BioOne COMPLETE

Sneak peek: Raptors search for prey using stochastic head turns

Authors: Ochs, Michael F., Zamani, Marjon, Gomes, Gustavo Maia Rodrigues, de Oliveira Neto, Raimundo Cardoso, and Kane, Suzanne Amador

Source: The Auk, 134(1) : 104-115

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-15-230.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 134, 2017, pp. 104–115
DOI: 10.1642/AUK-15-230.1

RESEARCH ARTICLE

Sneak peek: Raptors search for prey using stochastic head turns

Michael F. Ochs,[1] Marjon Zamani,[2] Gustavo Maia Rodrigues Gomes,[1] Raimundo Cardoso de Oliveira Neto,[1] and Suzanne Amador Kane[2]*

[1] Department of Mathematics and Statistics, The College of New Jersey, Ewing, New Jersey, USA
[2] Physics Department, Haverford College, Haverford, Pennsylvania, USA
* Corresponding author: samador@haverford.edu

Submitted December 12, 2015; Accepted August 29, 2016; Published November 16, 2016

ABSTRACT

The strategies by which foraging predators decide when to redirect their gaze influence both prey detection rates and the prey's ability to detect and avoid predators. We applied statistical analyses that have been used to study neural decision-making for gaze redirection in primates to 3 species of predatory birds with different sizes, visual systems, habitats, and hunting behaviors: the Northern Goshawk (*Accipiter gentilis*), Cooper's Hawk (*A. cooperii*), and Red-tailed Hawk (*Buteo jamaicensis*). The timing of head saccades was measured during visual searches using field video recordings of foraging raptors, and during a variety of behaviors using a miniature camera mounted on the head of a Northern Goshawk. The resulting statistical distribution of latencies (time between successive head saccades) was compared to predictions from various models proposed to describe visual search strategies. Our results did not support models that assume a constant probability of gaze redirection per unit time, a constant time for "giving up" on the visual search, or an initial setup time before visual search initiation. Instead, our data were fit best by a log-normal distribution, consistent with the raptors stochastically changing their gaze direction on the basis of accumulated environmental information. Specifically, this suggests that saccade initiation arises from a neural computation based on detection of a threshold level of a dynamically updated decision signal that encodes noisy sensory data, similar to the processes inferred from previous studies of visual search strategies in primates. The only significant between-species difference we found was a slower mean gaze-redirection rate for 2 larger species compared to the Cooper's Hawk, even though the latter has hunting behavior and maneuverability similar to that of the Northern Goshawk. Head-saccade latencies measured for a Northern Goshawk during different behaviors showed that the bird changed gaze direction significantly less frequently, on average, while perched than while in motion.

Keywords: foraging, latency, neural decision-making, predator, raptors, saccade, searching

Vista previa: Las aves rapaces buscan a sus presas usando giros de cabeza estocásticos

RESUMEN

Las estrategias con las que los depredadores en busca de alimento deciden cuándo redireccionar su mirada afectan la detección de las presas y la habilidad de las presas de detectar y evitar al depredador. En este estudio usamos análisis estadísticos que estudian la toma de decisiones neurales para redirigir la mirada en primates y los aplicamos en tres especies de aves depredadoras con diferencias en tamaño, sistemas visuales, hábitats y comportamiento de caza: *Accipiter gentilis, A. cooperii* y *Buteo jamaicensis*. La sincronización de los movimientos sacádicos se midió durante búsquedas visuales usando grabaciones de rapaces silvestres buscando alimento y durante varios comportamientos usando una cámara miniatura montada en la cabeza de un individuo de *A. gentilis*. La distribución estadística resultante de la latencia (tiempo entre movimientos sacádicos sucesivos) fue comparada con las predicciones de varios modelos propuestos para describir las estrategias de búsqueda visual. Nuestros resultados no sustentaron modelos que asumen una probabilidad constante de redirección de la mirada por unidad de tiempo, un tiempo constante para "rendirse" en la búsqueda visual o un tiempo inicial de ajuste anterior al inicio de la búsqueda visual. Por el contrario, nuestros datos se ajustaron mejor a una distribución log-normal consistente con la hipótesis de que las aves rapaces cambian estocásticamente la dirección de su mirada con base en información ambiental acumulada. Específicamente, esto sugiere que la iniciación de los movimientos sacádicos surge de un cómputo neural basado en la detección de un umbral en la señal de decisión dinámicamente actualizada que codifica los datos sensoriales ruidosos, similar a los procesos inferidos en estudios previos de estrategias de búsqueda visual en primates. En este estudio la única diferencia significativa encontrada entre especies fue una tasa más lenta de redirección de la mirada para las dos especies más grandes en comparación con *A. cooperii*, aún cuando este último tiene comportamientos de caza y de maniobrabilidad similares a las de *A. gentilis*. La latencia entre movimientos sacádicos medida en *A. genitlis* durante diferentes comportamientos mostró que, en promedio, esta ave cambia la dirección de su mirada significativamente menos frecuentemente cuando está perchada que cuando está en movimiento.

© 2017 American Ornithological Society. ISSN 0004-8038, electronic ISSN 1938-4254
Direct all requests to reproduce journal content to the Central Ornithology Publication Office at pubs@americanornithology.org

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Palabras clave: búsqueda, depredador, forrajeo, latencia, rapaces, sacudida, toma neural de decisiones

INTRODUCTION

Predatory birds must scan a complex three-dimensional environment to locate, track, and pursue prey. To do so, they change the direction of their gaze via saccades (rapid motions of the head or eyes) that alternate with long periods of visual fixation (Wallman and Letelier 1993, Land 2015). Because saccadic head motions are discrete, unambiguous events resolvable by field video recordings with good temporal resolution compared to the relevant behavioral timescales, they also enable the study of visual search dynamics during foraging and hunting (Land 1999b, Gall and Fernández-Juricic 2010, O'Rourke et al. 2010b). Past studies of visual searches by avian predators have explored the influence of factors such as hunting behavior (O'Rourke et al. 2010b), prey crypticity (Beauchamp and Ruxton 2012), the formation of an effective search image (Anderson et al. 1997, Alpern et al. 2011, Hein and McKinley 2013), and perch height (Andersson et al. 2009, Tomé et al. 2011). Specific models proposed for foraging searches by predatory birds have suggested that they redirect their attention at an average (possibly optimal) rate or do so with an average probability per unit time (Fitzpatrick 1981, Stephens and Krebs 1986) to optimize search efficiency and, hence, net energy intake. By contrast, it has been hypothesized that the mechanisms governing saccades in primates evolved early in evolutionary history, driven by the needs of both predator and prey for effective searching and unpredictable gaze shifts, to avoid signaling their next moves (Carpenter 1999). Indeed, members of many taxa, including birds, have been shown to react to the gaze direction of potential predators (Davidson et al. 2014), which suggests that unpredictable saccade timing can confer a fitness benefit. Each of these hypothesized models makes specific predictions for the distribution of saccade latencies (intersaccade intervals). For example, if saccades are initiated with a constant probability per unit time, their latency distribution should be a decaying exponential, while one would expect a normal distribution if there is a preferred (possibly optimal) saccadic latency. Therefore, we decided to measure this distribution for naturally foraging predatory birds as a proxy for determining the different mechanisms of neural decision-making that could be at work in this system.

