Behavioral correlates of semi-zygodactyly in Ospreys (*Pandion haliaetus*) based on analysis of internet images (#29375)

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Behavioral correlates of semi-zygodactyly in Ospreys (*Pandion haliaetus*) based on analysis of internet images

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Ospreys are renowned for their fishing abilities, which have largely been attributed to their specialized talon morphology and semi-zygodactyly−the ability to rotate the fourth toe to accompany the first toe in opposition of toes II and III. Anecdotal observations indicate that zygodactyly in Ospreys is associated with prey capture, although to our knowledge this has not been rigorously tested. As a first pass toward understanding the functional significance of semi-zygodactyly in Ospreys, we scoured the internet for images of Osprey feet in a variety of circumstances. From these we cross-tabulated the number of times each of three toe configurations (anisodactylous, zygodactylous, and an intermediate condition between these) was associated with different grasping scenarios (e.g., grasping prey or perched), contact conditions (e.g., fish, other objects, or substrate), object sizes (relative to foot size), and grasping behaviors (e.g., using one or both feet). Our analysis confirms an association between zygodactyly and grasping behavior; the odds that an osprey exhibited zygodactyly while grasping objects in flight were 5.7 times greater than whilst perched. Furthermore, the odds of zygodactyly during single-foot grasps were 4.1 times greater when pictured grasping fish compared to other objects. This suggests a functional association between predatory behavior and zygodactyly and has implications for the selective role of predatory performance in the evolution of zygodactyly more generally.

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ABSTRACT

Ospreys are renowned for their fishing abilities, which have largely been attributed to their specialized talon morphology and semi-zygodactyly–the ability to rotate the fourth toe to accompany the first toe in opposition of toes II and III. Anecdotal observations indicate that zygodactyly in Ospreys is associated with prey capture, although to our knowledge this has not been rigorously tested. As a first pass toward understanding the functional significance of semi-zygodactyly in Ospreys, we scoured the internet for images of Osprey feet in a variety of circumstances. From these we cross-tabulated the number of times each of three toe configurations (anisodactylous, zygodactylous, and an intermediate condition between these) was associated with different grasping scenarios (e.g., grasping prey or perched), contact conditions (e.g., fish, other objects, or substrate), object sizes (relative to foot size), and grasping behaviors (e.g., using one or both feet). Our analysis confirms an association between zygodactyly and grasping behavior; the odds that an osprey exhibited zygodactyly while grasping objects in flight were 5.7 times greater than whilst perched. Furthermore, the odds of zygodactyly during single-foot grasps were 4.1 times greater when pictured grasping fish compared to other objects. This suggests a functional association between predatory behavior and zygodactyly and has implications for the selective role of predatory performance in the evolution of zygodactyly more generally.

KEYWORDS: foraging; grasping; *Pandion haliaetus*; perching; zyg~~a~~odactyl; Osprey

INTRODUCTION

Ospreys (*Pandion haliaetus*) feed primarily on fish (accounting for ~99% of their diet) that they take from the water (Poole et al., 2002). They are able to achieve substantial prey-capture success rates for a predator (up to 82%; Poole et al., 2002), despite the difficulties inherent in penetrating an aquatic medium to pursue fish. This ability is afforded by several adaptive modifications of their foot form and function, compared to other birds of prey. Among these adaptations is the ability to rotate the fourth toe (digit IV) antero-posteriorly, and ~~apparently~~ toggle between anisodactyl (digits II-IV face anteriorly; digit I posteriorly) and zygodactyl (digits II and III face anteriorly; digits I and IV face posteriorly) toe arrangements (Shufeldt, 1909; Jollie, 1976, 1977; Raikow, 1985; Polson, 1993; Ramos and Walker, 1998) (Fig. 1). The ability to facultatively shift from anisodactyly to zygodactyly (i.e., semi-zygodactyly; Raikow, 1985; Botelho et al., 2015) is thought to enhance their extreme grasping capabilities. For instance, previous researchers have proposed that the facultative zygodactyl arrangement in predatory birds, such as owls and Black-shouldered Kites (Tsang, 2012), provides advantages for distributing the toes (and prey-contact surface area) more symmetrically (Payne, 1962; Goslow, 1972), as well as for generating greater grip strength (Ward et al., 2002; Einoder and Richardson, 2007). Both of these advantages ostensibly pertain to the Osprey, which grasps evasive, slippery fish from above by plunge-diving to capture prey well below the surface of the water (Polson, 1993).

