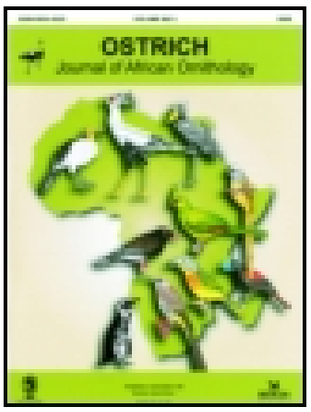

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THE FOOD HABITS OF THE BARN OWL TYTO ALBA AT THREE SITES ON MADAGASCAR

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THE FOOD HABITS OF THE BARN OWL *TYTO ALBA* AT THREE SITES ON MADAGASCAR

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SUMMARY

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Regurgitated food remains of the Barn Owl *Tyto alba* were collected within the rain forest of the Eastern Region of Madagascar (Andasibe and Manombo) and in the sub-arid thorn scrub of the Western Region (Beza Mahafaly). The material from Andasibe and Manombo represent single point samples, while 24 samples were collected from Beza Mahafaly between November 1990 and November 1991. A minimum of 176 individual vertebrates, representing 18 taxa, was identified from the Andasibe sample, and a minimum of 90 individual vertebrates of 5 taxa from the Manombo sample. The Beza Mahafaly samples included a minimum of 1 013 individual vertebrates of 22 taxa. At all three sites introduced rodents made up the bulk of the prey by number and by biomass, but at Beza Mahafaly lemurs and amphibia were also significant prey items. Insects constituted a small proportion of the prey. The results from these sites are compared with records of Barn Owl prey from mainland Africa.

RÉSUMÉ

Des pelotes de rejection de Chouette effraie *Tyto alba* ont été collectées au sein de la forêt pluviale de la Région de l'Est de Madagascar (Andasibe et Manombo) ainsi qu'au sein du bush épineux sub-aride dans la Région de l'Ouest (Beza Mahafaly). Le matérial collecté à Andasibe et Manombo correspond à une collecte unique alors que 24 collectes différentes ont été réalisées à Beza Mahafaly entre novembre 1990 et novembre 1991. Un minimum de 176 vertébrés, représentant 18 taxons différents a été identifié au niveau du site d'Andasibe et un minimum de 90 vertébrés appartenant à 5 taxons différents a été identifié à partir de la collecte réalisée à Manombo. Les échantillons collectés Beza Mahafaly comptent un minimum de 1 013 vertébrés appartenant à 22 taxons différents. Au sein des trois sites, les rongeurs introduits constituent la plus grande proportion de proie que ce soit en terme de nombre d'individus qu'en terme de biomasse; pour le cas de Beza Mahafaly les lémuriens et les amphibiens constituent cependant une part significative des proies identifiées. Les insectes comptent pour une faible proportion dans le nombre des proies. Les résultats des proies trouvées au niveau de ces sites sont comparés à ceux obtenus pour la Chouette effraie au niveau du continent africain.

INTRODUCTION

On Madagascar, the Barn Owl *Tyto alba affinis* is the most common and widely distributed nocturnal raptor (Langrand 1990). It occupies a variety of habitats from forest edge to grassland savanna, agricultural areas, and human habitation from sea level to 1 800 m. Little information is available on the food habits of the Madagascar population of Barn Owl. Rand (1936) noted that pellets found near a nest consisted of small mammal bones and fur, and that three stomachs contained remains of small mammals, including *Rattus*. Langrand (1990) mentioned that the Barn Owl's diet consisted of rodents, insectivores, primates (*Microcebus murinus*), bats, birds and insects. The principal purposes of this paper are to present quantified data on the diet of Barn Owls at three sites on Madagascar, to examine patterns of seasonal variation at one site, and to compare food habits of Barn Owls at several African localities.

STUDY AREAS AND METHODS

Andasibe: This sample was collected in June 1988 in the village of Andasibe (18 28S, 48 28E), which is about 800 m from the edge of the Réserve Spéciale d'Analamazaotra/Périnet (Fig. 1) 930 m above sea-level. The pellets were collected in a building in the village and nearby to a 12 m wide stream bordered by a grove of large *Eucalyptus* trees, and the natural forest starts another 400 m away. The vegetation of the reserve is typical of medium altitude tropical moist forest (Jenkins 1987) of the Eastern Region of the Central Domain. The average annual precipitation within the reserve is about 1 700 mm (Nicoll & Langrand 1989). The reserve is probably biologically the best known rain forest site in all of Madagascar and relatively complete lists are available for the local vertebrates.

Most of the pellets were found intact and all bones were removed after soaking in water. The average greatest length of the pellets was 45,5 mm

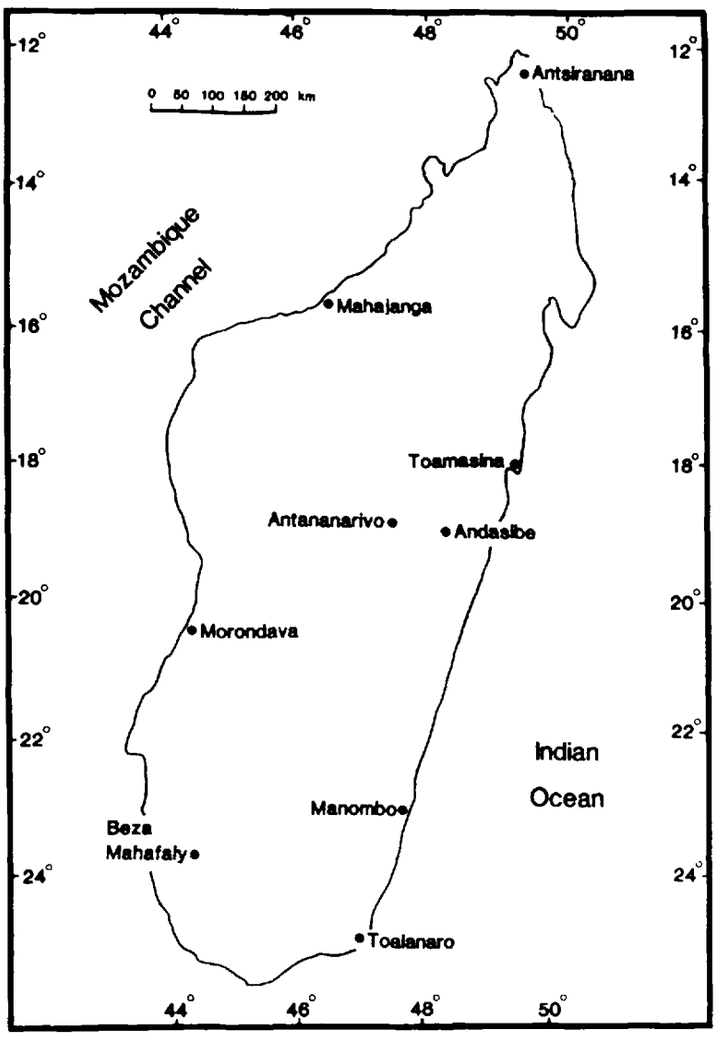

FIGURE 1.

