

A Bat Hawk *Macheiramphus alcinus* pair preyed primarily on bats and birds that forage in clutter-edge and open-air habitat groups

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This study aimed to analyse the diet of a pair of Bat Hawks *Macheiramphus alcinus*, based on regurgitated pellets, and the associated habitat-foraging groups the prey species belonged to. Nine-hundred-and-eight regurgitated pellets were collected from underneath one nest tree over a 12-month period. A total of 26 prey species were identified, of which 17 comprised bats and nine birds. Seven prey species qualified as common in the diet (≥ 11 individuals) and included *Pipistrellus hesperidus*, *Tadarida aegyptiaca*, *Scotophilus dinganii*, *Zosterops virens*, *Chaerephon pumilus*, *Afronycteris nana* and *Laephotis capensis*. The majority of prey individuals were clutter-edge foragers (birds 41 individuals, bats 181 individuals). Bat Hawks therefore foraged predominantly adjacent to vegetation. Future studies should examine the environmental factors that drive the abundance of insects in these habitats and the foraging techniques that bats and birds employ to prey upon them, to ultimately increase our understanding of the foraging framework the flying Bat Hawks exploit when hunting these flying animals.

Keywords: Diet, obligate predator, edge, open air, species richness, common species.

Introduction

Each prey community exhibits a unique spatial interaction with the ecosystem that it occupies (Pla *et al.* 2011). Moreover, due to shared morphological characteristics and foraging traits, prey species often inhabit the same foraging domain (Blaum *et al.* 2011). Therefore, such a prey community can provide a foraging framework for predators as the latter can select and focus on the attributes unique to that prey community (Risser *et al.* 1984; Blaum *et al.* 2011). The prey of insectivorous bats provides such an example as these invertebrates either forage in the open air, on edges, or within vegetation. They are followed by the bats and, as hypothesised, the bat predators (Schnitzler & Kalko, 2001, Monadjem *et al.* 2020).

Worldwide, the only bird that predominantly and routinely preys on bats is the Bat Hawk *Macheiramphus alcinus* (Fenton *et al.* 1977; Harris *et al.* 1990). To be able to catch multiple bats in a single foraging bout, especially under poor light conditions, this raptor has evolved several specialised morphological and behavioural adaptations such as large eyes, high-speed flying, echolocation and an enlarged gape (Eccles *et al.* 1969; Pulliam 1974; Black *et al.* 1979; Hartley and Hustler 1993; Hustler and Dean 2005; Jones *et al.* 2012; Mikula *et al.* 2016).

The Bat Hawk feeds primarily on small, insectivorous bats; avoiding larger bats weighing more than 30 g (Fenton *et al.* 1977; Black *et al.* 1979; Hustler and Dean 2005). The Bat Hawk also feeds on smaller (< 50 g) birds such as bushlarks, cisticolas, estrildid finches, flycatchers, hirundines, sunbirds, swifts, martins, nightjars and weavers, which it typically swallows whole and, on the wing, (Hustler and Dean 2005; BirdLife International 2016; Goodman *et al.* 2016). This raptor may occasionally take larger birds (≥ 50 g), e.g., buttonquails, cuckoos, doves, hoopoes and starlings. The 624 g Bat Hawk fulfils its energetic requirements by hunting mainly during dawn and dusk, chiefly from 17h00 to 20h00 and again from 04h00 to 06h00 (Bozinovic and Medel 1988; Harris *et al.* 2000; Hustler and Dean 2005, Sergio and Hiraldo 2008).

The main echolocation constraint that flying insectivorous bats face is clutter (or vegetation structure) as it provides obstacles they must detect and avoid (Aldridge & Rautenbach 1987; Fenton 1990). Bats therefore adapt their flight morphology and echolocation systems to the habitat structure in which they forage (Roemer *et al.* 2019). Sympatric bats can accordingly be classified in three forage-habitat groups based on their wing design and echolocation call, and the foraging terrain of the insects (Schnitzler and

Kalko 2001; Schoeman & Jacobs 2011; Maas et al. 2016). The open-air foraging bats are fast and agile flyers feeding exclusively on aerial prey high above the ground (Monadjem et al. 2022). Clutter-edge foragers hunt bats that glean insect prey from vegetation, such as forest edges and gaps. The clutter foragers are slow, manoeuvrable flyers and search for prey close to vegetation and on the ground.