Despite the common knowledge of Osprey semi-zygodactyly, it is not abundantly clear specifically when and how Ospreys employ one toe configuration over the other. Casual observations of ospreys captured in photographs reveal that the zygodactyl configuration is often assumed during perching as well as when clutching fish. Thus, the advantages to zygodactyly for grasping prey in Ospreys, although perfectly reasonable, remain somewhat speculative. Furthermore, it is unclear specifically how the change in toe configuration is controlled. Ospreys possess several anatomical peculiarities that are presumed to be associated with semi-zygodactyly. These include a relatively long digit IV that is semi-reversible, claws of near equal length across all toes, distinctly well-developed inner, and a truncated ventro-posteriorly-oriented lateral projection on the outer, trochleae of the distal tarsometatarsus, well-developed M. lumbricales, the absence of a membrane between digits III and IV, and a strongly developed M. abductor digiti IV (Hudson, 1948; Jollie, 1976, 1977; Tsang, 2012). However, the extent to which Ospreys are able to reposition digit IV voluntarily, or if such repositioning is mechanistically coupled with other hindlimb and/or digital movements (e.g., Ramos and Walker, 1998), or simply a consequence of the grasping scenario (i.e., the object is contacted between the third and fourth toes), is unclear.

As part of a larger project aimed at understanding the anatomy, control, and functional significance of semi-zygodactyly in Ospreys, we first set out to examine the behavioral correlates of semi-zygodactyly. We approached this by conducting a quantitative analysis of foot use behaviors captured in digital images and videos, publically available on the internet. We used data gleaned from these images specifically to test for associations among toe configurations, grasping scenario, and object size (Fig. 2). Following conventional wisdom, we predicted that Ospreys photographed clutching fish were more likely to display a zygodactyl (2×2) toe configuration. Furthermore, under the assumption that zygodactyly enhances grip force and/or the probability of prey contact (cited above), we anticipated that larger object (prey) sizes, (but not necessarily perching substrates), would also elicit a 2×2 toe configuration.

Materials and Methods

We searched the World-Wide Web (predominantly Google Images [English]) for photographs of Ospreys interacting with prey and/or various substrates, using the following search terms: “osprey,” “*Pandion haliaetus*,” and combinations of the previous two terms with “clutching,” "grasping,” "nest,” "fish,” and "photos.” We then moved on to searching personal/professional websites, and then videos (where we took screenshots of appropriate footage). Finally, we moved on to different languages of Google and repeated the above. Two observers independently scored each foot of each Osprey in every image for the characteristics described below and in Table 1.

A third independent observer served as a "moderator," by compiling the scores of the other two observers and resolving any disagreements. The three observers rotated among tasks, such that each one served as a moderator for one component of the data set or another. Although we made an effort to avoid scoring duplicated images, we cannot exclude the possibility that the same individual Ospreys may have appeared in more than one distinct image.

Each Osprey pictured in an image constituted a "subject," and each foot pictured was a replicate in the analyses. We used generalized estimating equations (a repeated-measures form of logistic regression; SPSS, 2013), with image identity included as a subject variable, and foot identity (left or right) included as a within-subjects variable, for which we specified an unstructured correlation matrix. We treated toe configuration as an ordinal (logistic) response variable ranging between 1 (= 3×1) and 3 (= 2×2), in which 2 (= 2.5×1.5) constituted an intermediate configuration analogous to Bock and Miller's (1959) "ectropodactyl" foot type (Fig. 2 B, C, F). We performed two series of analyses: one overall test to examine the effects of relative "object size" (ordinal variable ranging 0 [no object] to 4 [extra-large]; Table 1) and "grasping scenario" (0 = nothing in feet, P = perched on substrate, G = grasping an object), as well as their interaction. Although we were not specifically interested in the effects of foot identity (left or right), we performed an additional test including "foot identity" as a fixed effect to screen for any footedness biases. We then followed this analysis with a more refined test on data including only cases of contact between foot and object or substrate. For this test, we included an additional nested effect of "contact condition" (F = fish, O = other object, T = tree, S = other substrate; Table 1) within grasping scenario (P vs. G), to determine whether the general types of objects or substrates grasped have any further effects on toe configuration within each of the two main grasping scenarios. We also added an additional variable, "footing," indicating whether grasping was performed with one or both feet. For both sets of analyses, we began with full models (main effects and interactions) and successively removed non-significant interactions (by order of decreasing *P*-value) to obtain the most parsimonious final models. Significance was based on the Type III sums of squares, and an $\alpha = 0.05$.