Map of Madagascar showing localities mentioned in text and major cities.

(n=23, range 37-62 mm, S.D. 7,17) and greatest width 25,8 mm (n=23, range 21-33 mm, S.D. 2,77).

Manombo: The second site was 30 km south of Farafangana (Fig. 1), near the village of Mandovia, just at the edge of the Réserve Spéciale de Manombo (23 03S, 47 44E), and 30 m above sea-level. The bone remains were collected on 9 March 1991 under a cavity in a *Terminalia catappa* (Combretaceae) tree. The general area around the site had been cleared for agriculture and pasture lands, and the nearest relatively intact native forest was about 1 km away. A permanent river, about 5 m wide, passed within 1 m of the *Terminalia* tree, and was bordered on either side by a 5 m wide band of dense vegetation. The local natural vegetation is lowland rain forest of the Eastern Region of the Eastern Domain (Nicoll & Langrand 1989; pers. obs.). The average annual rainfall for the area is 2,500 mm (Nicoll & Langrand 1989). Only a few whole pellets were collected, as the vast majority had been dissolved by the regular local rains.

Beza Mahafaly: The third site is in the southwestern portion of the island at Ambinda (Fig. 1), at the edge of the Réserve Spéciale de Beza Mahafaly (23 38-23 42S and 44 31-44 34E). Material was collected on 24 occasions between November 1990 and November 1991. The reserve lies between 100 and 200 m above sea-level. The general habitat of this area is typical of sub-arid thorn scrub of the Southern Domain (Nicoll & Langrand 1989). (See Goodman *et al.* 1993 for a description of this locality).

Paired bones of any taxon within a sample were separated and the largest number of elements from either the left or right side was considered the minimum number of individuals (MNI). The

TABLE 1
MEAN BODY MASS (G), RANGE AND SAMPLE SIZES (N) OF VERTEBRATES IDENTIFIED FROM PREY REMAINS.

Taxa	n	Mean mass	Range
Amphibians			
Ptychadena mascareniensis	9	4,9	3,0-6,5
Boophis tephraeomystax (male)	5	4,0	3,0-5,0
Boophis opisthodon (male)	10	9,5	8,0-13,0
Scaphiophryne brevis or *calcaratus*	6	3,8	2,0-5,0
Plethodontohyla sp.	8	3,8	2,5-6,0
Reptiles			
Chamaeleo sp.		15,0	
Paroedura bastardi	9	6,3	4,0-9,0
Amphiglossus or *Geckolepis*		2,0	
Birds			
Turnix nigricollis	5	68,6	59-80
Charadrius sp.		32	
Agapornis cana	5	29,8	27,0-31,5
Merops superciliosus	3	44,2	39,5-48,0
Copsychus albospecularis	49	24,3	16,5-30,5
Hypsipetes madagascariensis	31	44,9	33,0-52,0
Neomixis tenella	21	7,3	6,5-8,5
Nectarinia souimanga	45	7,1	6,0-8,8
Leptopterus chabert	6	19,0	18,0-20,5
Foudia madagascariensis	22	16,9	13,0-19,5
Lonchura nana	2	8,8	8,5-9,0
Ploceus sakalava	26	23,8	19,5-27
Mammals			
Suncus madagascariensis	2	2,3	1,6-3,0
Suncus murinus	17	33,9	21,5-48,4
Geogale aurita	2	7,3	7,0-7,5
Taphozous mauritianus	4	55,5	49-62
Tadarida jugularis	43	10,0	8,4-11,5
Mops midas	13	43,8	37,5-48,0
Microcebus rufus	28	47,5	35-70
Microcebus murinus	163	60	39-98
Rattus rattus			
combined	63	102,7	26,1-174,3
sub-adult	7	45,4	26,1-56,1
adult	56	109,9	66,0-174,3
Mus musculus			
combined	21	9,7	4,5-16,6
sub-adult	3	5,0	4,5-5,4
adult	17	11,5	6,5-16,6

All mass measurements are based on our own field work on Madagascar with the exception of rodents, bats and some insectivores (specimens USNM), *Taphozous mauritanus* (specimens from East Africa in Field Museum of Natural History), *Microcebus rufus* (Harcourt 1987), and *M. murinus* (Martin 1973).

comparative skeletal collections housed in the Field Museum of Natural History, Chicago; the National Museum of Natural History (USNM), Washington, D.C.; and the University of Michigan Museum of Zoology, Ann Arbor, were used to identify the bone remains. Rodent mandibles were placed in two categories based on the condition of the teeth (when present), which are believed to represent different age classes: 1) sub-adult — teeth unworn, edges of M3 sharp, or newly or partially erupted and 2) adult — M3 from slightly worn, heavily worn or surface of teeth flat or concave. Mandibles without teeth were placed in the age category 'unknown'.

We are unaware of published mass information for Barn Owls on Madagascar. The same form occurs throughout much of sub-Saharan Africa (Benson 1960), and based on a sample of 24 adults from southern Africa this subspecies' average mass is 334 g with a range of 266-470 g (Fry *et al.* 1988). It is assumed that the mass of individuals of this subspecies occurring on Madagascar is similar to the mainland African population.

Mass information for animals identified from the pellet remains is given in Table 1; for rodents the category 'combined' is a summary statistic of the pooled sample, without regard to dental wear, and was used as the inferred mass for individuals identified from mandibles without teeth. The MNI was determined for mammals by mandibular counts, for birds by long bone or rostrum counts, for amphibians by ilia counts, for reptiles by dentary or maxillae counts, and insects by head or body part counts.