Quantitative neurophysiological models of decision-making have been used to explain the timing of eye saccades in humans and other primates (Carpenter 2012), with support from empirical data at the neural level (Gold and Shadlen 2001). These models have been used to explain several surprising features of primate eye saccades, such as the broad right-skewed probability distribution of saccade latencies and the fact that mean latencies are appreciably longer than the minimum time required for sensing visual stimuli and muscle activation (Carpenter 1999). The decision to initiate a saccade is assumed to be based on detection of a threshold level, S_T, of a decision signal, S, based on sensory data. This decision signal is assumed to start at an initial level, S_o, based on prior knowledge and to rise linearly at a rate, R, based on the output of a neural network that processes incoming sensory inputs. Such "rise-to-threshold" models provide a mechanism that introduces randomness in the decision-making process itself, in addition to randomness generated by noise arising from the environmental and sensory system (Carpenter and Williams 1995). The decision signal, S, is assumed to encode in some way the probability of a hypothesis being true (e.g., for a spontaneous saccade, "There are no objects of interest in the visual field"). For a fixed threshold and rate of rise, one would expect a normal distribution of latencies if the decision signal is proportional to the sum of a series of noisy, normally distributed sensory signals (a random-walk model). Alternatively, the LATER (Linear Approach to Threshold with Ergodic Rate) model assumes that the neural decision signal is proportional to the sum of the log probability of the hypothesis being true, and that the rate of rise to threshold, R, is randomly distributed, which predicts that the reciprocal latency, $1/T_L$, should be normally distributed (Carpenter 1999, Nakahara et al. 2006). A neural decision-making process in which the decision signal is updated by a factor proportional to the product (instead of the sum) of signals related to dynamically updated sensory and internal state inputs will generate a log-normal distribution; this distribution has been used to describe the reaction time for humans to initiate eye saccades in response to visual stimuli as well as the duration of visual fixations and saccade lengths (distance from start to stop) during human visual searches (Feng 2006, Gorea et al. 2014, Rhodes et al. 2014).

In birds, previous laboratory research has found right-skewed latency distributions that resemble those found in primate saccades for head saccades in white leghorn Domestic Chickens (*Gallus domesticus*; Pratt 1982) and Barn Owls (*Tyto alba pratincola*; Hausmann et al. 2008, Ohayon et al. 2008), and for eye saccades in head-immobilized Little Eagles (*Hieraaetus morphnoides*) and Tawny Frogmouths (*Podargus strigoides*; Wallman and Pettigrew 1985). While no studies have performed statistical modeling of saccade latency distributions measured in birds, the resemblance of their distributions

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

suggests that similar mechanisms may be at work in both birds and primates.

On the other hand, the visual systems of birds present many distinctive features that might have caused them to evolve novel visual search strategies; for example, birds lack pursuit (smooth tracking) eye movements and employ different fixational eye movements, including unique oscillatory eye saccades (Pettigrew et al. 1990, Martinez-Conde and Macknik 2008). In general, birds are reported to change the direction of their gaze predominantly by using head movements, even in species with relatively large ranges of eye motion (Land 2015). Diurnal raptors (falcons, hawks, accipiters, and eagles), in particular, have relatively frontally placed eyes, a limited range of eye motion (Land 1999a, Jones et al. 2007, O'Rourke et al. 2010a), and narrow binocular overlap (Martin and Katzir 1999). In general, birds perceive a wide swath of their environment for a fixed gaze direction by using their panoramic lateral visual fields to sense motion and their foveal field(s) for high resolution (Fernández-Juricic 2012). Diurnal raptors have 2 high-acuity foveae per eye (Fite and Rosenfield-Wessels 1975) oriented at different angles, resulting in a complex retinal visual field with a panoramic field of view and small blind region. They have been found to employ frequent head saccades to explore their visual environment, using rapid head saccades to shift their gaze direction and to view prey and other salient objects either at the center of their forward visual field or at one of the angles consistent with foveation at one of their high-acuity retinal fields (Land 1999a, Tucker 2000, Kane and Zamani 2014).

Data for the present study were drawn from online archives of field video recordings of 3 species of diurnal raptors foraging for prey in the field and from field video recorded by a miniature camera mounted on the head of a Northern Goshawk flown for falconry. Video field recordings made using animal-borne video cameras now make possible study of the behavior of unrestrained birds in natural settings (Rutz and Troscianko 2013), supplementing field video shot from the ground. Because birds maintain a level gaze via head nystagmus even during flight and rapid maneuvering (Warrick et al. 2002), cameras mounted on the bird's head also offer a new way to track its primary position of gaze and head motions in cases where eye motion is limited, as is the case for owls (Ohayon et al. 2008, Harmening et al. 2011) and diurnal raptors (Kane and Zamani 2014, Kane et al. 2015). The resulting head-mounted video is stable, apart from head motions that change the bird's primary direction of gaze. In addition, camera-based eye-trackers have been used to study eye saccades in chickens, peafowl, and starlings (Schwarz et al. 2013, Yorzinski et al. 2013, 2015, Tyrrell et al. 2014, 2015), although distributions for saccade latency, duration, or magnitude have not yet been reported.

Here, we consider the statistics of head saccades in 3 diurnal raptor species in the family Accipitridae. For logistical reasons related to the ease of recording video from the ground, we primarily studied sit-and-wait hunting, in which these birds forage for prey from a high perch. The Northern Goshawk (*Accipiter gentilis*; hereafter "goshawk") is a large accipiter that hunts in both forested and open habitats, preying primarily on small, ground-dwelling mammals (squirrels, rabbits, and hares) and birds (Kenward 2006). During foraging, the goshawk typically alternates between short ($\leq$20 s) flights from perch to perch, longer (median 3 min) intervals of sit-and-wait hunting from a perch, and rapid chases after prey (Squires and Reynolds 1997). We also decided to study 2 of the same raptor species, Cooper's Hawk (*Accipiter cooperii*) and Red-tailed Hawk (*Buteo jamaicensis*), for which mean head-saccade latencies and durations as well as the extent of eye motion and gaze orientation have been measured during foraging by perched birds (O'Rourke et al. 2010a, 2010b). Cooper's Hawk, a small, highly maneuverable accipiter, employs brief perch-and-scan foraging as well as ambush hunting and searches in flight (Curtis et al. 2006); this species preys primarily on smaller birds and mammals and prefers to hunt in forest, edge, and open habitats, in that order. Red-tailed Hawks hunt ground-dwelling small-to-medium mammals, reptiles, and birds primarily, and are less maneuverable in flight than either of the accipiters studied (Preston and Beane 2009). This species primarily uses sit-and-wait foraging from a high perch near an open or semi-open habitat and, to a lesser extent, forages for prey while soaring. Cooper's Hawks (♀ 273 g, ♂ 280 g) are much smaller than goshawks (♀ 1,152 g, ♂ 925 g) and Red-tailed Hawks (♀ 1,224 g, ♂ 1,028 g).