Results

The 1184 images of Osprey grasping behavior that we scored (Supplemental Data S1) fell into five main categories: (1) flying with fish, perching (2) with and (3) without fish, (4) nest-building, and (5) pre-contact with prey or substrate. Of these, obscured visibility of the feet and casewise deletions from one or more missing variables resulted in 1123 Osprey images of n = 1882 feet, both in contact with objects and not, entered into the analysis. Overall, there was no significant interaction between object size and grasping scenario on toe configuration (Type III Wald Chi-square (χ^2) test of model effects = 4.34, df = 2, $P = 0.114$). The effect of grasping scenario remained significant ($\chi^2 = 198.61$, df = 1, $P < 0.0001$), and the effect object size remained non-significant ($\chi^2 = 0.457$, df = 3, $P = 0.928$), after removing the non-significant interaction term from the model. The parameter estimates (*B*) revealed that the probability of zygodactyly significantly increased for the flying without an object and flying with an object scenarios, compared to the grasping while perched scenario (Table 2, Fig. 3). In particular, the odds that an osprey exhibited a zygodactyl toe configuration during flight were 5.7 times greater when pictured grasping objects, and 2.6 times greater when grasping nothing, than whilst perched. When "foot identity" was included as a fixed (between-subjects) effect in an auxiliary analysis implemented specifically to test for differences between left and right feet (rather than including it as a repeated effect, as in the omnibus analysis), there was no significant effect of foot identity, nor any interaction with objects size or grasping scenario, on toe configuration (Supplemental Table S1).

When considering object-contact cases only (n = 1503 feet from 995 images), all main effects and interactions were significant (Table 3). Both interaction effects (footing × contact condition within grasping scenario, and object size × contact condition within grasping scenario) reflect variation in responses between contact conditions within each perching and grasping scenarios (Fig. 4). In the former case, the interaction was due primarily to an increase in the probability of zygodactyly from dual- to single-foot grasping for fish, relative to the "other substrate" reference contact condition of perching ($B = 0.882 \pm 0.378$, df = 1, $P = 0.019$, Exp(B) = 2.42 [1.15-5.07, 95% CI]). The object size × contact condition within grasping scenario interaction was due to two marginally non-significant effects: a decrease in the probability of zygodactyly for small object sizes, relative to large, when grasping fish compared to the "other substrate"/perching reference category ($B = -1.08 \pm 0.598$, df = 1, $P = 0.072$, Exp(B) = 0.341 [0.106-1.10, 95% CI]), and an increase in the probability of zygodactyly for medium object sizes, relative to large, when perched in trees compared to the "other substrate"/perching reference category ($B = 1.14 \pm 0.631$, df = 1, $P = 0.071$, Exp(B) = 3.13 [0.908-10.79, 95% CI]). However, because these parameters were not significant, we felt justified in excluding the object size × contact condition within grasping scenario interaction effect in subsequent analyses (below).

In the subsequent model, all effects remained significant, with the exception of object size (Table 3). Because the effect of contact condition within grasping scenario depended upon whether or not the grasp was single- or dual-footed, we generated new models for dual-footed (n = 962) and single-footed (n = 541) grasps, separately (Fig. 4). In both models the main effect of grasping scenario was significant (Table 3), such that the odds of zygodactyl grasps were 2.8 and 6.4 times greater during flying than perching (Table 4). Furthermore, there was a significant effect of contact condition within grasping scenario for single-footed grasps, but not for bi-axial grasps (Table 3). For the former, the probability of zygodactyly was significantly greater for the fish, compared to the "other object" contact condition (Exp(B) = 4.05 [1.93-8.53, 95% CI]), as well as for the tree, compared to the "other substrate" contact condition (Exp(B) = 1.95 [1.03-3.69, 95% CI]; Table 4).

DISCUSSION

We analyzed grasping behavior of Ospreys from 1184 web images and videos of Ospreys in various states of utilizing their feet. Our results support predictions from casual observations, photographs, and anecdotal reports from the literature: that Ospreys tend to employ a zygodactylous foot configuration when grasping objects, and in particular when gripping fish. This suggests a functional association between predatory behavior and zygodactyly and has implications for the selective role of predatory performance in the evolution of zygodactyly more generally. Notably, the use of a zygodactylous configuration during single-foot grasps of fish (e.g., Fig. 4) strongly suggests that this toe configuration affords a performance advantage under the most challenging grasping conditions. Along these lines, however, it seems odd that object size was ostensibly unrelated to zygodactyly (e.g., Fig. 3), with a (non-significant) tendency for zygodactyl toe configurations to be pictured with smaller object sizes. On biomechanical grounds, very large and very small objects (relative to grasper size) pose greater challenges for grasping (e.g., Seo et al., 2008; Irwin & Radwin, 2008; Fok & Chou, 2010). Perhaps this is explained by the potential benefits of the multiarticular nature of their digital flexion mechanism (Backus et al., 2015), which might afford the ability to grasp a wide range of object sizes regardless of toe configuration (Dollar & Howe, 2011).