RESULTS

Andasibe

From the Andasibe material 1300 bones were recovered, representing a MNI of 176 (Table 2). The animals consisted of a variety of vertebrates, including frogs, lizards, birds, an insectivore, bats, a lemur, and rodents. By number the most common prey were *Mus* (29,5%), *Rattus* (28,4%), and *Ptychadena* (9,7%) and by biomass *Rattus* (73,8%), *Mus* (9,3%), birds (7,4%), reptiles (4,6%), and lemurs (2,5%). Insect remains included one Gryllidae, nine Blattidae (*Gromphadorina* sp.), and two Scarabaeidae (Table 3).

Manombo

The Manombo prey remains consisted of 586

TABLE 2
VERTEBRATE REMAINS IDENTIFIED FROM BARN OWL PELLETS COLLECTED IN JUNE 1988 AT ANDASIBE.

	MNI[1]	%total individuals	%total biomass
Amphibians			
Ptychadena mascareniensis	17	9,7	1,7
Boophis opisthodon	10	5,7	2,0
cf. *Plethodontohyla*	11	6,3	0,9
Total amphibians	38	21,7	4,6
Reptiles			
cf. *Amphiglossus* or *Geckolepis*	2	1,1	0,1
Birds			
Turnix nigricollis	1	0,6	1,4
Agapornis cana	4	2,3	2,5
Copsychus albospecularis	1	0,6	0,5
Hypsipetes madagascariensis	1	0,6	0,9
Neomixis cf. *tenella*	1	0,6	0,2
Leptopterus chabert	2	1,1	0,8
Foudia madagascariensis	1	0,6	0,4
Lonchura nana	4	2,3	0,7
Total birds	15	8,5	7,4
Mammals			
Suncus madagascariensis	12	6,8	0,6
Tadarida jugularis	4	2,3	0,8
Mops midas	1	0,6	0,9
Microcebus rufus	2	1,1	2,5
Rattus rattus			
sub-adult	29	16,5	27,4
adult	10	5,7	22,9
no teeth	11	6,3	23,5
Total	50	28,4	73,8
Mus musculus			
sub-adult	18	10,2	1,8
adult	18	10,2	4,3
no teeth	16	9,1	3,2
Total	52	29,5	9,3
Total mammals	121	68,8	87,9

[1]MNI = Minimum number of individuals.

bones, representing a MNI of 90 (Table 4). Identified species included a frog, an insectivore, a bird, and rodents. No lemur or insect material was recovered. *Rattus* accounted for 85,5% and *Ptychadena* 8,9% of the individuals taken, while birds and insectivores each made up less than 2,2%. When analyzed by biomass, *Rattus* represented over 96% of the prey eaten.

Beza Mahafaly

A MNI of 1 013 vertebrates was represented in the Beza Mahafaly samples (Table 5), constituting a biomass of about 15,2 kg. Animals identified include three species of amphibians, two reptiles, eight species of birds (all different genera), two insectivores, one bat, one lemur, and two rodents. By percent composition, the three most common prey items were: *Ptychadena* (35,3%), *Mus* (30,4%), and *Boophis* (8,0%). When the combined samples are analyzed by biomass there is a reordering of the most common prey taken: *Rattus* (34,8%), *Microcebus* (22,9%), *Mus* (21,4%), and *Ptychadena* (11,5%). By biomass, mammals represent 81,1%, amphibians 14,8%, birds 2,9% and reptiles 1,2%.

Insect remains were recovered from some pellets (Table 3) and consisted of Orthroptera, including the families Tettigoniidae, Gryllidae, Ac-

TABLE 3
INSECT REMAINS RECOVERED FROM BARN OWL PELLETS COLLECTED AT BEZA MAHAFALY FROM NOVEMBER 1990 TO NOVEMBER 1991.

	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Tettigoniidae					1[1]								
Gryllidae	23	1		1	12	1	15		3		9	4	3
Acrididae	6		3	1	9		1		2				3
Mantidae	1												
Blattidae[2]		2									2		2
Cerambycidae				1	1								
Scarabaeidae													
Dynastinae		3				1	3		1		2	3	2
Coprinae					3								
Hymenoptera	1												
Hemiptera													
Cydnidae				1	1								
Total	31	6	3	4	27	2	19	0	6	0	13	7	10

[1]Minimum number of individuals
[2]All *Gromphadorina* sp.

TABLE 4
VERTEBRATE REMAINS IDENTIFIED FROM BARN OWL PELLETS COLLECTED ON 9 MARCH 1991 AT MANOMBO.

	MNI[1]	%total individuals	%total biomass
Amphibians			
Ptychadena mascareniensis	8	8,9	0,7
Birds			
Merops superciliosus	1	1,1	0,8
Mammals			
Suncus murinus	2	2,2	1.4
Rattus rattus			
sub-adult	56	62,2	50,6
adult	21	23,3	46,0
Total	77	85,5	96,6
Mus musculus	2	2,2	0,4
Total mammals	81	90,0	98,4

[1] MNI = Minimum number of individuals

ridídae, Mantidae, and Blattidae; Coleoptera, including the families Cerambycidae and Scarabaeidae, including the subfamilies Dynastinae and Coprinae; Hymenoptera; and Hemiptera, including the family Cydnidae. The most commonly represented insect groups were Gryllidae, Acrididae, and Dynastinae.

When the Beza Mahafaly samples are analyzed by month there are differences in the types of prey taken by Barn Owls, which in part seems related to seasonality (Tables 3 & 6). In no case did insects comprise a substantial percentage of the biomass in any monthly sample. There is no clear seasonal pattern in the number of insects taken (Table 3). Seasonal patterns of vertebrate consumption by Barn Owls at Beza Mahafaly are discussed below.

DISCUSSION

Animals represented in the samples

Andasibe

The majority of amphibian prey taken at Andasibe is *Ptychadena mascareniensis* and *Boophis opisthodon*. The latter species is arboreal and common at the forest edge. It breeds in marshy

TABLE 5
SUMMARY OF VERTEBRATE REMAINS IDENTIFIED FROM BARN OWL PELLETS COLLECTED AT AMBINDA, BEZA MAHAFALY.

