
Robustness	0.733	-1.000
Reach	-0.514	-0.555
Overall strength	0.322	0.534
Strength digit I	-0.271	0.108
Proportion of variance explained	0.896	0.075

Bold values are the ones for which the discriminant coefficient values are the highest.

Table 5 Comparison of the 2 main discriminant morphological characteristics between owl species of each dietary group and all other owl species (Welsh t -test: t -value, degree of freedom, P values with Bonferroni correction for repeated tests)

FS vs. others	IS vs. Others	SMS vs. Others	G vs. others
Curvature			
$t = -1.00$	$t = 4.03$	$t = -3.65$	$t = -2.76$
d.f. = 3.90	d.f. = 8.46	d.f. = 10.47	d.f. = 11.83
$P = 1.000$	$P = 0.014^*$	$P = 0.017^*$	$P = 0.070^{**}$
Robustness			
$t = -3.63$	$t = 0.53$	$t = 1.64$	$t = -0.69$
d.f. = 3.64	d.f. = 11.95	d.f. = 2.65	d.f. = 8.30
$P = 0.10^{**}$	$P = 1.000$	$P = 0.844$	$P = 1.000$

Bold values highlight significant differences.

* $P < 0.05$.

** $P \leq 0.1$.

mammal and insect specialists, the small size of their prey enables owls to encircle them in the talons grasp and constrict them. This mode of prey restraint allows for straighter talons, which can therefore be longer and maximize the outlever strength and reach (Fowler *et al.*, 2009). By opposition, the highly curved talons of generalists suggest an adaptation to subdue and immobilize on the ground relatively stronger and heavier prey that cannot be readily constricted within the talon grasp. This suggests the ability to capture and subdue heavy prey has played a crucial role in the hindlimb evolution of owls. Our results suggests that talon curvature could be a very useful clue of owls' diet and prey type.

Robustness varied widely within dietary groups, with fish specialist species appearing to be among the ones with the most robust talons for their size, although we might not have had the statistical power to detect such a difference. The high

variability in talon robustness in other groups suggests that this morphological trait may be more related to hunting and capture techniques than prey type *per se*.

Reach also varied widely within dietary groups with no clear pattern. This might be due to the interaction of reach with other variables. For example, a higher curvature can often be associated with a lower reach. We could have expected small mammal specialists and insect specialists to show a greater reach, especially given their lower curvature. It is possible that the need for strength in these species was greater than the need for reach since a lower toe length for the same talon length