In this study we examined the diet of a pair of Bat Hawks based on pellets that was collected over a period of two years. Our first objective was to investigate which bird and bat prey they hunted, and particularly the number of individuals they caught of each species. The second objective was to examine to which habitat-foraging group the majority of prey species and individuals belonged. We investigated if there is a link between the Bat Hawks and the foraging traits of their dominant prey.

Fieldwork and Methods

An active Bat Hawk nest was discovered in the Agatha Forest Reserve, which is located 9.5 km southwest of the town of Tzaneen (23°49'S; 30°10'E; 1 083 m.a.s.l.), South Africa. The nest was located in a *Eucalyptus* tree in a free-growing *Eucalyptus* stand surrounded by a patchwork quilt of *Eucalyptus* stands, avocado (*Persea*) orchards, storage dams, public roads, farmhouses and outbuildings.

We collected Bat Hawks pellets over a 24-month period (May 1987 - April 1989). During this period, pellets were collected monthly, except during July and August of 1987 and January and February of both 1988 and 1989, when pellets were collected bimonthly. This collection also included the pellets regurgitated before the onset of the collection (May 1987). All pellets were gathered from within a 5 m radius of the base of the nest tree, and 908 regurgitated pellets were accumulated. The study pair bred at least once during the collection period; therefore, the pellets represent the diet of at least the roosting adults or breeding pair, and most likely one fledgling.

Upon collection, each pellet was labelled, placed in water, air-dried (for three weeks) and the macroscopic remains (bone and insect material) detected. The insect remains collected were too small and fragmented to be identified. Skeletal remains were facilitated by comparing remains with bones, teeth and mandible samples of avian and mammalian specimens from the collections of the Ditsong Museum of Natural History (Tshwane). For future reference, this entire pellet collection is stored at this Museum.

We separated the bird and bats remains. Thereafter the individual prey items from the pellets were identified to the lowest possible taxon. For each prey species identified, we calculated the minimum number of individuals in the diet by counting the number of unique bilateral elements of bones, teeth, and mandibles extracted from the pellets (Malan and Crowe 1996; Goodman et al. 2016). This approach allowed a calculation of the relative contribution of bat and bird prey in numbers of each prey taxon to the total diet of the Bat Hawks.

Since we only sampled the diet of a single pair of Bat Hawks, the results may not be representative of the prey selection by this species from the north-eastern region of South Africa. However, because our pellet collection of > 900 regurgitated pellets was collected over 24 months, we assumed that prey selection was representative of this pair's diet. The birds presumably hunted over a sizeable area as the study nest was located 14.5 km from its nearest neighbours (Engelbrecht 2015).

Bat and bird forage-habitat groups were characterised as follows: 1) open-air foragers that hunt prey above the canopy of vegetation; 2) clutter-edge foragers that capture prey on the clutter edges; 3) clutter foragers that obtain prey in dense vegetation such as the interior of forests, and 4) ground foragers that inhabit open vegetation (Schnitzler and Kalko 2001; Hockey et al. 2005; Monadjem et al. 2020).

The common species were identified as those species that contributed ≥ 11 individuals to the diet. Common species were thus prey that were frequently recorded in the diet, based on its overall presence in the sample (Gaston and Fuller 2008).

Results

Of the 37 prey taxa identified, 26 were recognised to species level, six to genus, four to family, and one to sub-order level (Table 1). Of the 37 taxa identified, 12 were from Aves and 25 from Mammalia. Of the 26 species identified, nine were birds and 17 were bats.

Numerically, the 25 Mammalia taxa contributed 433 individuals (88% of all individuals) and the 12 Aves taxa, 61 individuals (12%). The 17 bat species contributed 262 individuals (84%) and the nine bird species, 51 individuals (16%) (Table 1).