Compared to Cooper's Hawks, Red-tailed Hawks have been found to have a smaller binocular overlap region (33° vs. 36° full width), a larger blind area (82° vs. 60° full width), and smaller eye motion (5° vs. 8° full range) (values for Red-tailed Hawk and Cooper's Hawk, respectively; O'Rourke et al. 2010a). Although it has been noted that measurements of eye motions made when the bird's head is immobilized may overestimate eye motion when the head is free to move (Land 2015), the goshawk's limited range of eye motion has been estimated previously at up to $\pm$3° full range, from field video made with the head unrestrained (Kane et al. 2015). Goshawks and Red-tailed Hawks have similar retinal visual receptor densities, foveal geometries, and visual fields (Fite and Rosenfield-Wessels 1975) and similar eye axial lengths and corneal diameters (Hall and Ross 2007), which indicates that they should also have similar visual acuities (Land and Nilsson 2012). Although the visual anatomy of Cooper's Hawks has not been characterized, their smaller eyes presumably indicate that they have lower visual acuity than Red-tailed Hawks and goshawks.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

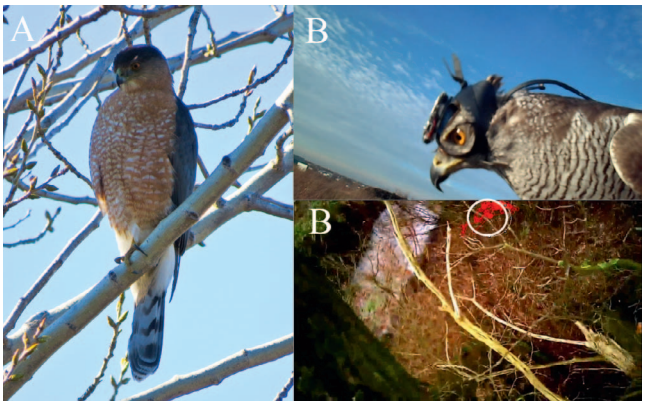


FIGURE 1. (**A**) Cooper's Hawk performing a visual search during sit-and-wait hunting (Vanillakirsky 2015). (**B**) Northern Goshawk wearing a head-mounted video camera (photo credit: Robert Musters). (**C**) Still image from head-mounted animal-borne video recorded while a goshawk observed a rabbit on the ground while perched in a tree. Red points indicate the tracked position of the prey on video as the goshawk turned its head to keep the prey on the center of its visual field, previously established to lie in the white circle (Kane et al. 2015).

METHODS

Animals

Field recording with the head-mounted camera (hereafter "head-camera") took place in the Netherlands on 6 days over a month-long period in December 2012 and January 2013. The goshawk (♀, 1.30 kg, 2.5 yr old) used in the head-mounted video studies was raised in captivity by a parent, trained for falconry, and flown by master falconer Robert Musters in her third hunting season. The falconer was licensed and had all necessary permits, and all activities followed all relevant regulations and laws of the Netherlands. A previous study has documented that the goshawk displayed normal flight and other behaviors while wearing the head-camera methods described here (Kane et al. 2015). Two types of natural goshawk prey were hunted by the goshawk: Ring-necked Pheasants (*Phasianus colchicus*; Giudice and Ratti 2001) and European rabbits (*Oryctolagus cuniculus*; Tislerics 2000), both common, non-endangered species. To minimize impact on prey animals, we used a combination of archival footage and videos filmed during ongoing existing falconry activities. All prey viewed by the goshawk during foraging were wild animals hunted in the field with no interventions by the experimenters or falconers, in order to avoid both altering predator or prey behavior and changing the prey's conspicuousness. Similar methods have been used in prior studies of raptors hunting wild prey in the field (Kenward 1978, Tucker et al. 2000, Kane and Zamani 2014, Kane et al. 2015).

Video Recording and Analysis

Head-mounted camera (hereafter "head-camera") video was recorded using model 808 store-onboard camcorders (Toplanter, Huizhou, China; 29.97 fps; 1,280 × 720 pixel resolution; shutter speed ≈ 0.01 s; 2 hr recording time) mounted in a customized fiberglass hood (total mass of 20 g = 1.5% body mass; Figure 1B). The camera was located a distance (± estimated instrumental uncertainty) $h = 2.4 \pm 0.5$ cm above the eyes. Because head nystagmus ensured that the video frame remained horizontal and stable during maneuvering, no deshake image-stabilization post-processing was used. Image analysis was performed using the Fiji installation of ImageJ (Schindelin et al. 2012; accessed March 26, 2015); an in-depth description of the video methods and image analysis is presented in Kane et al. (2015). Goshawk head-camera video was filmed during a wide variety of behaviors (see behavior codes in Table 1). For the sequences coded as foraging, no prey were visible on screen.

TABLE 1. Behavior codes for the goshawk head-camera video analysis.

Code	Behavior
A	Foraging from a perch (looking around without an obvious target)
B	Looking around while on the falconer's glove as he stood still or walked
C	Watching prey from a perch
D	Watching the falconer from a perch
E	Flying (no prey or perch in sight)
F	Flying toward perch
G	Pursuing prey by flying toward it

A total of 43 videos recorded by cameras on the ground, showing foraging goshawks, Cooper's Hawks, and Red-tailed Hawks, were obtained from the Macaulay Library Sound and Video Catalog (Cornell University, Ithaca, New York, USA; see Supplemental Material Table S1 for sources of all archived videos). Only videos of perched birds foraging undisturbed in the field using sit-and-wait hunting were analyzed. Six additional video sequences of a goshawk searching its environment visually (Buck 2013) were analyzed. Videos were selected to show primarily frontal close-up views to enable reliable detection of head saccades and to exclude sequences in which the birds were distracted by other behaviors (nest care, preening, etc.) or other factors (high winds, other birds, etc.). All videos that satisfied these requirements were analyzed, resulting in data for a total of $n = 584$ and 361 head latencies and durations scored by scorers 1 and 2, respectively. Because many of these videos were filmed in close-up, they also served to verify the small angular ranges of eye motion assumed and noted above.

Timing of head motions was determined from video recordings using the program VirtualDub (http://www.virtualdub.org/; accessed March 26, 2014) to examine each video frame-by-frame; videos were scored independently by 2 observers who recorded the times at which the bird's head motion began and ceased. The smallest detectable

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

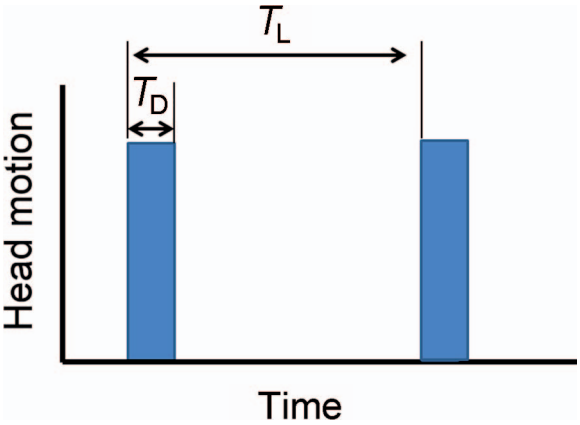


FIGURE 2. Definition of saccade latency, T_L, and duration, T_D. Shaded blue regions indicate intervals during which the bird's head moved. (The width of T_D in relation to T_L is exaggerated on the figure for clarity.)

head motions were estimated at ~1° for videos filmed from the ground and 0.4° for those filmed by the head-camera. The time resolution in the video measurements was 33 ms (due to video frame rate), which is smaller than the reported, measured avian sensorimotor response times of ≥60 ms (Hausmann et al. 2008) and 76 ± 15 ms (mean ± SD; Pomeroy and Heppner 1977). The time intervals between spontaneous eye blinks in goshawks (4.7 ± 0.6 s) and other raptors (range of means: 2.7–5.1 s) are also long in comparison to timescales of interest (Kirsten and Kirsten 1983). Although eye movements could not be measured for the head-camera video, we could see small eye-only saccades that occurred prior to ~6% of head saccades on the ground-camera video; these eye motions do not represent an additional source of gaze redirection because they always were observed to precede head saccades, confirming earlier reports that eye and head saccades in birds are often coupled (Land 2015). As a consequence, visual fixation on video was defined either by a lack of detectable head motion by the bird in ground-based video or by a stabilized image of any duration on the head-mounted video, in accordance with prior studies, as reviewed in Kjærsgaard et al. (2008). Head motion was visible directly on the ground-based video and/or defined on the head-mounted video as image motion not caused by body translation or rotations (i.e. the bird remained in a single location). Head-saccade latency, T_L, was defined as the time between initiations of head motion corresponding to changes in gaze direction, while saccade duration, T_D, was defined as time during which detectable head motion occurred (Figure 2). Head motions of the filmed raptors took several forms. We use the term "head saccade" to describe abrupt head turns resulting in a changed direction of gaze, and "head-bob" to describe motions in which the head was translated by approximately the interocular distance horizontally; head-bobs are presumed to provide depth information via parallax (Kral 2003). Perched raptors performed head-bobs much less often than head-turns, as previously reported (Tucker 2000, O'Rourke et al. 2010b). Furthermore, most head-bobs were performed as part of a single, uninterrupted head-turn–head-bob motion. Measured head-saccade durations (the time during which the head was in motion) for head turning were less than or equal to 2–3 video frames (66–100 ms), so we did not have sufficient time resolution to analyze their distribution. Uncertainties for both the latency and duration measurements were estimated at ±23 ms, determined primarily by the instrumental error introduced by the video frame-capture rate.