Embryological evidence supports developmental mechanisms as the primary drivers of toe configuration across taxa (Botelho et al., 2015). Semi-zygodactyly has apparently evolved only three times (Ospreys, turacos, and the common ancestor of owls and mousebirds), in each case in groups related to fully-zygodactylous clades, suggesting semi-zygodactyly as an intermediate stage (Botelho et al., 2015). However, semi-zygodactyl Ospreys (Pandionidae) are nested well within the predominantly anisodactylous Accipitriformes (Botelho et al., 2015), which, coupled with their extreme piscivorous specialization, suggests an adaptive, causal role for semi-zygodactyly. Furthermore, a recent analysis of the pedal flexibility of Australian raptors, including Osprey, has indicated that diurnal raptors do indeed possess a wider range of angle divarication of digits (i.e., the degree to which toes are splayed out from one another) as a group (Tsang & McDonald, *in press*). The Osprey exceeded the maximum digit angle divarication of digit IV (the digit that enables semi-zygodactyl grasping) of other anisodactylous raptors, achieving wider digit IV angle divarication results that overlapped with the digit IV angle divarications of the nocturnal owls. This degree of convergence between Ospreys and owls lends further support to the ecological, adaptive, origin of semi-zygodactyly, since Osprey (and owls) feed mostly on prey that can be difficult to capture (e.g. plunge-diving for slippery fish or nocturnally hunting small, fast moving prey). The observed lack of skin between digits III and IV in both species would no doubt facilitate wider lateral movement of digit IV.

The ability to transition between toe configurations is a feat of which very few species are capable, and ostensibly provides a performance advantage. We present quantitative data linking prey capture behavior with zygodactyly in Ospreys. Nevertheless, the extent to which semi- or full-zygodactyly provides a biomechanical/ functional advantage for grasping performance has yet to be explicitly tested. Thus, further work is required, supported by consistent field observations of reliably located individuals at close range, to facilitate further study of this unique behavior. Citizen science potentially has much to offer in this regard, via nest cams and/or automated cameras positioned near prime foraging grounds (Bierregaard et al., 2014). Another important avenue of inquiry currently underway is to uncover precisely how rotation of the outer toe is biomechanically accomplished; e.g., whether it is actively controlled via musculature or passively enabled by contact.

CONCLUSIONS

From our analysis of web images, we found that semi-zygodactylous Ospreys are pictured using three predominant toe configurations: anisodactylous, zygodactylous, and an intermedite condition we labeled “2.5×1.5”. Our generalized estimating equation models confirmed the oft-cited association between zygodactyly and grasping behavior in general; the odds that an osprey exhibited zygodactyly while pictured grasping objects in flight were 5.7 times greater than whilst perched. Contrary to our expectations, zygodactyly was unrelated to object size, but the odds of observing zygodactyly in single-foot grasps were 4.1 times greater with fish compared to other objects. This suggests a functional association between predatory behavior and zygodactyly, and ultimately has implications for the selective role of predatory performance in the evolution of zygodactyly.

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Table 1(on next page)

List of variables included in the analyses, along with descriptions of each category.

Statistical analyses were designed in such a way as to model the probability of zygodactyly (dependent variable) with each condition.

Variable/categories	Description	Additional notes/justification
Toe configuration		Treated as an ordinal logistic response variable
1 (3×1)	Anisodactyl (digits II-IV directed cranially, digit I directed caudally)	
2 (2.5×1)	Transitional; digit IV mid-way between digits III and I	
3 (2×2)	Zygodactyl (digits II and III directed cranially, digits I and IV directed caudally)	
Grasping scenario		To test how overall grasping behavior effects toe configuration
Free-footed (0)	Foot was empty; Osprey may have been landing, taking off, or diving	
Grasping object (G)	Object visibly clutched by foot; usually during mid-flight	
Perching (P)	Osprey was apparently motionless, with foot open against substrate	
Contact condition		Effect nested within grasping scenario, to determine whether the type of object/structure contacted within each scenario (G or P, above) affected toe configuration.
Fish (F)	Foot enclosed a fish; usually upon leaving the water or in mid-flight or landing	
Other object (O)	Foot enclosed something other than a fish; usually nesting material, occasionally the talons of other Ospreys	