	MNI[1]	%total individuals	%total biomass
Amphibians			
Ptychadena mascareniensis	358	35,3	11,5
Boophis tephraeomystax	81	8,0	2,1
Scaphiophryne brevis or *calcaratus*	48	4,7	1,2
Total amphibians	487	48,0	14,8
Reptiles			
Chamaeleo sp.	1	0,1	0,1
Paroedura bastardi	26	2,6	1,1
Total reptiles	27	2,7	1,2
Birds			
Turnix nigricollis	1	0,1	0,5
Charadrius sp.	1	0,1	0,2
Agapornis cana	1	0,1	0,2
Neomixis cf. *tenella*	5	0,5	0,2
cf. *Nectarinia souimanga*	2	0,2	0,1
Leptopterus chabert	1	0,1	0,1
Foudia madagascariensis	4	0,4	0,4
Ploceus sakalava	7	0,7	1,1
unidentified bird (±10 g)	1	0,1	0,07
Total birds	23	2,3	2,9
Mammals			
Suncus madagascariensis	18	1,8	0,3
Geogale aurita	28	2,8	1,3
Taphozous mauritianus	1	0,1	0,4
Microcebus murinus	58	5,7	22,9
Rattus rattus			
sub-adult	27	2,7	8,1
adult	37	3,7	26,7
Total	64	6,4	34,8
Mus musculus			
unknown	17	1,7	1,1
sub-adult	37	3,7	1,2
adult	253	25,0	19,1
Total	307	30,4	21,4
Total mammals	476	47,2	81,1
Total vertebrates	1013		

[1] MNI = Minimum number of individuals

TABLE 6
ANALYSIS OF VERTEBRATE REMAINS RECOVERED FROM BARN OWL PELLECTS COLLECTED AT BEZA MAHAFALY

	November (2)[1]	December (2)	January (2)	February (2)	March (2)	April (2)
Amphibians						
Ptychadena mascareniensis	66/50,8/21,1[2]	22/15,7/5,0	12/23,5/10,1	9/17,6/8,5	51/58,6/23,1	41/51,9/16,1
Boophis tephraeomystax		16/11,4/3,0	6/11,8/4,1	29/56,9/22,4	7/8,0/2,6	11/13,9/3,5
Scaphiophryne sp.	1/0,8/0,2	1/0,7/0,2		2/3,9/1,5		2/2,5/0,6
Reptiles						
Chamaeleo sp.						1/1,3/1,2
Paroedura bastardi					2/2,3/1,2	1/1,3/0,5
Birds						
Turnix nigricollis	1/0,8/4,5					
Charadrius sp.						
Agapornis cana		1/0,7/1,4				
Neomixis tenella						1/1,3/0,6
Nectarinia souimanga						
Leptopterus chabert						
Foudia madagascariensis					2/2,3/1,1	
Ploceus sakalava						
unidentified						
Mammals						
Suncus madagascariensis		2/1,4/0,2	1/2,0/0,4			2/2,5/0,4
Geogale aurita		2/1,4/0,7				1/1,3/0,6
Taphozous mauritianus					1/1,1/5,1	
Microcebus murinus	2/1,5/7,8	8/5,7/22,2		2/3,9/23,2	3/3,4/16,6	7/8,9/33,7
Rattus rattus						
sub-adult	3/2,3/8,9		2/3,9/15,6	1/2,0/8,8		
adult	3/2,3/21,5	5/3,6/25,5	1/2,0/18,9	1/2,0/21,3	3/3,4/30,4	4/5,1/35,3
Mus musculus						
unknown	4/3,1/2,5	10/7,1/4,5				
sub-adult	10/7,7/3,3	5/3,6/1,2	6/11,8/5,2	1/2,0/1,0	2/2,3/0,9	
adult	40/30,7/30,1	68/48,6/36,2	23/45,1/45,6	6/11,8/13,3	16/18,4/17,0	8/10,1/7,4

	May (2)	June (1)	July (2)	August (2)	September (2)	October (2)	November (1)
Amphibians							
Ptychadena mascareniensis	12/20,0/3,8	4/19,0/3,0	13/16,5/3,7	18/25,3/6,7	47/40,9/14,5	45/51,7/24,5	18/42,9/25,3
Boophis tephraeomystax	4/6,7/1,0	1/4,8/0,6	7/8,9/1,6				
Scaphiophryne sp.			1/1,3/0.2		22/19,1/5,3	15/17,2/6,3	4/9,5/4,4
Reptiles							
Chamaeleo sp.							
Paroedura bastardi				2/2,8/0,1	4/6,3/1,6	8/9,2/5,6	9/21,4/16,3
Birds							
Turnix nigricollis							
Charadrius sp.	1/1,7/2,0						
Agapornis cana							
Neomixis tenella	2/3,3/0,9			1/1,4/0,5	1/0,9/0,5		
Nectarinia souimanga				2/2,8/1,1			
Leptopterus chabert	1/1,7/1,2						
Foudia madagascariensis	1/1,7/1,1	1/4,8/2,6					
Ploceus sakalava	2/3,3/3,1		1/1,3/1,5	4/5,6/7,2			
unidentified (±10 g)						1/1,1/1,1	
Mammals							
Suncus madagascariensis	4/6,7/0,6	1/4,8/0,3	4/5,1/0,5		2/1,7/0,3	1/1,1/0,3	2/4,8/1,3
Geogale aurita	2/3,3/0,9		6/7,6/2,5	9/12,7/5,0	4/3,5/1,8		3/7,1/6,3
Taphozous mauritianus							
Microcebus murinus	17/28,3/65,8	9/42,9/81,7	6/7,6/20,6	3/4,2/13,8	1/0,9/3,8		
Rattus rattus							
sub-adult	2/3,3/5,9	1/4,8/6,9	8/10,1/2,8	3/4,2/10,4	5/4,3/14,3	2/2,3/10,1	
adult	1/1,7/7,1		5/6,3/31,5	4/5,6/33,5	6/5,2/41,6	3/3,4/36,7	1/2,4/31,6
Mus musculus							
unknown			2/2,5/1,2	1/1,4/0,7			
sub-adult	4/6,7/1,3	2/9,5/1,5	3/3,8/0,9	2/2,8/0,8	1/0,9/0,3		1/2,4/1,4
adult	7/11,7/5,2	2/9,5/3,5	23/29,1/15,2	22/31,0/19,3	22/19,1/16,0	12/13,8/15,4	4/9,5/13,2