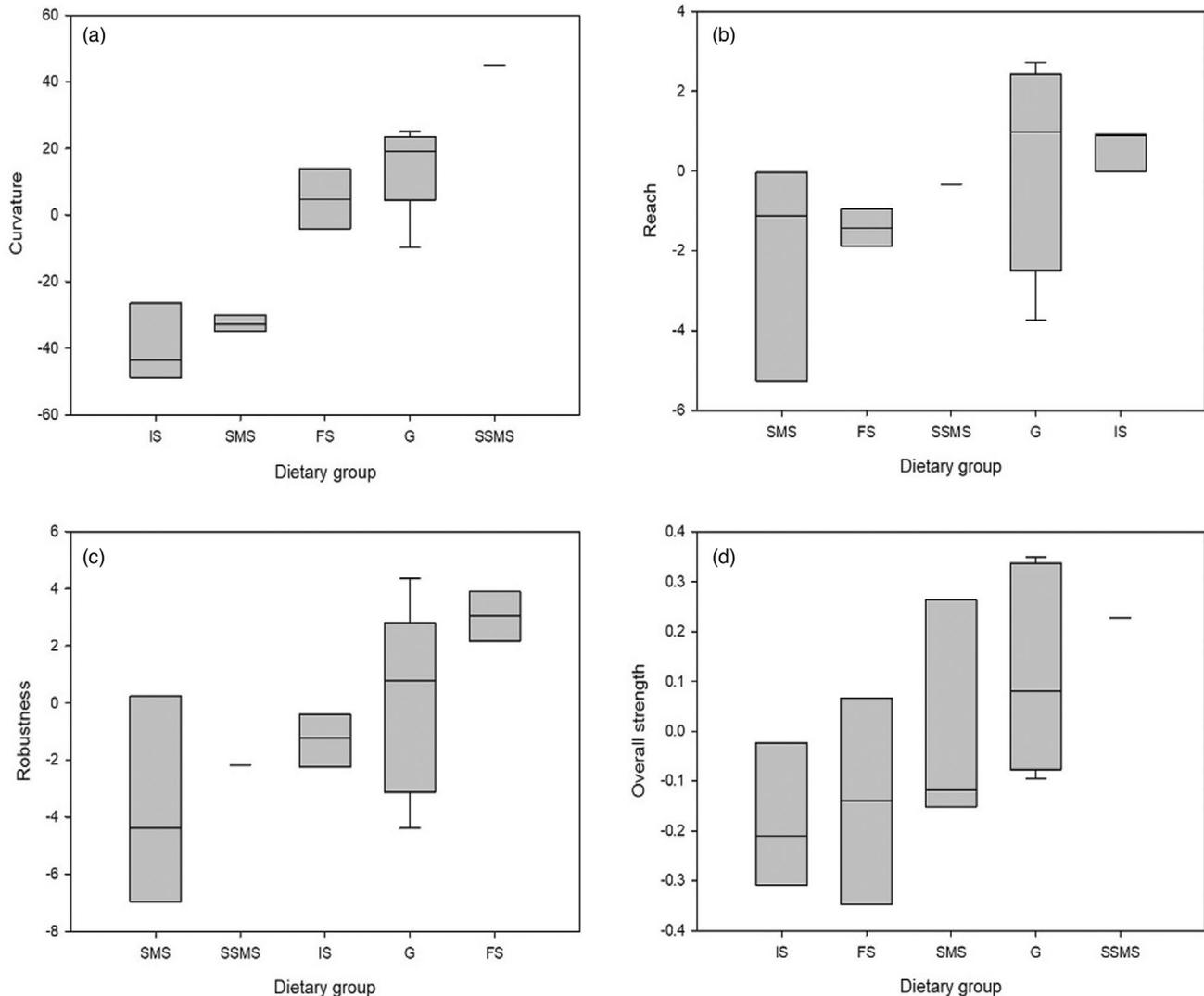


Figure 4 Ranked boxplot of morphological values (residuals or PC scores) by dietary type for (a) curvature, (b) reach, (c) robustness, and (d) overall strength (SMS, small mammal specialists; IS, insect specialists; FS, fish specialists; G, generalists; SSMS, seasonal small mammal specialists).

would increase digit strength but reduce overall reach (Fowler *et al.*, 2009).

Another interesting finding is that the strength component, as measured by the ratio talon/toe, was positively related to body size. This means that, in the species studied, bigger owls had a talon morphology that maximized strength. In our sample, these species are also the species we would expect to hunt prey that require more strength, such as small and medium-sized mammals. That relationship between body size and prey type might explain why we did not find any significant relationship between a talon morphology that maximize strength and diet after correction for body size.

A key finding is the fact that the seasonal small mammal specialist (the snowy owl), which feeds almost exclusively on small mammals during their breeding seasons but has a broad range of

prey in the winter (Robillard *et al.*, 2017; Therrien *et al.*, 2011; Williams & Frank, 1979) showed a very different hindlimb morphology compared to owls preying primarily on small mammals throughout the year. Their digits were similar in most respects (reach, strength, robustness; Fig. 4), but their curvature was strikingly more pronounced. The highly curved talons of seasonal small mammal specialists, like those of generalists, would be very useful in catching large prey by allowing retention of prey that are too large to be enclosed within the foot, using body weight to pin the prey to the ground. This behavior has indeed been recently described in snowy owl (Robillard *et al.*, 2017; Therrien *et al.*, 2011). Highly curved talons are likely essential to capture and retain large prey, and can still be used, though maybe not as efficiently, to capture small mammals, whereas the reverse might not be true. Therefore, such talon morphology appears essential

