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Source: Ardea, 95(1) : 75-82

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.095.0108

Spatial variation in the diet of the Barn Owl *Tyto alba* in the Caribbean

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Flikweert M., Prins T.G., de Freitas J.A. & Nijman V. 2007. Spatial variation in the diet of the Barn Owl *Tyto alba* in the Caribbean. Ardea 95(1): 75–82.

On Bonaire we assessed Barn Owl *Tyto alba* diets at four discrete sites. The 233 fresh pellets contained 755 identifiable prey items from four taxonomic orders. Average prey diversity differed two- to threefold between sites. Dietary composition showed large spatial variations between sites, from predominantly insectivorous to avian. Between-island variation was assessed by comparing the dietary composition of populations of Barn Owls on nine islands throughout the Caribbean region as reported in the literature. On 8/9 islands mammals (mainly rodents and bats) formed the main diet. On half of the islands about a fifth or more of the prey comprised birds. Reptiles and/or insects were eaten on 5/9 islands, but rarely dominated the diet. These large within-island dietary differences reflect differential prey availabilities in the Caribbean, possibly enhanced locally by specialisation.

Key words: *Tyto alba*, diet, variation, Caribbean

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INTRODUCTION

The Barn Owl *Tyto alba* has a cosmopolitan distribution, with populations occupying temperate and tropical zones. The Barn Owl is arguably the best-studied owl worldwide showing large temporal and spatial variation in the dietary composition within and between study areas (e.g. Bunn *et al.* 1982, Taylor 1994, Bruce 1999, Köning *et al.* 1999). Our knowledge of the biology of Barn Owls and, more specifically, of its diet is strongly biased towards studies from temperate regions (Taylor 1994). Relatively few data are available on the dietary composition of Barn Owls from tropical regions, and in particular from (small) tropical islands. Given that these islands typically have depaupered faunas (Woods & Sergile 2001) we expect that Barn Owls on these islands have a less diverse diet compared with those breeding on the mainland. On many islands exotic animals (rats, mice, rabbits) have been introduced and these may provide alternative food sources. Our aim is to quantify and analyse the diet of Barn Owls breeding in the Caribbean, and to quantify the spatial variation in diet between and within these isolated tropical islands.

MATERIAL AND METHODS

Study area

We selected the Caribbean as our study region (Fig. 1) as the Barn Owl is widespread in the area and data on the dietary composition of several resident island populations is available. Within the Caribbean several island populations have been described as different at the subspecific level, viz *T. a. pratincola* in the north, *T. a. furcata* in the north and east, and *T. a. bargei* in the south (König *et al.* 1999; Prins *et al.* 2003). In much of the region only one species of barn owl is present, i.e. *Tyto alba*, but on Hispaniola and Tortuga the Ashy-faced Owl *T. glaucops* occurs sympatrically (König *et al.* 1999).

For our within-island comparison the island of Bonaire, Netherlands Antilles, was chosen. The island occupies a land surface of c. 288 km^2 and is situated 87 km north of Venezuela from which it is separated by the 1700 m deep Bonaire Trench. Bonaire has an arid climate (mean annual rainfall 463 mm; mean annual temperature 28°C: Meteorological Service of the Netherlands Antilles and Aruba) with about 50% of rainfall recorded in October to December. The amount of permanent available surface water has increased the last decades following the construction of dams and ponds (Prins & Nijman 2005). The Barn Owl is the only owl species present on Bonaire; in addition a small number of resident and migrant birds of prey occur (Nijman *et al.* 2005).

Data acquisition

Barn Owl pellets on Bonaire were collected in February–May 2003. The species proved to have a patchy distribution with concentrations along limestone escarpments within the terraced landscapes that rim the island. Areas to be searched were identified by the presence of Middle and Higher Terrace units (de Freitas *et al.* 2005). Accumulation of pellets was considered evidence for the presence of a roost. Roosts were clustered around four sites, i.e. Bolivia (a continuous stretch