Statistical Methods

The measured head-saccade latency distributions were fitted to 4 models: normal, log-normal, Weibull, and normal distribution of reciprocal latency ($1/T_L$) (details and rationale are discussed below). All analysis was conducted in R 3.2.1 (R Development Core Team 2015); all code and datasets required to reproduce these calculations are included in the Supplemental Materials ZIP folder. Parameters for each model were estimated using maximum likelihood. Parameters were estimated independently for each of the 2 scorers' saccade latency and duration datasets, and 3 statistical goodness-of-fit tests (Kolmogorov-Smirnov, Anderson-Darling, and Cramér-von Mises) were performed to determine whether the data were consistent with random variables generated from the distributions.

We considered 3 possible probability distributions here that arise naturally from the hypotheses of decision-making in visual search. In addition, we considered the normal distribution, which would result from models that assume a preferred (possibly optimal) saccade latency or a random-walk model of neural decision-making. The normal distribution for the saccade latency, T_L, is defined as

$$f(T_L;\mu,\sigma) = \frac{1}{\sqrt{2\sigma^2\pi}} e^{-\frac{(T_L-\mu)^2}{2\sigma^2}} \quad (1)$$

where the parameters μ and σ are the mean and standard deviation, respectively. If the probability of head-saccade initiation can be described by a constant rate per unit time, then the distribution of latencies would be a decaying exponential. To test this and other scenarios parameterized by decay rate, we fit to the Weibull distribution:

$$f(T_L;\lambda,k) = \frac{k}{\lambda}\left(\frac{T_L}{\lambda}\right)^{k-1} e^{-(x/\lambda)^k} \quad (2)$$

where λ is the scale parameter and $k > 0$ is the shape parameter that determines decay rate. Exponential decay corresponds to $k = 0$, and $k > 1$ and $k < 1$ to decay rates that increase or decrease, respectively, with latency. For

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 2. Range of *P* values for rejection of the data matching the proposed distribution for 4 potential models for the 2 scorers (bold indicates data consistent with the proposed distribution).

	Perching				Flying
Distribution	Cooper's Hawk (video)	Red-tailed Hawk (video)	Northern Goshawk (video)	Northern Goshawk (head-camera)	Northern Goshawk (head-camera)
Normal	$<2.3 \times 10^{-6}$ 0.003–0.0003	$<3.8 \times 10^{-6}$ $<4.2 \times 10^{-6}$	0.005–0.001 <0.00049	$<1.1 \times 10^{-6}$ 0.0045–0.003	$<2.8 \times 10^{-6}$ 0.007–0.003
Log normal	**0.55–0.28** **0.99–0.95**	**0.20–0.13** **0.26–0.21**	**0.86–0.70** **0.98–0.95**	**0.24–0.091** **0.70–0.49**	**0.25–0.11** **0.13–0.11**
Weibull	0.024–0.007 **0.43–0.28**	0.074–0.046 0.048–0.030	**0.45–0.34** **0.45–0.19**	0.074–0.030 **0.15–0.10**	**0.15–0.060** 0.042–0.037
LATER	$<2.3 \times 10^{-6}$ 0.001–0.0002	$<3 \times 10^{-6}$ 0.002–0.0008	$<3 \times 10^{-6}$ 0.0007–0.0003	$<2 \times 10^{-6}$	$<3 \times 10^{-6}$

decision processes that use a rise-to-threshold multiplicative model, the log-normal distribution is predicted, given by

$$f(T_L;\mu,\sigma) = \frac{1}{T_L\sqrt{2\pi}\sigma} e^{-\frac{(\ln T_L-\mu)^2}{2\sigma^2}} \quad (3)$$

Here the shape and scale parameters μ and σ are related to the mean, *m*, and variance, *v*, by

$$m = e^{\mu+\frac{\sigma^2}{2}} \quad (4)$$

$$v = e^{2\mu+\sigma^2}(e^{\sigma^2}-1) \quad (5)$$

The LATER model of neural decision-making described above predicts that the reciprocal latency, $1/T_L$, should be normally distributed, so that $1/T_L$ replaces T_L in Equation 1. We hereafter refer to this as a "reciprocal normal" distribution.

The goshawk head-camera dataset was also analyzed with analysis of variance (ANOVA) to compare the mean latencies found for different behaviors. Because the distributions were not normal, log-transformation of the latency data was performed and the resulting distributions reviewed. The latter were substantially more normal and, hence, were used when testing for significance with Tukey's HSD method. Approximate 95% confidence intervals on differences of the mean latencies were calculated in the original data space.

RESULTS

Our results for the 3 raptor species studied indicate that their head-saccade distributions most closely follow a log-normal distribution for video filmed from the ground and using a head-camera. Although a few isolated datasets were borderline for rejection of the Weibull distribution for one observer, taken as a whole the data are consistent only with the log-normal distribution, and in all cases the log-normal was the best fit to the data. Table 2 presents results from the statistical analysis of the head-saccade distributions for all 3 species, summarized as the range of *P* values from the 3 goodness-of-fit tests for the rejection of the null hypothesis that the data are distributed according to the statistical distribution under consideration (for full results, see Supplemental Material Table S2). Thus, low *P* values indicate that the data are not consistent with the proposed distribution. Figure 3 shows plots of the probability distributions for head-saccade latency data from video filmed from the ground along with the 3 log-normal, normal, and Weibull models for each species together with fits to the reciprocal normal model for scorer 1. In Figure 4, fits to distributions for the goshawk head-camera data are shown for scorer 1.

The head-camera video was analyzed to determine how head-saccade latencies were distributed for a variety of behaviors not feasibly studied using field video. We were able to analyze 4 different head-camera videos in which the goshawk performed a variety of behaviors: sitting on an elevated perch (a tree, post, or hill) while foraging for prey or watching either a prey animal or the falconer moving around on the ground below, flying after prey, flying with no target in sight, and other behaviors. In each case, the goshawk visually tracked the motion of the object of interest in a well-defined retinal fixation area, using rapid head saccades to keep the object at the same point in the image. Comparison with results from a previous study showed that this retinal fixation area was consistent with the center of the bird's visual field, determined by finding the center of motion in the optical flow field during level flight (Kane et al. 2015). Since the goshawk flies with its head axis aligned with its body axis and forward velocity, this confirmed that the goshawk tracked objects of interest at the center of its visual field, which corresponds to the head and body's forward direction. When the goshawk wearing the head-camera perched on the glove of a walking falconer, it periodically translated its head forward-and-backward, similar to the vision-stabilizing head motions seen in walking pigeons (Kral 2003).