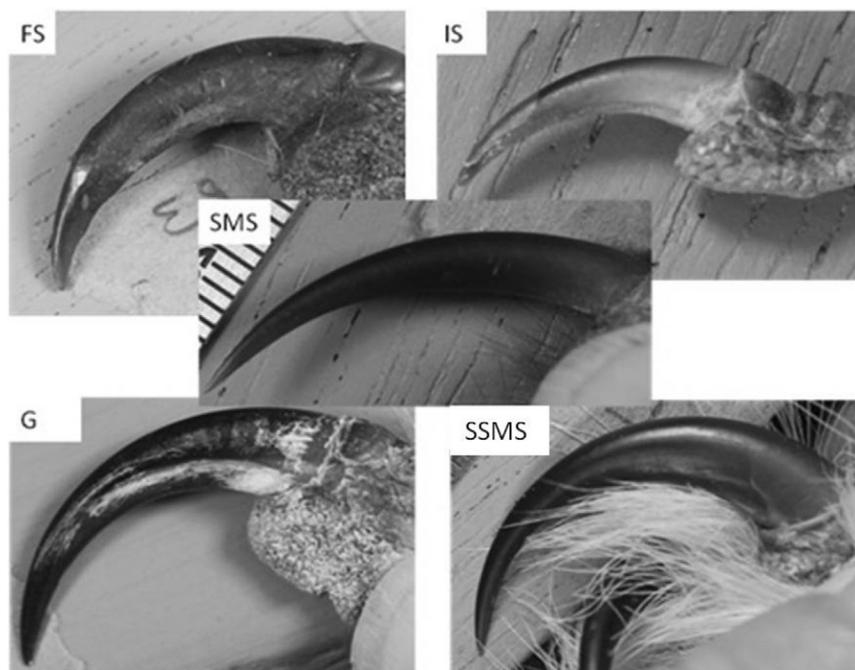


Figure 5 Talon comparison between owl specimen of the 5 diet types—Fish specialists (FS, *Bubo blackistonii*): thick talons; insect specialists (IS, *Otus socotranus*) and small mammal specialist (SMS, *Strix nebulosa*): straight talons; generalists (G, *Bubo virginianus*) and seasonal small mammal specialists (SSMS; *Bubo scandiacus*): highly curved talons.

to allow a diverse diet even when large prey are an important item during a relatively small portion of the year. These findings reinforce how important alternative prey might be for this species outside the breeding season.

Other studies have compared raptor hindlimb characteristics between raptor groups and with non-raptors. The present study includes a great diversity of owl species and is the first to investigate, to our knowledge, potential differences in hindlimb morphology within Strigiformes. It is therefore interesting to compare how the hindlimb morphology of different dietary owl groups varies compared to other raptors and to non-raptors. Fowler *et al.* (2009) reported that non-raptors have weakly curved talons compared to raptors, with average outer curvature (same measurement methodology as in the present study) of about 100° , which is very similar to the curvature we observed in small mammal specialists ($101 \pm 2^\circ$) and insect specialists ($99 \pm 6^\circ$). However, the average outer curvature we found in generalists ($126 \pm 7^\circ$) is more in line with the average curvature reported in Accipitridae (123°) and Falconidae (124°). The snowy owl, with its average curvature of $140^\circ (\pm 9)$, clearly does not fit the overall description of weakly curved talons associated with Strigiformes. They are closer in curvature with what is reported for the Bald Eagle (146°), a species also known for preying on waterfowl (König & Weick, 2008) like snowy owls (Robertson & Gilchrist, 2003, Williams & Frank, 1979). We could have expected fish specialist owls to present an extreme talon curvature resembling that of other fish specialist raptors such as the osprey (166°). While fish diet may not impact their curvature, other functional factors or drift could be behind their lower curvature ($121 \pm 6^\circ$).

Overall, talon curvature seems to be strongly linked to diet in raptors, a character likely primarily driven by the need for higher talon curvature with increased prey size.

Conclusion

Our results show that different owl species have specific and pronounced hindlimb adaptations related to their diet and prey types. These results could be used to extrapolate diet in species for which data on hunting techniques and diet are scarce. This would be particularly relevant in the management and conservation of those species, as owls are often elusive, and some populations are very small, with species listed as endangered or critically endangered (e.g. forest owl, *Athene blewitti*; flores scops-owl, *Otus alfredi*, IUCN, 2022). The findings of this study could also be very useful in ecological studies of sympatric species and could help to understand resource partitioning between competing species belonging to the same guild (e.g. Seyer *et al.*, 2020). Furthermore, it suggests a way we could study resource partitioning between sexes in the same species and test the hypothesis of resources partitioning to avoid competition between mating partners.

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