[1] Figure in parentheses represents the number of samples analyzed.
[2] Figures are minimum number of individuals/% total individuals/% total biomass.

areas, often sympatrically with *Ptychadena*. *Boophis* is sexually dimorphic, with adult males being about 60% smaller than adult females (Blommers-Schlösser 1979). On the basis of this dimorphism, all of the *Boophis* bones recovered were males or perhaps a few juvenile females. Males of this species call from leaves or branches, usually 1-4 m above stagnant water, and always at the forest edge. It appears that Barn Owls hunt these frogs by acoustic orientation and home in on vocalizing males in relatively exposed areas. *Ptychadena* is a ground-dwelling, largely nocturnal, frog which is generally found in marshy, typically disturbed, open areas, and rice fields (Blommers-Schlösser & Blommers 1984). It usually does not occur in primary forest. This owl hunts *Ptychadena* in mar-

shy areas, probably in close proximity to native forest. Amphibians made up a small proportion of the individuals and biomass consumed by Barn Owls at this site. Two lizard maxillae were recovered from the pellet remains that belong to a species of *Amphiglossus* or *Geckolepis*.

Eight different species of diurnal birds were identified in the Andasibe pellets, none of which are obligate forest species. These birds occur in open areas within the forest, and at the edge or in degraded areas (*Turnix nigricollis, Agapornis cana, Copsychus albospecularis, Hypsipetes madagascariensis, Neomixis* cf. *tenella, Leptopterus chabert, Lonchura nana,* and *Foudia madagascariensis*). Many of them roost during the night in partially exposed places, such as on outer limbs or crowns of trees or shrubs, and would presumably be accessible to hunting owls. Birds constituted 8,5% of the individuals and 7,4% of the biomass.

One species of insectivore, *Suncus (etruscus) madagascariensis*, was identified from the pellets. *S. madagascariensis* weighs on average 2,3 g and is the smallest mammal identified from any of the pellet remains. It made up 6,8% of the prey taken and 0,6% of the biomass at Andasibe. This species occurs in areas with dense grass, often considerable distances from the forest (Nicoll *et al.* 1988), although it has been captured in primary forest within about 300 m of the forest edge (Raxworthy unpubl.).

Nicoll & Langrand (1989) list seven species of relatively small nocturnal insectivores in the genus *Microgale* (Tenrecidae, sub-family Oryzoryctinae) as occurring in the nearby Réserve Spéciale d'Analamazaotra/Périnet, all of which live in relatively intact forest (Nicoll *et al.* 1988) and many weigh less than 10 g (Eisenberg & Gould 1970). No *Microgale* sp. was recovered from the owl pellets. The small size of these animals cannot explain their absence from the diet of this owl, since it takes the smallest insectivore on the island, *S. madagascariensis*. Further, *Microgale* spp. have been identified from Barn Owl pellets collected elsewhere on the island (Heim de Balsac 1972; MacPhee 1987).

Two species of Molossidae bats, *Tadarida (Mormopterus) jugularis* (MNI=4) and *Mops midas* (MNI=1), were identified from the pellets; these species have not been previously recorded from the reserve (Nicoll & Langrand 1989). *T. jugularis* is widespread on the island and remains of it have been found in pellets of Madagascar Long-eared Owls *Asio madagascariensis* collected at Beza Mahafaly (Goodman *et al.* 1993). Considerable numbers of this bat frequent day roosts and at dusk exit in mass. Bats made up less than 3% of the prey and 2% of the biomass in this sample.

A MNI of two *Microcebus rufus* were identified from the Andasibe pellets. This species is relatively common in both intact and secondary humid forest areas of eastern Madagascar (Tattersall 1982). It has been commonly observed in the *Eucalyptus* plantation at the edge of Andasibe.

The two species of rodents recovered from the pellets, *Rattus rattus* and *Mus musculus*, are not native to the island. They are generally found as human commensals. *Rattus* made up about 28% of the individuals and 74% of the biomass taken, and approximately half of the *Rattus* identified were sub-adults. *Mus* constituted about 30% by number and 9% by biomass of the prey consumed; nearly one-third of the individuals identified were sub-adults. In the Andasibe area *Mus* have been collected in grassy fields or at the edge of agricultural areas and *Rattus* from these same habitats and also within the rain forest, often along stream beds (specimens in USNM; Nicoll *et al.* 1988). The reserve has a relatively diverse fauna of native forest rodents, consisting of *Brachytarsomys albicauda, Eliurus minor, E. myoxinus tanala, Gymnuromys roberti,* and *Nesomys rufus audeberti* (Nicoll *et al.* 1988; Carleton & Schmidt 1990), but none of these rodents was found in the pellet remains.

On the basis of the animals identified from this sample, the Barn Owl is hunting locally in areas of slightly to completely disturbed habitats and not intact forest.

Manombo

At Manombo relatively few types of animals were recorded in the Barn Owl pellets. The only amphibian was *Ptychadena* which accounted for 8,9% of the individuals and 0,7% of the biomass taken. A river a few meters from the owl nest site, which meanders through deforested agricultural and pastural areas, would be appropriate habitat for this frog.

One species of insectivore, *Suncus murinus*, was identified from the Manombo material. This species is not native to the island (Hutterer & Trainer 1990), and it made up a small percentage of the owls' diet. There is a difference between Manombo and Andasibe in the consumption of this insectivore. At the latter locality, *Suncus* is common (specimens in USNM; Nicoll *et al.* 1988), particularly as a human commensal and in degraded areas at the edge of the forest and near agricultural fields. However, we found no evidence of it being preyed upon at Andasibe by Barn Owl.

Two species of rodents were identified from the pellets, *Rattus* and *Mus*. *Rattus* made up the largest portion of the owl's diet, 85,5% by individuals and 96,6% by biomass; while *Mus* constituted 2,2% and 0,4% respectively. Two species of native forest rodents, *Eliurus myoxinus webbi* and *Nesomys rufus*, are known from Manombo (Carleton & Schmidt 1990), but neither was found in the pellet remains. During a visit to the reserve in March 1991, *Microcebus rufus* was relatively common in forest about 1 km from the owl site; no remains of this lemur were found in the pellets.

