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

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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; zygaodactyl; Osprey

INTRODUCTION

Ospreys (*Pandion haliaetus*) feed virtually exclusively 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;

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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).

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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 of 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 or digital movements (e.g., Ramos and Walker, 1998), or simply a

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consequence of the grasping scenario (i.e., the object is contacted between the third and fourth toes), is unclear.

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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, publicly 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 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.

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MATERIALS AND METHODS

We searched the World-Wide Web (predominantly Google Images [English]) for photographs of Ospreys interacting with prey 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

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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 ± 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 ± 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 ± 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 using 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).

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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, because 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

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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 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.

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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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