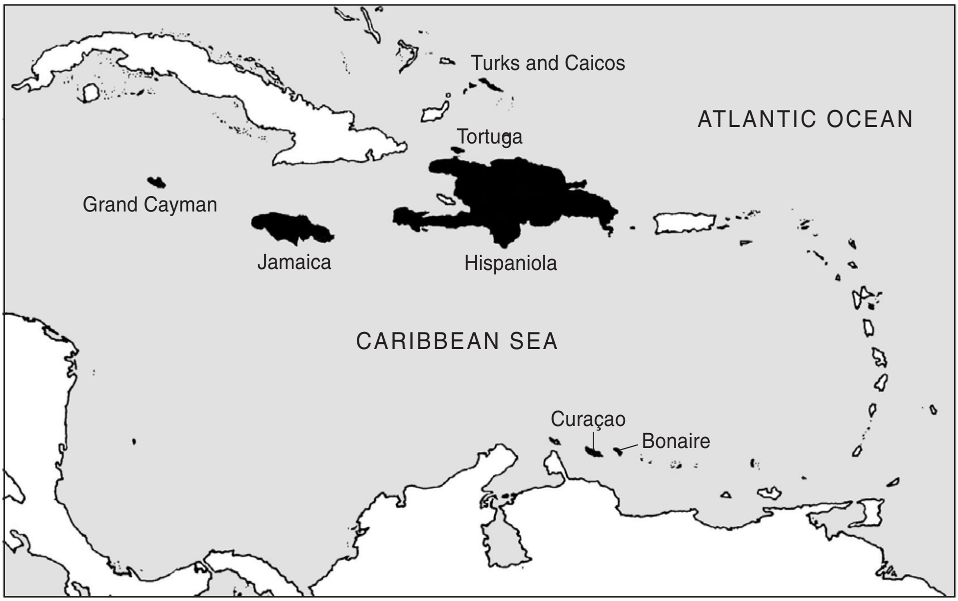

Figure 1. The Caribbean region, indicating the location of the island of Bonaire, and other localities mentioned in the text.

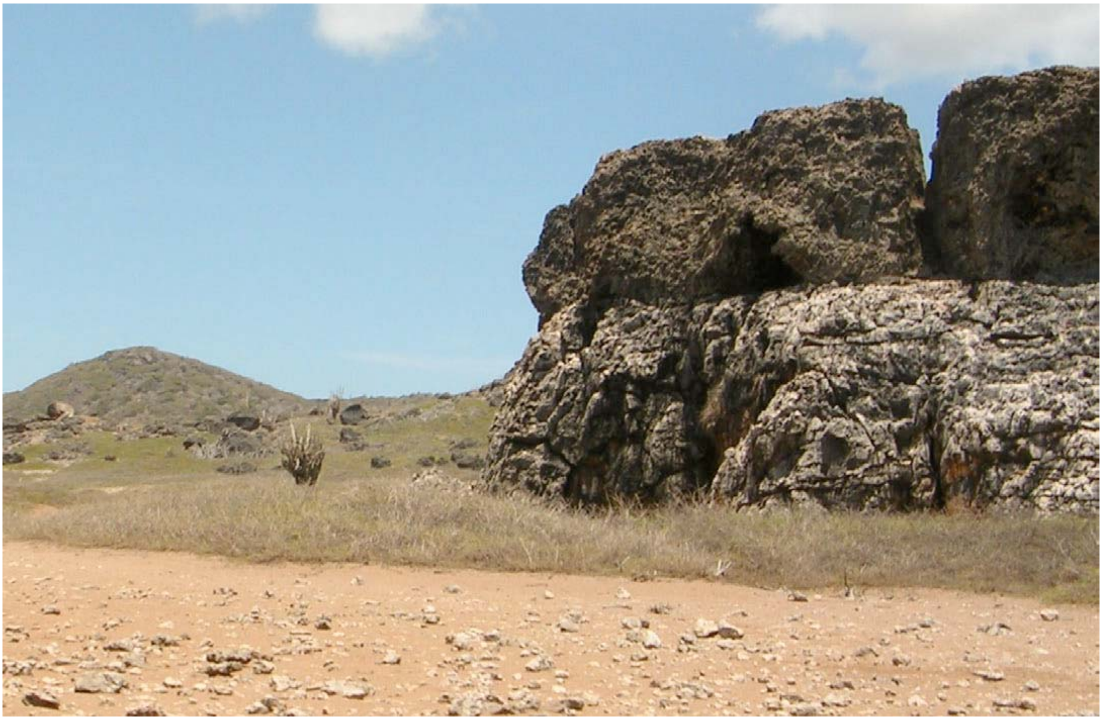

Figure 2. Barn Owl habitat on Bonaire, showing one of the higher limestone terraces near Fontein (photo Mansour Aliabadian, Archive ZMA)

of the Middle Terrace on the windward coast of the central part of the island), Roi Sangu (a gorge bordered by high limestone escarpments in the Higher Terrace landscape unit in the southern part of the island), Playa Frans (isolated limestone hill in an undulating landscape unit of volcanic origin) and Fontein (Middle and Higher limestone terraces; Fig. 2). Within the four sites we identified 25 individual roosts (see Table 1 for details). Only fresh pellets (<2 months old) were collected, and later analysed at the Zoological Museum Amsterdam (ZMA). We collected 233 fresh pellets, with a total of 755 identified prey items.