On the basis of the animals identified from the pellet remains it appears that this local pair of Barn Owls does not enter undisturbed portions of the forest to hunt.

Beza Mahafaly

Three species of frogs were identified from the pellets. Two of these, *Ptychadena* and *Scaphioph-*

TABLE 7
COMPARISON BY MONTH OF DIFFERENT PREY TYPES TAKEN BY BARN OWL AT BEZA MAHAFALY BETWEEN NOVEMBER 1990 AND NOVEMBER 1991

	November (2)[1]	December (2)	January (2)	February (2)	March (2)	April (2)
Total number of vertebrates taken	130	140	69	51	87	79
Calculated prey mass (g)	1530	2158	580	517	1083	1245
Average mass of individual prey (g)	11,8	15,4	8,4	10,1	12,4	15,8
Amphibians	51,6/21,3[2]	27,8/8,2	35,3/14,2	78,4/32,4	66,6/25,7	68,3/20,2
Reptiles	-	-	-	-	2,3/1,2	2,6/1,7
Birds	0,8/4,5	0,7/1,4	-	-	2,3/3,1	1,3/0,6
Microcebus	1,5/7,8	5,7/22,2	-	3,9/23,2	3,4/16,6	8,9/33,7
Rattus	4,6/30,4	3,6/25,5	5,9/34,5	4,0/30,1	3,4/30,4	5,1/35,3
Mus	41,5/35,9	59,3/41,9	56,9/50,8	13,8/14,3	20,7/17,9	10,1/7,4
Insectivores	-	2,8/0,9	2,0/0,4	-	-	3,8/1,0
Bats	-	-	-	-	1,1/5,1	-

	May (2)	June (1)	July (2)	August (2)	September (2)	October (2)	November (1)
Total number of vertebrates taken	60	21	79	71	115	87	42
Calculated prey mass (g)	1550	661	1625	1312	1585	899	348
Average mass of individual prey (g)	25,8	31,5	20,6	18,5	13,8	10,3	8,3
Amphibians	26,7/4,8	23,8/3,6	26,7/5,5	25,3/6,7	60,0/19,8	68,9/30,8	52,4/29,7
Reptiles	-	-	-	2,8/0,1	6,3/1,6	9,2/5,6	21,4/16,3
Birds	11,7/8,3	4,8/2,6	1,3/1,5	9,8/8,8	0,9/0,5	1,1/1,1	-
Microcebus	28,3/65,8	42,9/81,7	7,6/20,6	4,2/13,8	0,9/3,8	-	-
Rattus	5,0/13,0	4,8/6,9	16,4/52,3	9,8/43,9	9,5/55,9	5,7/46,8	2,4/31,6
Mus	18,4/6,5	19,0/5,0	35,4/17,3	35,2/20,8	20,0/16,3	13,8/15,4	11,9/14,6
Insectivores	10,0/1,5	4,8/0,3	12,7/3,0	12,7/5,0	5,2/2,1	1,1/0,3	11,9/7,6
Bats	-	-	-	-	-	-	-

[1] Figure in parentheses represents the number of samples analyzed.
[2] Figures are % total individuals/% total biomass.

ryne brevis or *S. calcaratus*, are ground-dwelling nocturnal frogs and are known to aestivate during the dry season; while *Boophis tephraeomystax* probably is not active until after the rains commence, when local water pools are filled. The majority of frog bones identified from the Beza Mahafaly samples were collected between September and April (Tables 6 & 7), which would coincide with the rainy season and when breeding habitat for frogs was available. *Scaphiophryne* was rare or absent in pellet remains collected throughout most of the year, except from September to November; this suggests that as conditions dry out, these partly fossorial toads became more difficult for the owls to find. *Scaphiophryne* are presumably eaten by owls when they congregate around water pools to breed. Between May and August the representation of amphibians in the diet, as measured by both number of individuals and biomass, drops off substantially. Even during the dry season this owl is still feeding on some *Ptychadena* and *Boophis*, and these two species may not aestivate for some dry-season months or may remain active year round. *Ptychadena* made up 35% of the individuals represented in the sample and over 11% of the biomass. Amphibians were found in every monthly sample.

Two species of lizards were identified. *Paroedura bastardi* is nocturnal and partly arboreal and *Chamaeleo* is diurnal and arboreal. The single *Chamaeleo* skeleton is either a young *C. verrucosus* or adult *C. lateralis*; both of which are known from the reserve (Nicoll & Langrand 1989). *Chamaeleo* spp. often roost for the night at the tips of branches or other vegetation, where they would be relatively exposed to owl predation. Between November 1990 and August 1991 reptiles, if present at all, made up less than 3% of the individuals and 2% of the biomass taken by this owl. Starting with the September sample there was an increase in the prevalence of reptiles in the diet, which culminated with the final November sample, when 21,4% of the individuals and 16,3% of the biomass was reptilian prey. Reptiles were identified in six of the 13 monthly samples.

Eight species of birds were identified from the Beza Mahafaly sample (Table 6), all of which occur in open habitat and are diurnal (Langrand 1990). Barn Owls do not specialize upon any particular species of bird. The highest single monthly samples were May and August, when a MNI of seven was identified (Table 6). Four of the seven individuals in the May material had partially ossified bones and were recent fledglings. This owl may exploit a post-breeding increase in the number of birds and/or the greater vulnerability of young birds to predation. In the combined Beza Mahafaly sample, birds made up 2,3% of the individuals and 2,9% of the biomass. Birds were identified in 10 of the 13 monthly samples (Table 7).

Two species of insectivores, *Suncus madagascariensis* and *Geogale aurita*, were identified from the pellets (Table 5). Both of these species were previously known from the reserve (Nicoll & Langrand 1989). *Geogale* was identified from the December, April, May, July, August, September, and November samples. The austral winter months, the hottest and driest period of the year,

is when this animal might be torpid. However, *Geogale* seems to be active throughout the year. On the whole, insectivores made up a small proportion of the Barn Owl's diet, never exceeding 12,7% of the individuals nor 7,6% of the biomass in a monthly sample (Table 7). Insectivores were identified in 10 of the 13 monthly samples, and there does not appear to be any clear seasonal bias in the number of insectivores taken by this owl.