Tree (T)	Foot was enclosed around a tree branch while Osprey was perched	Trees were distinguished from other perching substrates to account for Ospreys' tendencies to wrap their toes around branches, as opposed to standing flat-footed
Other substrate (S)	Foot was in contact with perching substrates other than a tree branch; usually a post, rock, or ground	
Object size		Assessed visually, relative to the extent to which toes encircled the object
0	No object in foot	
1	Small/very small: foot encircled between 67 and ≥100% of object "diameter".	By "diameter" we refer roughly to the cross-sectional dimension of the grasped object
2	Medium: foot encircled between 34-66% of object "diameter".	
3	Large: foot encircled 33% of object or less of object "diameter".	
4	Extra-large: foot did not really "wrap" around the object at all (e.g. ground, nest surface).	
Foot identity	Left or right foot scored	Included as a within-subjects variable to account for covariation in the responses between feet
Footing	Whether object was grasped with one (1) or both (2) feet	Included specifically to test whether single-foot grasps were more apt to exhibit zygodactyly, perhaps to enhance purchase on objects when unaided by the other foot

Table 2(on next page)

Parameter estimates and test statistics from a generalized estimating equation (GEE) model.

Toe configuration (toe code; 1 = 3×1, 2 = 2.5×1.5, 3 = 2×2) was modeled as a function of grasping scenario (graspscen; free-footed, grasping, perched), object size (objsize; no object [0] – extra-large [4]), and their interaction (graspscen × objsize), for the complete data set (*n* = 1882 feet [of 1123 Osprey images]).

Parameter*	*B*	Std. Error	Hypothesis Test: Type III Wald χ^2	Hypothesis Test: df	Hypothesis Test: *P*	Odds ratio Exp(*B*)	95% CI Exp(B): Lower	95% CI Exp(B): Upper
Threshold toecode=1	.172	.2226	.595	1	.440	1.187	.768	1.837
toecode=2	.173	.2236	11.942	1	.001	2.166	1.397	3.357
graspscen=0	.963	.2517	14.629	1	.0001	2.619	1.599	4.289
graspscen=G	1.739	.3139	30.678	1	<.0001	5.690	3.075	10.527
objsize=1	.308	.2472	1.550	1	.213	1.360	.838	2.208
objsize=2	.046	.2533	.033	1	.856	1.047	.637	1.720
objsize=3	.116	.2719	.181	1	.671	1.123	.659	1.913
graspscen=G × objsize=1	-.415	.3548	1.367	1	.242	.660	.330	1.324
graspscen=G × objsize=2	.078	.3661	.045	1	.831	1.081	.528	2.216
(Scale)	1							

Table 3(on next page)

Test of model effects from generalized estimating equation (GEE) models restricted to cases in which feet were observed contacting objects or substrates (*n* = 1503).

Toe configuration (toe code; 1 = 3×1, 2 = 2.5×1.5, 3 = 2×2) was modeled as a function of grasping scenario (graspscen; free-footed, grasping, perched), contact condition (contcond; F = fish, O = other object, T = tree, S = other substrate) within grasping scenario, object size (objsize; small [1] – extra-large [4]), and footing (dual- or single-foot grasps). The reduced model shows results after excluding an interaction term with marginally non-significant parameter estimates; this model was further decomposed into separate models for each single (*n* = 541) and dual (*n* = 962) footing condition.

Source	**Type III Wald χ^2**	**df**	***P***
graspscen	23.68	1	<.0001
objsize	8.33	3	.040
footing	5.20	1	.023
graspcond(graspscen)	18.68	2	<.0001
footing × graspcond(graspscen)	18.58	3	.0003
objsize × graspcond(graspscen)	18.27	7	.011
Reduced model			
graspscen	98.86	1	<.0001
objsize	0.464	3	.927
footing	5.25	1	.022
graspcond(graspscen)	15.29	2	<.0001
footing × graspcond(graspscen)	16.38	3	.001
Footing = single-footed			
graspscen	27.95	1	<.0001
objsize	.339	3	.952
graspcond(graspscen)	18.30	2	<.0001
Footing = dual-footed			
graspscen	86.66	1	<.0001
objsize	.791	3	.852
graspcond(graspscen)	1.92	2	.383

Table 4 (on next page)

Parameter estimates and test statistics from generalized estimating equation (GEE) models for single-footed (n = 541) and dual-footed (bi-axial; n = 962) contact cases.

Toe configuration (toe code; 1 = 3×1, 2 = 2.5×1.5, 3 = 2×2) was modeled as a function of grasping scenario (graspscen; free-footed, grasping, perched), contact condition (contcond; F = fish, O = other object, T = tree, S = other substrate) within grasping scenario, and object size (objsize; small [1] – extra-large [4]).