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

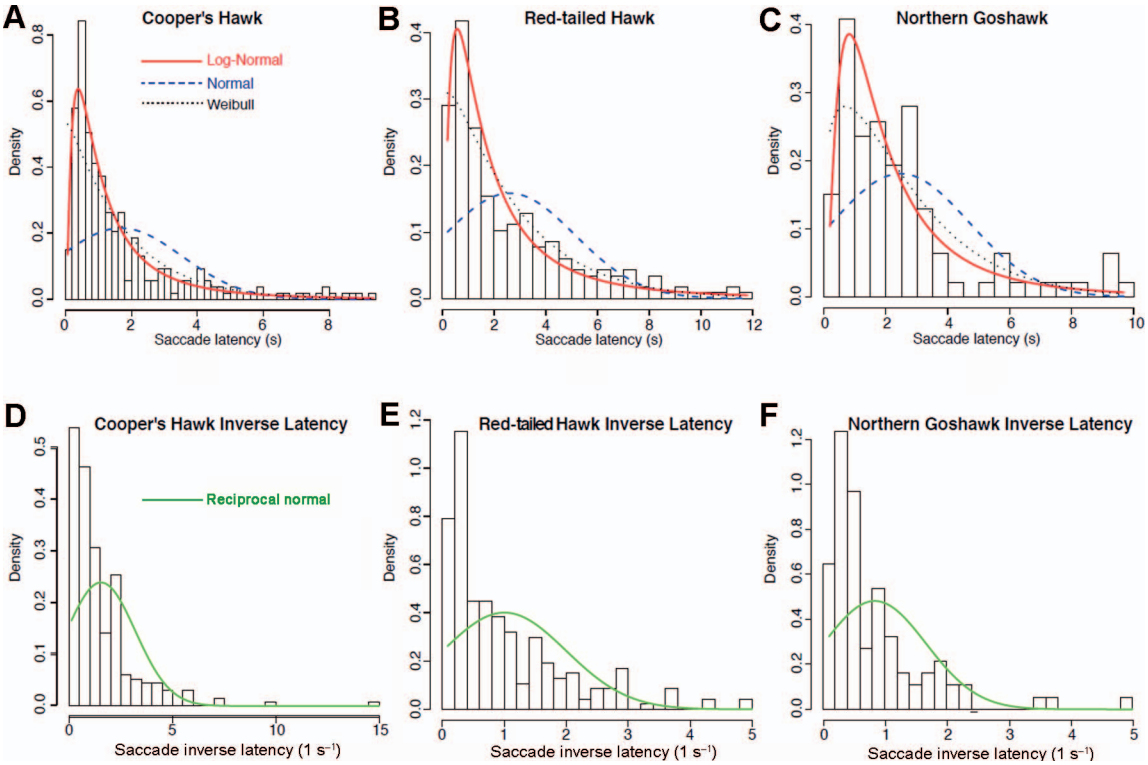


FIGURE 3. Head-saccade latency distribution plots made using videos, recorded from the ground, of perched raptors foraging in the field. (**A**–**C**) Probability densities vs. head-saccade latency data for each species, with best fits to log-normal, normal, and Weibull distributions. (**D**–**F**) The same empirical probability densities plotted vs. reciprocal latency ($1/T_L$) for comparison with the best fits to the reciprocal normal model (solid green line).

The differences in head-saccade latencies between different goshawk behaviors measured using the head-camera (Figure 5) were analyzed with ANOVA, and significance was determined with Tukey's HSD test (Table 3). Significant differences were found between foraging from a perch (dataset A) and these 3 behaviors: sitting on the falconer's glove (dataset B, adjusted $P < 0.001$), flying with no prey in sight (dataset E, adjusted $P < 0.001$), and

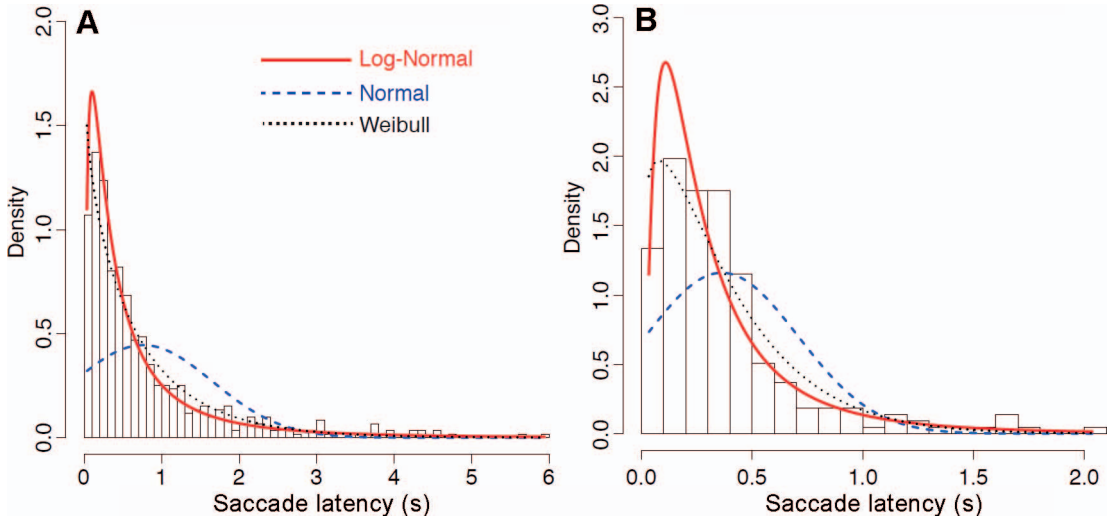


FIGURE 4. Head-saccade latency distribution plots for the Northern Goshawk using head-camera data for (**A**) foraging from a perch with no prey in sight and (**B**) flying with no prey or perch in sight. Probability densities vs. head-saccade latency data (histograms) for the goshawk with best fits to log-normal, normal, and Weibull distributions.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

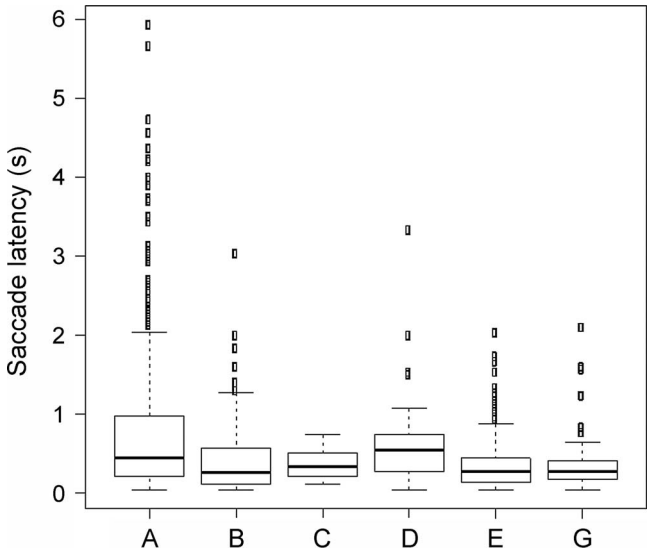


FIGURE 5. Head-saccade latency by behavior for a Northern Goshawk wearing a head-mounted video camera. Black bars denote the median, the box encloses the first and third quartiles, lower whiskers show minimum value, and upper whiskers give a corrected range based on the number of observations, as is standard in R. Open circles show outliers. Letter codes indicate the behaviors (Table 1); category F was omitted here because of a low number of data points.