Table 1: Regurgitated pellets were collected over a 2-month period from below one Bat Hawk nest and the minimum number of prey individuals in the diet calculated from prey remains identified from bone, tooth and mandible fragments. All individual prey items were identified to the lowest possible taxon, but individual prey items that could not be identified to species level were recorded as Present (P). Bat and bird forage-habitat groups were characterised as open-air foragers, clutter-edge foragers, clutter foragers and ground foragers. Common species (≥ 11 individuals) are underlined

Taxa	Forage-habitat group	Minimum number of individuals	% Minimum number of individuals
AVES			
Turnicidae			
<i>Turnix sylvatica</i> (Kurrichane Buttonquail)	Ground	5	1.6
Apodidae			
<i>Apus</i> * (swifts)		P	
<i>Apus affinis</i> (Little Swift)	Open-air	1	0.3
<i>Cypsiurus parvus</i> (African Palm Swift)	Open-air	3	1.0
Hirundinidae* (swallows and martins)		P	
<i>Psaldoprocne holomelas</i> (Black Saw-wing)	Open-air	1	0.3
Platysteiridae			
<i>Batis capensis</i> (Cape Batis)	Cutter-edge	9	2.9
Fringillidae			
<i>Crithagra gularis</i> (Streaky-headed Seedeater)	Cutter-edge	2	0.6
Emberizidae			
<i>Emberiza tahapisi</i> (Cinnamon-breasted Bunting)	Cutter-edge	1	0.3
Monarchidae			
<i>Terpsiphone viridis</i> (African Paradise Flycatcher)	Cutter-edge	1	0.3
Zosteropidae			
<i>Zosterops virens</i> ** (Cape White-eye)	Cutter-edge	<u>28</u>	8.9
Columbidae* (pigeons and doves)		P	
Subtotal birds		51	16
MAMMALIA			
Rhinolophidae			
<i>Rhinolophus</i> * (horseshoe bats)		P	
<i>Rhinolophus darlingi</i> (Darling's Horseshoe Bat)	Clutter	1	0.3
<i>Rhinolophus simulator</i> (Bushveld Horseshoe Bat)	Clutter	1	0.3
Emballonuridae			
<i>Taphozous mauritanus</i> (Mauritian Tomb Bat)	Open-air	6	1.9
Molossidae*		P	
<i>Chaerephon pumilus</i> (Little Free-tailed Bat)	Open-air	<u>26</u>	8.3
<i>Mops condylurus</i> (Angolan Free-tailed Bat)	Open-air	2	0.6
<i>Mops midas</i> (Midas Free-tailed Bat)	Open-air	2	0.6
<i>Tadarida</i> * (free-tailed bats)		P	
<i>Tadarida aegyptiaca</i> (Egyptian Free-tailed Bat)	Open-air	<u>42</u>	13.4
Miniopteridae			
<i>Miniopterus natalensis</i> (Natal Long-fingered Bat)	Cutter-edge	1	0.3
Vespertilionidae*		P	
<i>Myotis</i> * (Myotis)		P	
<i>Myotis tricolor</i> (Temminck's Myotis)	Cutter-edge	2	0.6
<i>Laephotis capensis</i> (Cape Serotine)	Cutter-edge	<u>11</u>	3.5
<i>Afronycteris nana</i> (Banana Bat)	Cutter-edge	<u>17</u>	5.4
<i>Neoromicia zuluensis</i> (Zulu Serotine)	Cutter-edge	1	0.3
<i>Nycteris thebaica</i> (Egyptian Slit-faced Bat)	Clutter	1	0.3
<i>Nycticeinops schlieffeni</i> (Schlieffen's Twilight Bat)	Cutter-edge	7	2.2
<i>Pipistrellus</i> * (Pipistrelles)		P	
<i>Pipistrellus hesperidus</i> (Dusky Pipistrelle)	Cutter-edge	<u>91</u>	29.1
<i>Pipistrellus rusticus</i> (Rusty Pipistrelle)	Cutter-edge	10	3.2
<i>Scotophilus</i> * (house bats)		P	
<i>Scotophilus dinganii</i> (Yellow-bellied House Bat)	Cutter-edge	<u>41</u>	13.1
Unidentified insect-eating bats*		P	
Subtotal bats		262	84
Grand total		313	100

*taxa not included in abundance and biomass analyses as species could not be identified

**Thompson and Taylor 2014

Of the nine bird species found in the diet, one species of ground forager contributed 10% to the diet, and three species of open-air foragers contributed 10% to the diet, whereas five species of clutter-edge bats contributed 80% to the diet (Table 1). Of the 17 bat species found in the diet, three species of clutter foragers contributed 1% to the diet, and nine species of clutter-edge foragers contributed 69% to the diet, whereas five species of open-air foragers contributed 30% to the diet.