Parameter		B	Std. Error	Hypothesis Test: Type III Wald χ^2	df	P	Odds ratio Exp(B)	95% CI Exp(B): Lower	Upper
Single-footed grasps									
Threshold	toecode=1	.093	.3531	.070	1	.792	1.098	.549	2.193
	toecode=2	.731	.3549	4.245	1	.039	2.077	1.036	4.165
graspscen=G		1.025	.4664	4.826	1	.028	2.786	1.117	6.950
graspscen=P		0					1		
objsize=1		-.064	.4638	.019	1	.890	.938	.378	2.327
objsize=2		-.085	.4461	.036	1	.850	.919	.383	2.203
objsize=3		-.193	.4261	.204	1	.651	.825	.358	1.902
objsize=4		0[a]					1		
contcond=F(graspscen=G)		1.400	.3793	13.619	1	.0002	4.054	1.928	8.527
contcond=O(graspscen=G)		0[a]					1		
contcond=T(graspscen=P)		.666	.3270	4.145	1	.042	1.946	1.025	3.694
contcond=S(graspscen=P)		0					1		
(Scale)		1							
Dual-footed grasps									
Threshold	toecode=1	.373	.3168	1.389	1	.239	1.453	.781	2.703
	toecode=2	1.208	.3208	14.188	1	.0002	3.347	1.785	6.277
graspscen=G		1.849	.3149	34.456	1	<.0001	6.352	3.426	11.775
graspscen=P		0					1		
objsize=1		.091	.3589	.064	1	.800	1.095	.542	2.213
objsize=2		-.031	.3538	.007	1	.931	.970	.485	1.940
objsize=3		.122	.3735	.107	1	.744	1.130	.543	2.349
objsize=4		0					1		
contcond=F(graspscen=G)		-.142	.2706	.276	1	.599	.867	.510	1.474
contcond=O(graspscen=G)		0					1		
contcond=T(graspscen=P)		.296	.2257	1.722	1	.189	1.345	.864	2.093
contcond=S(graspscen=P)		0					1		
(Scale)		1							

1

Figure 1

Examples of pedal digit (DI-DIV) configurations of avian feet.

(A) “Raptorial” foot of a Wedge-tailed Eagle (*Aquila audax*), (B) Anisodactyl foot of an Australian Raven (*Corvus coronoides*), (C) a zygodactyl foot of a Galah (*Eolophus roseicapilla*), and (D) a facultative zygodactyl foot of an Eastern Barn Owl (*Tyto javanica*).

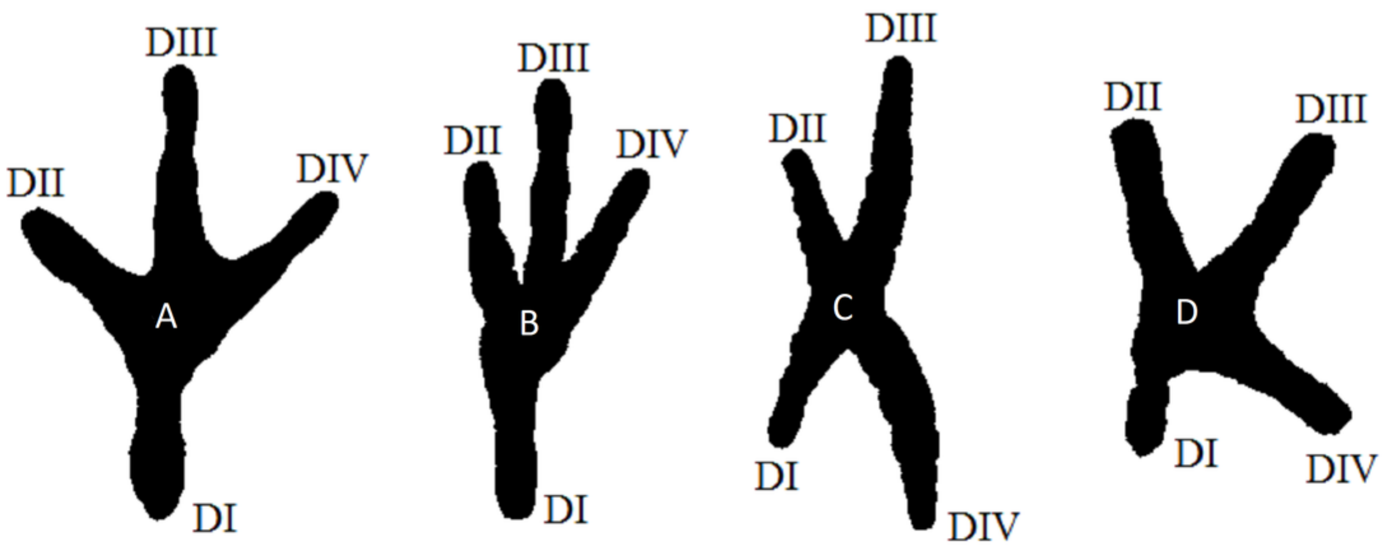

Figure 2

Photos of Osprey showing grasping scenarios and representative object types and sizes.