The lemur, *Microcebus murinus*, is relatively common but little information is available on its habits in the sub-arid thorn scrub region. The *Microcebus* remains recovered from owl pellets at Beza Mahafaly provide some insight into the seasonality of this species. This lemur represented 5,7% of the individuals and 22,9% of the biomass taken by the owls over a 13 month period (Table 5). There is a distinct seasonal shift in the number of *Microcebus* taken (Table 6): the average biomass for the November 1990 to April 1991 monthly samples was 17,3% (n=6, range 0-33,7%), the May sample 65,8%, the June sample 81,7%, and the July to November samples 7,6% (n=5, range=0-20,6%). *Microcebus* was identified in 10 of the 13 monthly samples and during this period the owls consumed a MNI of 58 lemurs. During May and June, a hot and dry portion of the austral winter and when it would be assumed that this lemur might aestivate, there is a pronounced increase in the number of animals taken by the Barn Owl. Because of their small size, non-gregarious foraging patterns, and arboreal habits *Microcebus* spp. are highly vulnerable to predation by nocturnal foraging raptors. The implications of the high level of predation on the population of *Microcebus* is considerable, and this is discussed elsewhere (Goodman *et al.* in press).

Two species of rodents were recovered from the pellet remains, *Rattus* and *Mus*. *Rattus* constituted 6,4% of the individuals and 34,8% of the biomass consumed, while *Mus* represented 30,4% and 21,4% respectively (Table 5). *Mus* and *Rattus* were identified in all of the monthly samples (Tables 6 & 7). The representation of *Rattus* in pellets collected between November 1990 and April 1991 was relatively constant, but dropped between May and June, and then increased between July and November. The pattern with *Mus* was similar, although the decrease in their consumption started in February rather than April. The decline in the number of rodents taken during the austral winter coincided with an increase in lemur consumption. Next to *Ptychadena*, *Mus* was the animal most commonly taken by this owl No native rodent has been recorded within the reserve (Richard *et al.* 1987; Nicoll & Langrand 1989); although *Eliurus m. myoxinus* and *Macrotarsomys bastardi* are known from the general area (Carleton & Schmidt 1990).

An important question associated with seasonal or cyclic variation in the diet of the Barn Owl at Beza Mahafaly, is if the material analyzed represented the majority of prey consumed by the pair between November 1990 and 1991? There were considerable differences between months in the number of vertebrates and the biomass consumed by the owls (Table 7). For example, limiting comparisons to months when two samples were collected, the number of vertebrates taken varied from 140 in December to 51 in February and the calculated prey mass varied from 2158 g in December to 517 g in February. One explanation is that the site where pellets were collected was not used by the owls on a regular basis, and that in some months they regurgitated pellets in other areas of the forest. Given these points, it follows that there would also be considerable differences between the months in the average body mass of each prey item (Table 7). Between November 1990 and April 1991 the average body mass of individual animals taken by the owls was relatively constant, ranging from 8,4 to 15,8 g; between May and August the average body mass of prey increased substantially, ranging from 18,5 to 31,5 g; and between September and November the average mass of prey returned to the former level, ranging from 8,3 to 13,8 g. The explanation for this change during the austral winter can be explained by clear dietary shifts of this owl. In May there was a pronounced increase in the consumption of *Microcebus* and a substantial decline in the number of small-bodied animals (e.g. amphibians) and *Mus*. Thus, the average animal eaten by the owls was larger during this period. This trend continued through the end of August and then returned to the types and proportions of animals taken before May.

Information is available from Beza Mahafaly on the food habits of one of the other nocturnal owls, Madagascar Long-eared Owl, which also took primarily rats and lemurs (Goodman *et al.* 1993). Thus, there is considerable overlap in the prey taken by Barn Owls and Madagascar Long-eared Owls at this site. Barn Owls seasonally catch more frogs than the Madagascar Long-eared Owl, which in turn takes more *Rattus* than Barn Owls do, and both owls take considerable numbers of lemurs.

Comparison of Barn Owl food habits on Madagascar with African populations

Numerous studies have been published on the food habits of the Barn Owl in mainland Africa and adjacent islands (summarized in Cramp 1985; Fry *et al.* 1988). These studies are largely based on the analysis of prey remains recovered from regurgitated pellets. In this section we compare the types and proportions of prey taken at various localities and in different habitats.

In Table 8 summary information is presented on the food habits of Barn Owls from a variety of sites (habitat type presented in parentheses): three sites on Madagascar described herein, one in South Africa (semi-succulent thorn scrub (Perrin 1982)), two in Nigeria (both woody savanna (Demeter 1981)), one in Tanzania (sparse acacia woodland (Laurie 1971)), one in Kenya (tropical semi-evergreen forest, now mostly suburban (Gichuki 1987)), one in Egypt (agricultural area in Nile Valley (Goodman 1986)), and one in the Canary Islands (mostly cultivated areas (Martin *et al.* 1985)). It is important to consider that inter-site

TABLE 8
COMPARISON OF THE FOOD HABITS OF BARN OWL IN MADAGASCAR, MAINLAND AFRICA AND THE CANARY ISLANDS[1]

	insects	amphibians	reptiles	birds	mammals	source[2]
Madagascar						
Beza Mahafaly						
individuals	+	48,0	2,7	2,3	47,2	1
biomass		14,8	1,2	2,9	81,1	
Manombo						
individuals		8,9		1,1	90,0	1
biomass		0,7		0,8	98,4	
Andasibe						
individuals	+	21,6	1,1	8,5	68,8	1
biomass		4,5	0,1	7,4	87,9	
South Africa						
Eastern Cape Province						
individuals	+	+	+	+	100,0	2
Nigeria						
Yankari Game Reserve						
individuals	32,0		4,0		64,0	3
biomass	7,3		3,4		89,4	
Futuk						
individuals	5,9	5,5	1,3	3,4	83,0	3
biomass	1,6	1,2	0,6	2,8	93,0	
Kenya						
Nairobi						
individuals	+	17,5	+	4,3	78,3	4
Tanzania						
Serengeti						
individuals	+		0,1	2,8	97,1	5
Egypt						
Karnak[3]						
individuals				45,3	45,3	6
biomass				51,0	48,9	
Canary Islands						
Tenerife						
individuals	18,3	1,7	4,6	0,9	74,5	7
biomass	1,3	0,6	2,5	2,2	93,3	

[1] information is presented as the percent total individuals in the sample and percent total biomass in the sample. + = present, but in negligible amount.
[2] 1 - this study, 2 - Perrin (1982), 3 - Demeter (1981), 4 - Gichuki (1987), 5 - Laurie (1971), 6 - Goodman (1986), 7 - Martin *et al.* (1985).
[3] also included fish remains.

comparisons are not always equivalent, since the number of pellets analyzed, temporal variation in the types of prey available, and preferential selection cannot be controlled for.