TABLE 3. Comparison between Northern Goshawk head-camera behaviors (for behavior codes, see Table 1; time in seconds) using ANOVA and Tukey's HSD test (significance based on log-transformed data; $***P < 0.001$, $**P < 0.01$, $*P < 0.05$).

		95% confidence limits		
Behaviors	Difference	Lower	Upper	Significance
B–A	−0.363	−0.533	−0.193	***
C–A	−0.392	−0.818	0.034	
D–A	−0.066	−0.441	0.309	
E–A	−0.396	−0.555	−0.237	***
G–A	−0.424	−0.649	−0.199	**
C–B	−0.029	−0.473	0.415	
D–B	0.297	−0.098	0.693	**
E–B	−0.033	−0.234	0.169	
G–B	−0.061	−0.317	0.196	
D–C	0.326	−0.23	0.882	
E–C	−0.004	−0.444	0.436	
G–C	−0.032	−0.5	0.436	
E–D	−0.33	−0.721	0.061	*
G–D	−0.358	−0.78	0.064	
G–E	−0.028	−0.278	0.222	

pursuing prey in flight (dataset G, adjusted $P < 0.01$) (Figure 5). In addition, significant differences were found between behaviors related to watching the falconer from the perch (dataset D) and sitting on the falconer's glove (dataset B, adjusted $P < 0.01$) and flying with no prey in sight (dataset E, adjusted $P < 0.05$) (Figure 5). In comparisons to foraging from the perch, the 3 identified behaviors exhibited significantly shorter mean latencies, and the perching latencies are right-skewed toward longer latencies with a large number of outliers.

DISCUSSION

Our analysis suggests that the head-saccade latency data for all 3 species of diurnal raptors and all behaviors studied here are consistent with a log-normal distribution, and that they are highly unlikely to have been generated from the other distributions considered. There was no evidence in favor of bimodal distributions, which can be interpreted as indicative of multistage decision-making. Although we did not find agreement between our data and either the random-walk or reciprocal normal (LATER) models used to model human and primate saccade latencies, the log-normal distribution found to best describe the head-saccade latency distributions for raptor species is consistent with a process based on similar underlying mechanisms. This is because the log-normal distribution should apply if the random variables determining the observed latency combine multiplicatively (rather than additively, as in the normal distribution; or as a sum of logarithms, as in the LATER model) to generate the head-saccade initiation signal. These results can be thought of as linking head-movement behavior to prey detection rates, because the sensory inputs that determine the decision signal also, presumably, encode evidence for the probability that prey are present or not.

The fact that the 3 raptor species studied exhibit the same saccade latency distribution is consistent with, but not a proof of, the same underlying neural processes being at work. The parameters in the log-normal distributions for the 2 larger raptor species, the Red-tailed Hawk and goshawk, were not significantly different. Our mean head-saccade latencies are consistent with previously published values for Cooper's Hawks and Red-tailed Hawks (O'Rourke et al. 2010b). The smaller Cooper's Hawk made more frequent saccades, on average, than either of the 2 larger raptors (mean = 1.68 s, 2.61 s, and 2.47 s for Cooper's Hawk, Red-tailed Hawk, and goshawk, respectively). While the Red-tailed Hawk and goshawk are similar in mass, and their visual systems share many similar features, the hunting behavior and maneuverability of the 2 accipiters are more similar to each other than to that of the Red-tailed Hawk. Thus, saccade latency distributions alone are not predictive of foraging and hunting behavior. In the case of data gathered from the goshawk with the head-camera, we found that some behaviors differ significantly in mean saccade latency based on ANOVA analysis. Analysis of the saccade distribution for the goshawk in flight and perching confirmed this. The goshawk wearing a

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

head-camera moved its head more frequently, with fewer long-latency outliers, when in motion than when foraging from a perch (i.e. actively searching for prey); this is consistent with the presumed need of the bird to scan its environment more quickly as its speed increases.

The shapes of our distributions agree with the general shape of head-saccade latency distributions previously reported for Domestic Chickens (Pratt 1982) and Barn Owls (Hausmann et al. 2008, Ohayon et al. 2008), as well as with eye-saccade data for the Little Eagle and Tawny Frogmouth (Wallman and Pettigrew 1985). To analyze the means and variances of diurnal raptor head-saccade frequency distributions, O'Rourke et al. (2010b) reported using a log $(x + 1)$ transform to meet normality assumptions, which is also consistent with our log-normal distributions.

We surveyed the literature for studies of visual search that measured the time during which predatory birds using pause-travel foraging paused to scan their locality visually. These studies considered motions other than saccades that resulted in a change of visual scene and assumed that such birds primarily search for prey in between such moves (Tye 1989), in part to avoid motion blur (Kramer and McLaughlin 2001). These measures of time spent visually scanning the environment have been called, variously, pause times or search times. If a similar decision-making process governs the timing of scene shifts during pause-travel foraging in general, then we would expect the distributions of pause times to agree with those found for head-saccade latencies in our study. Two studies have noted the resemblance between the log-normal distribution and the probability distributions found for the pause times of various bird species foraging for insect prey, including Northern Wheatears (*Oenanthe oenanthe*) and Stonechats (*Saxicola torquata*; Moreno 1984) and tyrant flycatchers (Aves: Tyrannidae; Fitzpatrick 1981); similar right-skewed distributions of foraging pause times were also noted for thrushes (Smith 1974), Spotted Flycatchers (*Muscicapa striata*; Davies 1977), and goshawks (Kenward 1982). This similarity between multiple sets of data related to visual searches during foraging is especially striking because the study species differ in size, hunting habitat, and time-scale between moves. In a different context, studies of antipredator vigilance by foraging birds have examined the tradeoff between random and periodic intervals spent scanning their environment visually in the context of different predator tactics (Bednekoff and Lima 2002). We do not consider antipredator vigilance behavior here, however, because it should be influenced by factors not relevant for predators, such as the need to forage in between bouts of vigilance (Beauchamp and Ruxton 2016) or the wider range of eye motion found in many prey birds (Tyrrell et al. 2014).

Foraging predatory birds must balance competing needs: They must react to environmental stimuli that require rapid, urgent decisions (e.g., when to launch an attack on a prey animal, which could use the predator's head motion to detect its presence, allowing the animal to flee or find cover) as well as more deliberate ones (e.g., absent evidence of prey, deciding when to search a new part of its environment). Unlike models that have assumed an average pause time or a fixed search rate, a stochastic decision-making strategy based on accumulating sensory inputs allows a balance between these multiple constraints without providing prey with predictable feedback. Our measured log-normal distributions don't agree with visual search models that assume an optimal pause time, because these imply a hard cutoff at long times; they also don't agree with models that posit a fixed interval of time during which birds assess their new visual scene before starting to search actively (Fitzpatrick 1981), because the latter predict a distribution truncated at short times, at a value longer than typical avian sensorimotor response times. If saccades were initiated with a constant probability per unit time, then one would expect their distribution to decay exponentially, again in contradiction to the observed distributions.

Our study methods were limited in several ways compared to those used to study eye saccades in humans. In the present study, head-camera data were collected only for the goshawk, although in the future the development of smaller and more streamlined cameras should allow their use in a wider context. Eye-tracking techniques used successfully in other bird species would prove useful for measuring both head and eye motions. Modern saccadometers enable extremely high statistics (of order 10^4 saccades per trial per subject), whereas low yield and difficulties in obtaining field data limited the number of saccades studied here. We were also unable to record angular motion or to resolve the distribution of durations. Now that high-speed video and stereometric three-dimensional video are becoming more feasible in field settings (Theriault et al. 2014), these limitations should be resolvable in future studies. On the other hand, combining archived video recordings with head-mounted video offers the advantage of sampling a fuller behavioral and environmental context of the visual search (flying vs. perched, searching vs. fixing on and pursuing prey, etc.) than would be allowed by ground-based data alone. This provides information complementary to the rich datasets that are becoming available through the use of other biologging sensors (e.g., acceleration and depth; Watanabe and Takahashi 2013) and allows validation of these techniques in certain circumstances (e.g., one can omit from analysis sequences where the birds are preening, which accelerometers would record as motion.)