From the literature we selected studies from other islands in the region, if samples were specifically collected from just one island (as opposed to an aggregate of islands), and prey identification included all taxonomic orders.

Analysis

Prey remains were identified using keys published in Husson (1960) and Voous (1983), and a reference collection in the ZMA. Identification of insects was mostly restricted to family level. For vertebrates we determined the minimal number of prey items in pellets by tallying the number of skulls and mandibles. Mean prey mass was taken from Dunning (1993), Nowak (1999), and ZMA collections. Rodent body masses were calculated following Morris (1979) and de Groot (1983). Frequency analysis followed the method of de Groot (1983). Many diversity indexes tend to be sensitive to differences in sample sizes (Magurran 1988). For each site, therefore, we calculated an average prey diversity index when sample size exceeded 53 prey items (the smallest sample size for Bolivia) with EcoSim software (using a rarefaction analysis) allowing direct comparisons between

Table 1. Frequency of prey items in pellets of Barn Owl at four sites in Bonaire, Netherlands Antilles. For each site the number of pellets and the number of individual roosts is given in parentheses. Biomass is given as a percentage of the total biomass for the sites.

Site	Bolivia (45, 6)	Roi Sangu (125, 13)	Playa Frans (55, 3)	Fontein (8, 4)	Biomass (% of total)
ARTHROPODA					
Gryllidae	0	1	0	0	<0.1
Hemiptera	0	1	0	0	<0.1
Coleoptera; Carabidae	0	35	0	0	<0.1
Coleoptera; Cerambycidae	0	1	0	0	<0.1
Coleoptera; Curculionidae	0	22	1	1	<0.1
Coleoptera; Elateridae	0	3	0	0	<0.1
Coleoptera; Scarabidae	0	1	1	0	<0.1
Coleoptera; Tenebrionidae	0	353	11	7	<0.1
Coleoptera; Buprestidae	0	25	0	0	<0.1
Scorpionidae	0	1	0	0	<0.1
REPTILIA					
Cnemidophorus murinus	1	9	9	2	7.7
AVES					
Columba corensis	1	1	0	0	4.7
Zenaida auriculata	0	3	3	0	6.1
Columbina passerina	1	3	13	4	5.6
Leptotila verreauxi	0	0	0	1	1.4
Sublegatus arenarum	0	0	2	2	0.4
Myiarchus tyrannulus	0	0	0	1	0.4
Tyrannus spp.	0	1	0	3	1.6
Dendroica spp.	0	0	8	0	0.7
Dendroica petechia	27	3	7	8	4.0
Coereba flaveola	2	3	3	11	1.6
Tiaris bicolor	0	1	6	6	2.2
Icterus icterus	0	0	1	0	0.6
Icterus nigrogularis	0	0	0	1	0.4
Passer domesticus	0	0	0	1	0.2
MAMMALIA					
Glossophaga longirostris	0	0	13	0	1.4
Mus musculus	0	8	2	14	3.0
Rattus rattus	21	36	25	24	55.9
Mean prey biomass (g)	35.7	6.9	30.3	29.8	14.8
Total prey items	53	511	105	86	755

sites (Gotelli & Entsminger 2001). The options were set at 100 iterations and independent sampling of randomly chosen items from the total prey-item pool. For within- and between-island comparisons, spatial variation in dietary composition of the major prey items was tested with a χ^2-test, with number of prey items or summed body mass within each category as independent variables (Sokal & Rohlf 1995). To reduce the number of low expected values in the analysis, arthropods were pooled and birds and mammals were analysed at the family level (with Coerebidae, Ichteridae and Passeridae pooled). Yates' correction for continuity was applied to the χ^2-test, where appropriate. We made multiple comparisons; to reduce the overall experiment-wise error, we set significance at $P < 0.01$ in two-tailed tests.

RESULTS

Within-island variation

Diet composition, expressed as number of prey items and biomass, differed significantly at the spatial level (number of prey items: $\chi^2 = 791$, $df = 9$, $P < 0.001$; biomass: $\chi^2 = 559$, $df = 9$, $P < 0.01$). Pair-wise comparisons, with each area tested for similarity against the other areas pooled together, revealed that differences between sites were significant.

Diet diversity, expressed as Average Prey Diversity Index (APDI), differed between the four sites, with APDIs at Playa Frans and Fontein (13 and 12, respectively) being much higher than those observed at Roi Sangu and Bolivia (8 and 5, respectively).