(A) Perched, grasping a tree branch (small) with a 2×2 configuration in the left foot and a 3×1 configuration in the right foot. (B) Perched, grasping a tree branch (small) with a 2.5×1.5 configuration in the left and right foot. (C) Perched, grasping a tree branch (medium) with a 3×1 configuration in the left foot and a 2.5×1.5 configuration in the right foot. (D) Perched, grasping (single-footed) a fish (large), with a 2×2 configuration in the left foot. (E) Flying, grasping (dual-footed) a twig (small) using a 2×2 configuration in the left and right foot. (F) Schematic diagrams of a left foot showing foot types scored in A-E.

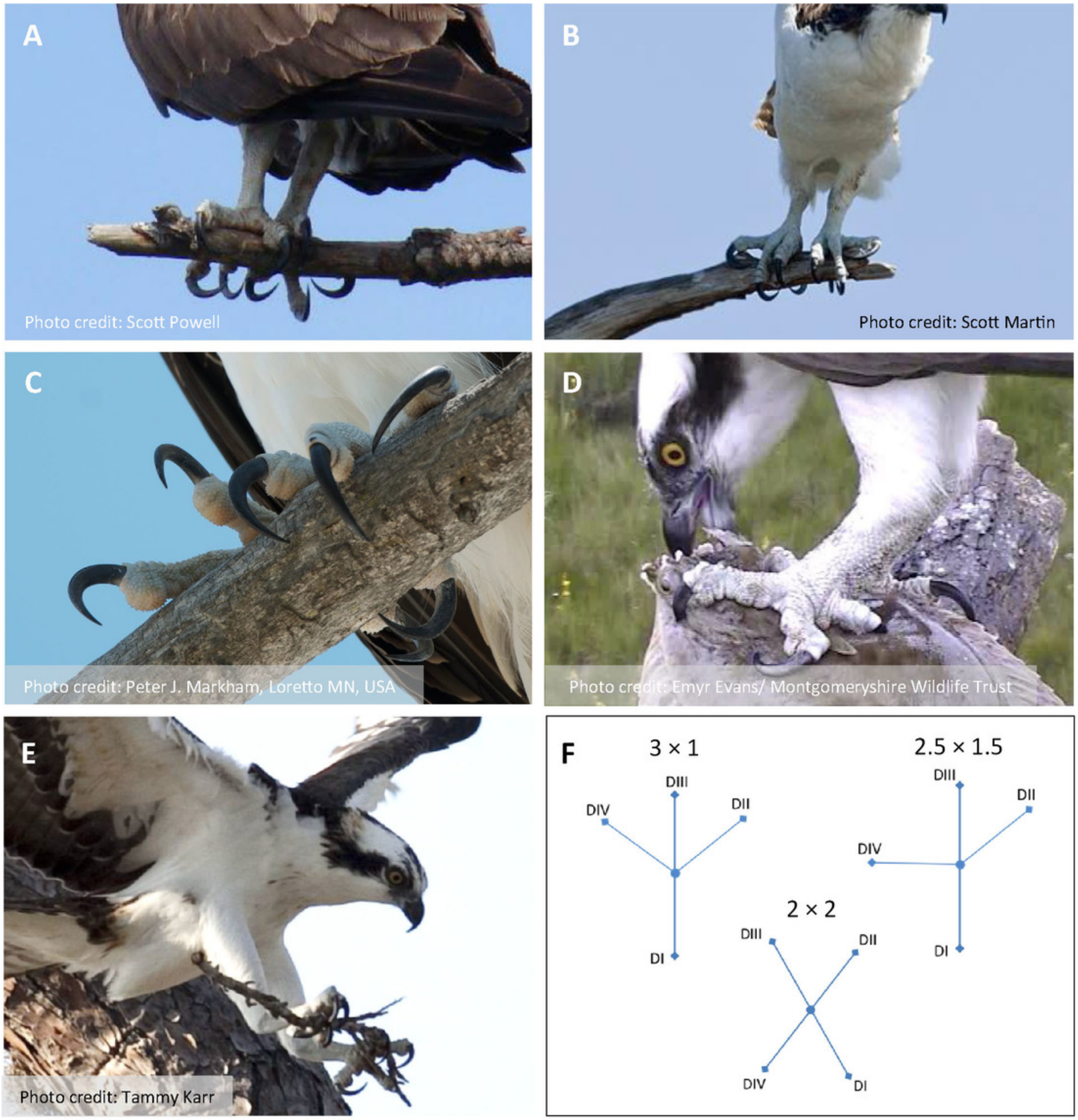
A
Photo credit: Scott Powell
B
Photo credit: Scott Martin
C
Photo credit: Peter J. Markham, Loretto MN, USA
D
Photo credit: Emyr Evans/ Montgomeryshire Wildlife Trust
E
Photo credit: Tammy Karr
F
3 × 1
DIII
DIV
DII
DI
2.5 × 1.5
DIII
DII
DIV
DI
2 × 2
DIII
DII
DIV
DI