Insects, if consumed at all, generally made up an insignificant portion of this owl's diet. The exception is at one of the Nigerian localities (Yankari Game Reserve), where insects comprised 32,0% of the individuals and 7,3% of the biomass taken by this owl; this is compared to the second Nigerian site, where insects made up 5,9% and 1,6% respectively. Although the habitat of these two sites is similar and the pellets were collected during the same period (Demeter 1981), there appears to be some local variation in the prevalence of insects in the diet of this owl.

There is considerable variation among sites in the number of amphibians in the diet. Reptiles, in comparison, are rarely taken. Amphibian bones do not always withstand the digestive process of owls and may be under-represented in pellet remains (Fry *et al.* 1988). No clear pattern exists between habitat type and prevalence of amphibians in the diet of this owl. In the Beza Mahafaly sample, collected over the course of one year at a semi-arid thorn scrub site, amphibians comprised 48,0% of the individuals and 14,8% of the biomass. This is compared to the rain forest site of Andasibe, in which amphibians constituted 21,6% of the individuals from a single sample, and the tropical semi-evergreen locality near Nairobi, in which they made up 17,5% of the individuals from material collected over the course of more than two years. Generally, amphibians were either absent from the diet or comprised a small proportion. Throughout the range of the Barn Owl, there is considerable variation in the number of amphibians taken. For example, European populations of the Barn Owl rarely consume amphibians (Cramp 1985), yet frogs made up a significant portion of a sample from Hungary (Marián & Marián 1973). In Mali, certain owls feed almost exclusively on frogs and toads (Fry *et al.* 1988).

In most of the samples birds were present, but formed a small portion of the Barn Owl's diet. The major exception was the Egyptian sample, in which 45,3% by number and 51,0% by biomass was composed of birds. Two species, *Streptopelia senegalensis* and *Passer domesticus*, made up over 48,5% of the biomass in this sample (Goodman 1986).

At all of the sites, mammals made up the largest proportion of prey taken by this owl in both number of individuals and biomass. With the exception of Egypt, mammals comprised more than 75% of the biomass taken by this owl; in Egypt it was less than half. The proportion of mammal species varied widely between localities. For ex-

ample, insectivores made up 55,8% of the individuals identified from the Serengeti sample, 29,4% from Nigeria, 11,9% from the Nairobi, 10% from the Eastern Cape Province, 1,7% from Egypt, and were absent from the Canary Island sample. However, because of their small size, insectivores generally represent a small portion of the biomass consumed by this owl. Primates were only identified from the Madagascar material. Bats, if present at all, formed a small proportion of this owl's diet. However at some localities such as Bamako, Mali, bats are well represented in the pellet remains of the Barn Owl (Heim de Balsac 1965). A range of rodents are taken by this owl, a significant proportion of which include introduced species.

The Barn Owl occupies different habitats across its African range and is able to exploit a wide variety of animals for food. Even within a relatively small geographical region, with subtle differences among local habitats, there are pronounced differences in the food habits of this owl that cannot be related to temporal variation in seasonality (Macdonald & Dean 1984). The remarkable hunting skills of this owl, combined with its ability to take a variety of prey, including locally common human-commensal species and animals whose abundance varies seasonally, helps to explain its broad diet and distribution across most of the temperate and tropical areas of the world.

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REVIEWS

MALCOLM, S.B. & ZALUCKI, M.P. 1993 **Biology and conservation of the Monarch Butterfly**. Los Angeles CA: Natural History Museum of Los Angeles Country science series no. 38. 419 pp. Many text figures and tables, a few coloured and black white photographs.

This handsomely produced book is based upon the proceeding of the Second International Conference on the Monarch Butterfly held at the Los Angeles County Museum in September 1986, but contains much updated material. It is divided into 10 sections containing one to eight papers. It covers most of what is known about the American Monarch Butterfly *Danaus plexippus*, a close relative of the African Monarch *D. chrysippus*.

Why should a treatise on one butterfly be noticed, even briefly, in an ornithological journal? The American Monarch has probably the most complex distributional and biological history of any insect, and a good deal more complex than that of most birds. During the Holocene this butterfly has taken to migrating in the sense that birds do. They breed over much of the USA, laying their eggs on milkweeds of the Family Asclepiadaciae. In autumn the butterflies move south and southwest to winter in great numbers (up to 1 million) in tall trees in southern California and central Mexico. In spring the surviving butterflies return to the southern USA to breed and die. Their progeny move northwards, breeding as they go, and eventually providing the autumn butterflies that will migrate to their progenitors' wintering areas. Then the cycle starts again.

In the last century the American Monarch suddenly expanded its range which now includes various Pacific and Indian Ocean islands, including Australia and Mauritius, as well as various North Atlantic islands, and even eastern Spain. It has been suggested that this expansion was the result of clearing the north American forests for agriculture, permitting a great increase in the number of milkweeds and of the butterflies whose larvae feed on them. The butterfly population exploded in the middle decades of the last century across half the world until the main populations standardized their range by migrating to cluster in southern California and central Mexico. The recency of their expansion is witnessed by the lack of other butterflies which mimic them to obtain protection from vertebrate predators. These usually find American Monarchs distasteful and poisonous. The similarly distasteful and poisonous African Monarch has a suite of mimics befitting its long residence in Africa.

Much attention has been given to the study and conservation of these concentrations of butterflies because it is a unique spectacle in the insect world. The techniques and insights developed, and set out in this volume, warrant attention by conservationists generally.

R.K. Brooke

NOTICE

OWL PELLETS REQUIRED

Material from the Cape Province is needed for a revision of the rodent genus *Otomys*, which is being investigated at the Transvaal Museum. Owl pellets are an excellent source of samples of rodent skulls, and anyone who can provide a series of owl pellets from any locality in the Cape Province should please contact:

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