In terms of frequency of prey items in pellets, the diet of Barn Owls from Bolivia differed from the other sites combined ($\chi^2 = 193$, $df = 7$, $P < 0.001$), especially in the marked abundance of Yellow Warblers *Dendroica petechia* and Black Rats *Rattus rattus* and the absence of arthropods. Dietary composition at Roi Sangu differed from the other sites combined ($\chi^2 = 380$, $df = 7$, $P < 0.001$), with a preponderance of darkling beetles (Coleoptera; *Tenebrionidae*), whilst New World warblers (large *Dendroica* spp.), Bananaquits *Coereba flaveola*, Black-faced Grassquits *Tiaris bicolor*, Common Ground Doves *Columbina passerina* and Black Rats were underrepresented. The dietary composition at Playa Frans differed from the other sites combined ($\chi^2 = 197$, $df = 7$, $P < 0.001$) with a relatively large number of Common Ground Doves, New World warblers (small *Dendroica* spp.), Rufous-collared Sparrows *Zonotrichia capensis*, Miller's Long-tongued Bat *Glossophaga longirostris*, Black Rats and Bonaire Whiptails *Cnemidophorus murinus*. Also, in terms of number of items present in pellets, Fontein differed from the other three sites combined ($\chi^2 = 137$, $df = 7$, $P < 0.001$) with significantly more Bananaquits, Black-faced Grassquits, tyrants (*Tyrannus* spp.) and Common House Mouse *Mus musculus* than the other sites combined.

When comparing spatial variation in dietary composition in terms of biomass, a similar pattern emerged as with the frequency analysis. Although the relative importance of the larger species increased, each of the sites differed significantly in species composition from the other sites combined. Most prominent were the small contributions of reptiles in the diet of the Barn Owls at Fontein (3% vs. 7%; $\chi^2 = 94.4$, $df = 1$, $P < 0.01$), and birds at Roi Sangu (24% vs. 32%; $\chi^2 = 172.4$, $df = 1$, $P < 0.01$). At Playa Frans there was a relative large amount of birds but a small amount of mammals in the Barn Owls diet (birds 42% vs. 32%; mammals 47% vs. 60%; both $\chi^2 > 212.4$, $df = 1$, $P < 0.01$).

Between-island variation

Data on dietary composition of the Barn Owl was available from nine islands in the Caribbean, i.e. the Netherlands Antilles, the Turks and Caicos Islands, the Cayman Islands, Hispaniola, and Jamaica (Table 2). Almost 90 different species were found in Barn Owl pellets throughout the Caribbean, clearly an underestimate because many insects and some birds were not identified to the species level. The differences in dietary composition of Barn Owls between the islands were significant ($\chi^2 = 5281$, $df = 24$, $P < 0.001$); exclusion of

Table 2. Dietary composition of Barn Owls on Caribbean Islands by percentage (number of items) of total number of prey items identified.

Territory and islands	Mammals	Birds	Reptiles	Insects	Reference
Jamaica	97.2 (1027)	2.6 (28)	0 (0)	-	McFarlane & Garrett 1989
Turks and Caicos Islands					
Middle Caicos	95.4 (62)	4.6 (3)	0 (0)	0 (0)	Buden 1974
Crooked Island	94.8 (73)	5.2 (4)	0 (0)	0 (0)	Buden 1974
Providenciales	73.1 (136)	26.9 (50)	0 (0)	0 (0)	Buden 1974
Mayaguana	70.3 (19)	18.5 (5)	11.1 (3)	0 (0)	Buden 1974
Hispaniola	81.6 (250)	14.2 (43)	4.2 (13[a])	-	Wetmore & Bradshaw 1931
Cayman Islands					
Grand Cayman	58 (32)	40 (22)	2 (1)	0 (0)	Johnston 1974
Netherlands Antilles					
Curaçao	62.6 (1040)	30.5 (506)	3.5 (58)	3.4 (57)	Debrot *et al*. 2001
Bonaire	18.9 (143)	16.9 (128)	2.8 (21)	61.4 (464)	This study
Minimum number of species	21	50	6	12	

[a]Includes 12 Giant Tree-toads *Hyla dominicensis*.

insects did not alter this picture ($\chi^2 = 769$, $df = 16$, $P < 0.001$). The observed between-island variation is not an artifact of different methodologies employed: within the Turks and Caicos Islands and within the Netherlands Antilles the observed differences were significant ($\chi^2 = 63.9$, $df = 6$, $P < 0.001$ and $\chi^2 = 1049.0$, $df = 3$, $P < 0.001$ for the Turks and Caicos Islands, and the Netherlands Antilles, respectively).