Figure 3

Raw proportional distributions of toe configurations with respect to grasping scenario and object size, scored from 1123 web images of Ospreys.

Toe configurations were classified as: 2×2 = zygodactyl, 3×1 = anisodactyl, and 2.5×1.5 = intermediate condition. The proportions of observations for each toe configuration across each grasping scenario (A), and relative object size class (B), were based on *n* = 1882 feet (left and right combined). When these variables were considered in the analysis simultaneously, the probability of zygodactyly (2×2) was significantly greater when Ospreys were photographed grasping objects, or nothing, than when perched, and there was no significant effect of object size.

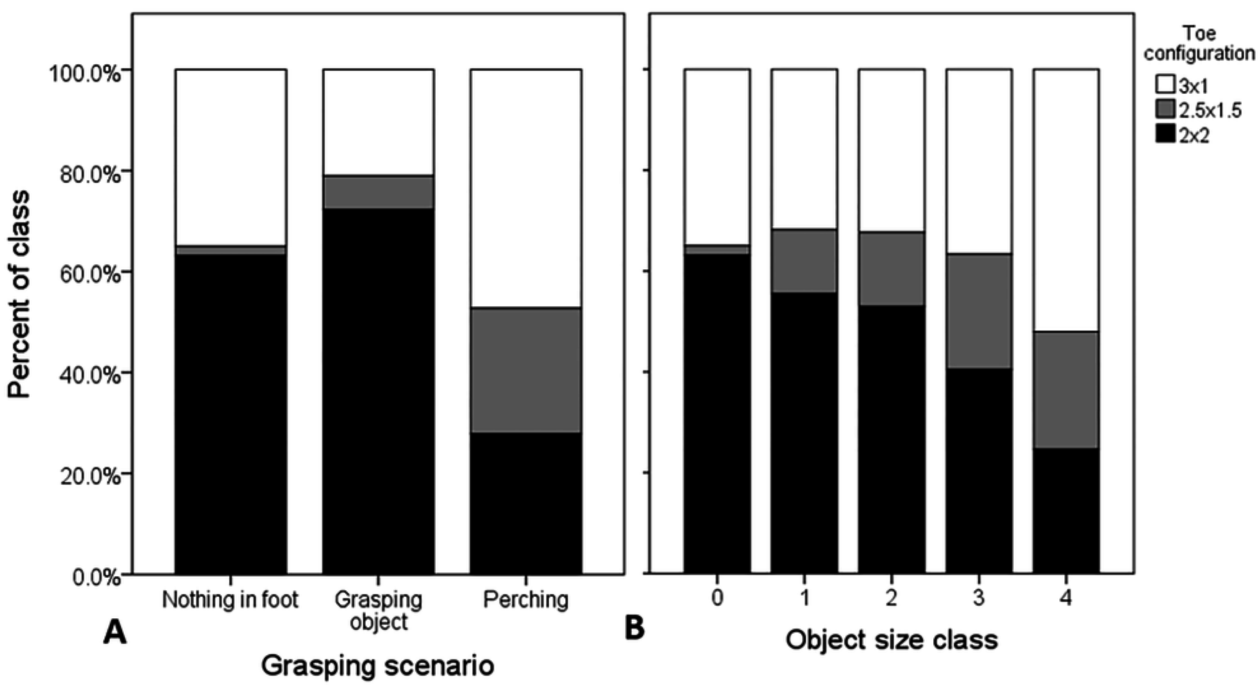

Figure 4

Raw proportional distributions of each toe configuration scored from 995 web images of Ospreys for single- and dual-foot grasps.

Toe configurations were classified as: 2×2 = zygodactyl, 3×1 = anisodactyl, and 2.5×1.5 = intermediate condition. Single-foot (A) and dual-foot (B) cross-tabulations with respect to grasping scenario and contact condition were based on *n* = 1503 feet. When these variables were considered in the analysis simultaneously, the probability of zygodactyly (2×2) was significantly greater, overall, when Ospreys were photographed grasping compared to perching, and specifically for single-foot grasps of fish compared to other objects, and trees compared to other substrates.