Seven prey species qualified as common in the diet, and included *Pipistrellus hesperidus*, followed by *Tadarida aegyptiaca*, *Scotophilus dinganii*, *Zosterops virens*, *Chaerephon pumilus*, *Afronycteris nana* and *Laephotis capensis* (Table 1). Of these common species, six were bats and one a bird, and five were clutter-edge foragers and two open-air foragers.

Of the eight taxa not identified to species, five could be identified to genus level including *Rhinolophus* a clutter forager, *Myotis*, *Pipistrellus* and *Scotophilus* as clutter-edge foragers, and *Tadarida* an open-air forager.

Discussion

This study revealed that, in time, the study pair of Bat Hawks caught mostly bats, but the diet included two bird-prey taxa which were unexpected. The hawks caught one ground foraging species, *Turnix sylvatica*, which tend to be sedentary and reluctant to fly (Hockey et al. 2005). However, they migrate at night (Herholdt 2001) and during this period most likely fall prey to the Bat Hawks. Comparatively in Madagascar, Bat Hawks caught four ground-living species, of which *Turnix nigricollis*, a ground-foraging buttonquail, was one (Goodman et al. 2016).

Zosterops virens was the dominant bird caught, and during the day, occasionally sally from a perch to capture flying insects (Smith 2005; Thompson and Taylor 2014). However, before dawn pairs or small parties of this species are known to gather in large trees before starting to forage (Eccles et al. 1969; Black et al. 1979; Smith and Bowie 2005). It is likely that during this period that these small birds were susceptible to predation by hunting Bat Hawks. It is not known if *B. capensis* also gather in groups during the daybreak period.

In terms of space, clutter-foraging bats were almost absent from the diet. *Nycteris thebaica*, *Rhinolophus darlingi* and *Rhinolophus simulator* are largely confined to dense vegetation, and only occasionally transverse open-air (Monadjem et al. 2020).

Open-air foraging Bat Hawks habitually hunt over grasslands, water bodies, forests and plantations (Brown and Amadon 1968; Monadjem et al. 2020) which were abundant in the birds' territory. However, in this study, they caught far less open-air foragers than clutter-edge foragers. In a comparison between the proportions of open-air versus clutter-edge foragers caught, the clutter-edge foragers outnumbered the open-air foragers for species caught. Of the bats and birds caught, for clutter-edge foragers a total 14 species and 222 individuals were caught, whereas for open-air foragers 8 species and 83 individuals were caught.

Although open-air foraging bats are fast and agile fliers (Noer et al. 2012), and a wing-hunting Bat Hawk can attain considerable open-air flight speeds (44 m.s^{-1} ; McCracken et al. 2016) and flight heights ($\leq 600 \text{ m}$ above ground; Fenton and Griffin 1997), we do not have information as to how the open-air flying speed of the Bat Hawks compare to that of the open-air foraging bats. In addition, swallows and swifts are regularly cited as prey of the Bat Hawk (Steyn 1982; Hustler and Dean 2005; Global Raptor Information Network 2021), but in this study, only five individuals of these open-air foraging birds were caught (*Apus affinis*, *Cypsiurus parvus*, *Psalidoprocne holomelas*).

Clutter-edge bats display intermediate manoeuvrability and fly comparatively slow when flying close to dense vegetation (Monadjem et al. 2020). It is therefore perhaps no surprise that nine clutter-edge bat species were caught in relatively large numbers (181 individuals: 69% of bats). The clutter edges of particularly *Eucalyptus* stands and avocado orchards were abundant in the hawks' territory, and may provide some, as yet undetected, cover benefit to the hunting Bat Hawks (Kenward 1982).

Despite sampling the diet of only one Bat hawk pair, this study produced one useful observation result. It showed that these Bat Hawks foraged predominantly adjacent to vegetation. We demonstrated a link between the diet of the world's only obligate bat predator, the Bat Hawk, and the foraging trait of its dominant prey. This finding will stimulate future studies to unravel the intricacies of the foraging framework the Bat Hawks exploit when hunting bats and birds foraging near or above vegetation, as well as the relationship between the prey species caught and their flight speed and manoeuvrability.

A future study should also investigate the association between the prey species of the Bat Hawks and the abundance of these prey in the different foraging groups (see Owen-Smith and Mills 2008; Barnes et al. 2010). Of particular interest would be to examine

if the Bat Hawks select their prey or catch them opportunistically (randomly), therefore if the common prey species represent the abundance or a selection of prey species.

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