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Studies that integrate measurements of locomotion with vision during foraging and hunting promise a deeper understanding of how animals search efficiently and target their prey (Ben-Simon et al. 2012, Gabay et al. 2013). More generally, understanding the head motions made by birds and other animals during visual searches offers insights into how widely distributed different decision-making mechanisms may be across vertebrate taxa with different sensorimotor processes—and, hence, how widely conserved they are throughout evolutionary history.

ACKNOWLEDGMENTS

We thank R. Musters for designing the falconry hood for the head-camera video and for flying Shinta the goshawk wearing the head-camera, and A. H. Fulton and L. Rosenthal for assisting with preliminary data analyses of the head-camera data.

Funding statement: M.F.O. was partially supported by the National Institutes of Health (R01 LM011000). S.A.K. received funding from the Marian E. Koshland Integrated Natural Sciences Center and Haverford College.

Ethics statement: All fieldwork was conducted in accordance with the rules and regulations of the Haverford College Institutional Animal Care and Use Committee (protocol sa050411) and the animal welfare standards for wildlife research outlined in Paul et al. (2016).

Author contributions: S.A.K., M.F.O., and M.Z. conceived of the study design and hypotheses. S.A.K. conceived the data collection methods. M.F.O. designed and supervised the statistical analysis. All authors were involved in the data analysis. S.A.K. and M.F.O. wrote the paper.

LITERATURE CITED

Alpern, S., R. Fokkink, M. Timmer, and J. Casas (2011). Ambush frequency should increase over time during optimal predator search for prey. Journal of the Royal Society Interface 8:1665–1672.

Anderson, J. P., D. W. Stephens, and S. R. Dunbar (1997). Saltatory search: A theoretical analysis. Behavioral Ecology 8: 307–317.

Andersson, M., J. Wallander, and D. Isaksson (2009). Predator perches: A visual search perspective. Functional Ecology 23: 373–379.

Beauchamp, G., and G. D. Ruxton (2012). Changes in antipredator vigilance over time caused by a war of attrition between predator and prey. Behavioral Ecology 23:265–270.

Beauchamp, G., and G. D. Ruxton (2016). Modeling scan and interscan durations in antipredator vigilance. Journal of Theoretical Biology 390:86–96.

Bednekoff, P. A., and S. L. Lima (2002). Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. Journal of Avian Biology 33:143–149.

Ben-Simon, A., O. Ben-Shahar, G. Vasserman, and R. Segev (2012). Predictive saccade in the absence of smooth pursuit: Interception of moving targets in the archer fish. Journal of Experimental Biology 215:4248–4254.

Buck, L. (2013). Goshawk BM8E—goshawk close up on head real time. [Video.] Birds in Slow Motion, Newtownmountkennedy, Ireland. http://birdsinslowmotion.com/goshawk/

Carpenter, R. H. S. (1999). A neural mechanism that randomises behaviour. Journal of Consciousness Studies 6:13–22.

Carpenter, R. H. S. (2012). Analysing the detail of saccadic reaction time distributions. Biocybernetics and Biomedical Engineering 32:49–63.

Carpenter, R. H. S., and M. L. L. Williams (1995). Neural computation of log likelihood in control of saccadic eye movements. Nature 377:59–62.

Curtis, O. E., R. N. Rosenfield, and J. Bielefeldt (2006). Cooper's Hawk (*Accipiter cooperii*). In Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/075

Davidson, G. L., S. Butler, E. Fernández-Juricic, A. Thornton, and N. S. Clayton (2014). Gaze sensitivity: Function and mechanisms from sensory and cognitive perspectives. Animal Behaviour 87:3–15.

Davies, N. B. (1977). Prey selection and the search strategy of the Spotted Flycatcher (*Muscicapa striata*): A field study on optimal foraging. Animal Behaviour 25:1016–1033.

Feng, G. (2006). Eye movements as time-series random variables: A stochastic model of eye movement control in reading. Cognitive Systems Research 7:70–95.

Fernández-Juricic, E. (2012). Sensory basis of vigilance behavior in birds: Synthesis and future prospects. Behavioural Processes 89:143–152.

Fite, K. V., and S. Rosenfield-Wessels (1975). A comparative study of deep avian foveas. Brain, Behavior and Evolution 12:97–115.

Fitzpatrick, J. W. (1981). Search strategies of tyrant flycatchers. Animal Behaviour 29:810–821.

Gabay, S., T. Leibovich, A. Ben-Simon, A. Henik, and R. Segev (2013). Inhibition of return in the archer fish. Nature Communications 4:1657.

Gall, M. D., and E. Fernández-Juricic (2010). Visual fields, eye movements, and scanning behavior of a sit-and-wait predator, the Black Phoebe (*Sayornis nigricans*). Journal of Comparative Physiology A 196:15–22.

Giudice, J. H., and J. T. Ratti (2001). Ring-necked Pheasant (*Phasianus colchicus*). In Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/572

Gold, J. I., and M. N. Shadlen (2001). Neural computations that underlie decisions about sensory stimuli. Trends in Cognitive Sciences 5:10–16.

Gorea, A., D. Rider, and Q. Yang (2014). A unified comparison of stimulus-driven, endogenous mandatory and 'free choice' saccades. PLoS ONE 9:e88990.

Hall, M. I., and C. F. Ross (2007). Eye shape and activity pattern in birds. Journal of Zoology 271:437–444.

Harmening, W. M., J. Orlowski, O. Ben-Shahar, and H. Wagner (2011). Overt attention toward oriented objects in free-viewing Barn Owls. Proceedings of the National Academy of Sciences USA 108:8461–8466.

Hausmann, L., D. T. T. Plachta, M. Singheiser, S. Brill, and H. Wagner (2008). In-flight corrections in free-flying Barn Owls (*Tyto alba*) during sound localization tasks. Journal of Experimental Biology 211:2976–2988.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Hein, A. M., and S. A. McKinley (2013). Sensory information and encounter rates of interacting species. PLoS Computational Biology 9:e1003178.

Jones, M. P., K. E. Pierce, Jr., and D. Ward (2007). Avian vision: A review of form and function with special consideration to birds of prey. Journal of Exotic Pet Medicine 16:69–87.

Kane, S. A., A. H. Fulton, and L. Rosenthal (2015). When hawks attack: Animal-borne video studies of goshawk pursuit and prey-evasion strategies. Journal of Experimental Biology 218: 212–222.

Kane, S. A., and M. Zamani (2014). Falcons pursue prey using visual motion cues: New perspectives from animal-borne cameras. Journal of Experimental Biology 217:225–234.

Kenward, R. E. (1978). Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. Journal of Animal Ecology 47:449–460.

Kenward, R. E. (1982). Goshawk hunting behaviour, and range size as a function of food and habitat availability. Journal of Animal Ecology 51:69–80.

Kenward, R. [E.] (2006). The Goshawk. T & AD Poyser, Oxford, UK.

Kirsten, S. J., and E. B. Kirsten (1983). Spontaneous blink rates of birds. The Condor 85:92–93.

Kjærsgaard, A., C. Pertoldi, V. Loeschcke, and D. W. Hansen (2008). Tracking the gaze of birds. Journal of Avian Biology 39:466–469.