The analysis shows that, apart from Bonaire, small mammals (mainly rats and mice but also various species of bats) and to a lesser degree birds, make up the majority of the Barn Owls' diet in the Caribbean. Insects and reptiles are preyed upon by Barn Owls on few islands, but rarely feature prominently in the species' diet.

DISCUSSION

We found large spatial differences in diets within Bonaire. At one roost, 86% of all prey items were Arthropoda, but this taxonomic group was rare at other roosts. Lizards were important prey for owls at one site (9% of all prey items), but were almost completely absent at other. Only at the roosts of Playa Frans, bats featured in the Barn Owl's diet (12% of all prey items). Prey diversity differed almost threefold between sites. Between islands the variation was almost as large. On 8 out of 9 islands small mammals (mainly rodents and bats) form the bulk of the Barn Owl's diet. On half of the islands about a fifth or more of the prey comprise birds, but reptiles and/or insects rarely dominated the diet although found in pellets on half of the islands.

Taylor (1994) reviewed the dietary composition of Barn Owls worldwide and concluded that in 80% of the cases small mammals made up >90% of the total number of prey items. On some small island ecosystems this general conclusion seems to hold, as for instance studies from the Turks and Caicos Islands (Buden 1974), the Cayman Islands (Johnston 1974), and coastal islands off West Australia (Dickman *et al.* 1991) indicate that rats and/or mice are important prey items. It seems that in more arid tropical islands Barn Owls often catch a greater proportion of non-mammalian prey, as for instance in the Galapagos Islands insects made up 63% of prey items (de

Groot 1983), and our results indicate a similar picture for Bonaire. In arid areas Barn Owls seem to have a catholic diet, taking a wide variety of insects, lizards, birds and small mammals (Taylor 1994; cf. Debrot *et al.* 2001).

This large spatial variation in dietary composition may point at (a) temporal and geographic variations in the species composition and abundance of food supply, or (b) some degree of local specialization. Given the small size of Bonaire, the proximity of study sites, and distances covered by hunting Barn Owls (1–5 km from nest sites), the latter hypothesis may have some support. However, as we have no information on variations in prey availability within and between islands, the more likely first explanation cannot be ruled out. We feel that pinpointing proximate causes of local variations in diet would be an interesting avenue for further research.

ACKNOWLEDGEMENTS

Fieldwork on Bonaire was made possible through generous financial contributions from the Prins Bernhard Cultuurfonds Nederlandse Antillen en Aruba and the P.A. Hens Memorial Fund. We thank W. Bergmans (ZMA), A.O. Debrot (CARMABI), G. van Hoorn (DROB), P. Montanus (DROB), and C.S. Roselaar (ZMA) for help and support. We thank the two reviewers for their suggestions and comments.

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SAMENVATTING

De kosmopolitische Kerkuil *Tyto alba* is de enige uilensoort die op Bonaire, Nederlandse Antillen, voorkomt. De soort zit vooral op de kalksteenhellingen die het eiland omzomen. Bonaire is slechts 288 km^2 groot, en ligt 87 km ten noorden van Venezuela. Er heerst een aride klimaat met een gemiddelde temperatuur van 28°C en een gemiddelde neerslag van 463 mm per jaar. Over het menu van de Kerkuilen van Bonaire is niets bekend. In februari–maart 2003 werden daarom op 25 verschillende roestplekken 233 verse braakballen verzameld; deze waren goed voor 755 identificeerbare prooiresten. Er werden opvallende verschillen in samenstelling van menu gevonden, afhankelijk van de verzamelplek. Waar op de ene locatie insecten ontbraken in het menu, en een zangertje *Dendroica petechia* en Zwarte Ratten *Rattus rattus* de hoofdtoon voerden, bestonden de braakballen op andere plekken overwegend uit insecten, of uit verschillende vogelsoorten, al dan niet aangevuld met reptielen. Deze verschillen bleven overeind als de prooikeus werd uitgedrukt in biomassa. In vergelijking met braakbalanalyses van Kerkuilen elders uit het Caribische gebied, waaronder de rest van de Nederlandse Antillen, de Turks - en Caicos Eilanden, de Kaaimaneilanden, Hispaniola en Jamaica, bleken de uilen van Bonaire veel insecten en vogels te vangen. Elders betrof dat overwegend ratten en muizen, en in mindere mate vogels. Mogelijk dat het aride klimaat van Bonaire tot een veelzijdiger menu heeft geleid, waarbij insecten en reptielen een groter aandeel in de voedselkeus vormen. Daarnaast is het mogelijk dat sommige uilen van Bonaire zich hebben gespecialiseerd in bepaalde prooisoorten. (RGB)

Corresponding editor: Rob G. Bijlsma
Received 31 March 2006; accepted 13 February 2007