Kral, K. (2003). Behavioural–analytical studies of the role of head movements in depth perception in insects, birds and mammals. Behavioural Processes 64:1–12.

Kramer, D. L., and R. L. McLaughlin (2001). The behavioral ecology of intermittent locomotion. American Zoologist 41: 137–153.

Land, M. F. (1999a). Motion and vision: Why animals move their eyes. Journal of Comparative Physiology A 185:341–352.

Land, M. F. (1999b). The roles of head movements in the search and capture strategy of a tern (Aves, Laridae). Journal of Comparative Physiology A 184:265–272.

Land, M. F. (2015). Eye movements of vertebrates and their relation to eye form and function. Journal of Comparative Physiology A 201:195–214.

Land, M. F., and D. E. Nilsson (2012). Animal Eyes. Oxford University Press, Oxford, UK.

Martin, G. R., and G. Katzir (1999). Visual fields in Short-toed Eagles, *Circaetus gallicus* (Accipitridae), and the function of binocularity in birds. Brain, Behavior & Evolution 53:55–66.

Martinez-Conde, S., and S. L. Macknik (2008). Fixational eye movements across vertebrates: Comparative dynamics, physiology, and perception. Journal of Vision 8:28.

Moreno, J. (1984). Search strategies of wheatears (*Oenanthe oenanthe*) and stonechats (*Saxicola torquata*): Adaptive variation in perch height, search time, sally distance and inter-perch move length. Journal of Animal Ecology 53:147–159.

Nakahara, H., K. Nakamura, and O. Hikosaka (2006). Extended LATER model can account for trial-by-trial variability of both pre- and post-processes. Neural Networks 19:1027–1046.

Ohayon, S., W. Harmening, H. Wagner, and E. Rivlin (2008). Through a Barn Owl's eyes: Interactions between scene content and visual attention. Biological Cybernetics 98:115–132.

O'Rourke, C. T., M. I. Hall, T. Pitlik, and E. Fernández-Juricic (2010a). Hawk eyes I: Diurnal raptors differ in visual fields and degree of eye movement. PLoS ONE 5:e12802.

O'Rourke, C. T., T. Pitlik, M. Hoover, and E. Fernández-Juricic (2010b). Hawk eyes II: Diurnal raptors differ in head movement strategies when scanning from perches. PLoS ONE 5:e12169.

Paul, E., R. S. Sikes, S. J. Beaupre, and J. C. Wingfield (2016). Animal welfare policy: Implementation in the context of wildlife research—policy review and discussion of fundamental issues. ILAR Journal 56:312–334.

Pettigrew, J. D., J. Wallman, and C. F. Wildsoet (1990). Saccadic oscillations facilitate ocular perfusion from the avian pecten. Nature 343:362–363.

Pomeroy, H., and F. Heppner (1977). Laboratory determination of startle reaction time of the starling (*Sturnus vulgaris*). Animal Behaviour 25:720–725.

Pratt, D. W. (1982). Saccadic eye movements are coordinated with head movements in walking chickens. Journal of Experimental Biology 97:217–223.

Preston, C. R., and R. D. Beane (2009). Red-tailed Hawk (*Buteo jamaicensis*). In Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/052

R Development Core Team (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rhodes, T., C. T. Kello, and B. Kerster (2014). Intrinsic and extrinsic contributions to heavy tails in visual foraging. Visual Cognition 22:809–842.

Rutz, C., and J. Troscianko (2013). Programmable, miniature video-loggers for deployment on wild birds and other wildlife. Methods in Ecology and Evolution 4:114–122.

Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longair, T. Pietzsch, S. Preibisch, C. Rueden, S. Saalfeld, B. Schmid, J. Y. Tinevez, et al. (2012). Fiji: An open-source platform for biological-image analysis. Nature Methods 9:676–682.

Schwarz, J. S., D. Sridharan, and E. I. Knudsen (2013). Magnetic tracking of eye position in freely behaving chickens. Frontiers in Systems Neuroscience 7:91.

Smith, J. N. M. (1974). Food searching behaviour of two European thrushes. I. Description and analysis of search paths. Behaviour 48:276–302.

Squires, J. R., and R. T. Reynolds (1997). Northern Goshawk (*Accipiter gentilis*). In Birds of North America Online (A. Poole, Editor). Cornell Laboratory of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/298

Stephens, D. W., and J. R. Krebs (1986). Foraging Theory. Princeton University Press, Princeton, NJ, USA.

Theriault, D. H., N. W. Fuller, B. E. Jackson, E. Bluhm, D. Evangelista, Z. Wu, M. Betke, and T. L. Hedrick (2014). A protocol and calibration method for accurate multi-camera field videography. Journal of Experimental Biology 217:1843–1848.

Tislerics, A. (2000). *Oryctolagus cuniculus:* European rabbit. In Animal Diversity Web. University of Michigan Museum of Zoology. http://animaldiversity.org/accounts/Oryctolagus_cuniculus/

Tomé, R., M. P. Dias, A. C. Chumbinho, and C. Bloise (2011). Influence of perch height and vegetation structure on the foraging behaviour of Little Owls *Athene noctua*: How to

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

achieve the same success in two distinct habitats. Ardea 99: 17–26.

Tucker, V. A. (2000). The deep fovea, sideways vision and spiral flight paths in raptors. Journal of Experimental Biology 203: 3745–3754.

Tucker, V. A., A. E. Tucker, K. Akers, and J. H. Enderson (2000). Curved flight paths and sideways vision in Peregrine Falcons (*Falco peregrinus*). Journal of Experimental Biology 203:3755–3763.

Tye, A. (1989). A model of search behaviour for the Northern Wheatear *Oenanthe oenanthe* (Aves, Turdidae) and other pause-travel predators. Ethology 83:1–18.

Tyrrell, L. P., S. R. Butler, and E. Fernández-Juricic (2015). Oculomotor strategy of an avian ground forager: Tilted and weakly yoked eye saccades. Journal of Experimental Biology 218:2651–2657.

Tyrrell, L. P., S. R. Butler, J. L. Yorzinski, and E. Fernández-Juricic (2014). A novel system for bi-ocular eye-tracking in vertebrates with laterally placed eyes. Methods in Ecology and Evolution 5:1070–1077.

Vanillakirsky (2015). Adult Cooper's Hawk. Wikimedia Commons.

Wallman, J., and J.-C. Letelier (1993). Eye movements, head movements, and gaze stabilization. In Vision, Brain, and Behavior in Birds (H. P. Zeigler and H.-J. Bischof, Editors). MIT Press, Cambridge, MA, USA. pp. 245–263.

Wallman, J., and J. D. Pettigrew (1985). Conjugate and disjunctive saccades in two avian species with contrasting oculomotor strategies. Journal of Neuroscience 5:1418–1428.

Warrick, D. R., M. W. Bundle, and K. P. Dial (2002). Bird maneuvering flight: Blurred bodies, clear heads. Integrative and Comparative Biology 42:141–148.

Watanabe, Y. Y., and A. Takahashi (2013). Linking animal-borne video to accelerometers reveals prey capture variability. Proceedings of the National Academy of Sciences USA 110: 2199–2204.

Yorzinski, J. L., G. L. Patricelli, J. S. Babcock, J. M. Pearson, and M. L. Platt (2013). Through their eyes: Selective attention in peahens during courtship. Journal of Experimental Biology 216:3035–3046.

Yorzinski, J. L., G. L. Patricelli, M. L. Platt, and M. F. Land (2015). Eye and head movements shape gaze shifts in Indian Peafowl. Journal of Experimental Biology 218:3771–3776.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use