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Estimation of Biological Indices for Little-known African Owls

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ABSTRACT

Biological indices for 16 little-known species of African owls are estimated. The estimations are based, primarily, on allometric scaling relationships derived from the biological indices reported for some 40 well-studied species of owls. This comparative approach is offered as a preliminary method of deriving the basic information necessary for conservation planning and management. Such an approach should be applicable to all homeotherms, in particular those species that are rare, inaccessible or, for some other reason, difficult to study.

INTRODUCTION

To develop management plans for the conservation of a bird species, it is necessary to know as much about the biology of that species as possible. Information of particular importance includes its habitat preference, its home range requirements, its feeding requirements, its breeding season, its reproductive capacity, the duration of its incubation, nestling and post-fledging periods, its age at first breeding and its life expectancy.

The contention of this paper is that it is possible to estimate many of these indices from information available in museum collections and the literature. The stimulus for this analysis came from preparing texts on strigid owls for *Birds of Africa, Vol 3* (Kemp in press). Basic details of the biology of 13 of the 23 species endemic to the continent were lacking. There are about 140 species of owls in the world and my search of the literature for this paper has revealed basic biological indices for only 40 species, most of the undocumented species existing in tropical rainforest. It should be noted that the more indices available for analysis, the greater the precision with which predictions can be made.

It is suggested that the approaches presented here offer sufficient precision for preliminary planning of the conservation of these little-known species. Furthermore, these plans can be made with minimum expenditure of time, funds and manpower. The approach is applicable to most other groups of homeotherms and the work of Newton (1979), in the context of this conference, provides an excellent platform for predictions about diurnal birds of prey.

METHODS

Indices of the body size and biology of as many species of owls as possible were tabulated from information available in the literature, personal research and personal communications. Data were obtained for most species in the Holarctic region, for some species in the Afrotropical and Australasian regions, but for none of the species endemic to the Neotropical or Oriental regions.

Data on body mass and wing length were taken from as large a sample size as possible for each sex. Where variations in mass or wing length were recorded over the range of a species, then the largest sample from where other biological indices were recorded was included. Mean egg size was tabulated, together with an index of egg size formed by adding together the mean length and mean breadth.

These data were used, directly or indirectly, as a measure of body size in subsequent allometric regressions.

The following biological indices were also tabulated. The minimum mean home range was taken from the largest sample size available for prime habitat and was chosen to indicate the density which a species might attain in optimum habitat. Mean clutch size was tabulated, but where only ranges of clutch size were given, then the median value was used. Median values were taken for incubation and nestling periods, due to lack of means or sample sizes being given. The nestling period was taken as the time to making the first flight, as an indication of co-ordination and ability to avoid predators, rather than time to leaving the nest. The latter depends on the nest site and is shorter for open- or ground-nesting species due to their more rapid nestling growth (Saunders *et al.* 1984; Wijnandts 1984). Incubation and nestling periods were also combined to tabulate the total nesting cycle. The post-fledging period was taken as the minimum time from flying to leaving the parental territory, the latter often coinciding with attainment of the first full plumage of feathers. Age at first breeding was taken as the youngest age recorded, not necessarily the mean value for any population. Longevity records were derived from survival of wild birds as well as captives. The former give more an indication of lifespan than potential longevity, but more detailed information was not available.

COMMENTS ON TAXONOMY

Predictions from comparisons between species are most precise when the species are closely related. Unfortunately, the higher taxonomy of owls appears to be poorly resolved. There is general agreement that the orders Strigiformes and Caprimulgiformes are sister groups (Sibley & Ahlquist 1972, Sibley pers. comm.). There is also general agreement that the families Phodilidae, Tytonidae, and Strigidae are the primary divisions of the owls. The Phodilidae (2 species of *Phodilus*) and Tytoninae (12 species of *Tyto*) are often combined (Burton 1984, but see Marshall 1966).

It is within the 24 genera and 126 species of Strigidae that there is least consensus (e.g. Cramp 1985). The groupings of species used in this paper are based on the preliminary DNA-DNA hybridisation results of Sibley and Ahlquist (pers. comm.). Unfortunately, there are too few species studied to permit separate analyses of each clade or comparisons between clades. Fortunately, owls are conservative in their design and habits, compared to many other groups of birds, including diurnal raptors, so that comparisons across clades are unlikely to be too biased by effects of differences between clades.

RESULTS

Table 1 presents information, for as many species as possible, on mass, wing length, egg size and index of egg size, minimum mean home range, mean clutch size, incubation period, nestling period, post-fledging period, age at first breeding and longevity. Results of regression analyses of these data are represented in Table 2. Details of and commentary on these and other indices of comparative owl biology are presented below.

Habitat preference: First-order habitat preferences are evident from the geographical distribution of a species. More details may be derived from analysis of location and altitude on labels of museum specimens or in publications, and comparison with topographical and vegetation maps.

Mass, wing length and egg size: An accurate measure of body size is essential for any allometric comparisons. Body mass is the best index of body size, in theory but not in practice. Mass may differ with age, sex, condition and season, and adequate samples are lacking for all but the most common species. For example, Marshall (1978) could list masses for only 24 of the 78 taxa of *Otus* that he reviewed, with a mean of three masses per taxon. It is useful, therefore, to establish some practical estimate of body mass. High correlation coefficients were found for female and male mass versus wing length and female mass versus the egg size index (.948, .945 and .981 respectively, Table 2). The egg size index shows the highest correlation to female mass and is a practical alternative from which to estimate female mass since egg sizes are available for at least 86 of the 140 owl species, as well as many subspecies (e.g. Schönwetter 1964). Wing length can be used to estimate body mass when the mass or eggs of a species are not described.

Table 2. Results, in logarithms, of regression analyses on the data in Table 1, transformed into logarithms for calculations of the equation log y = log a + b log x.

INDEPENDENT VARIABLE (x axis)	DEPENDENT VARIABLE (y axis)	SCALING FACTOR b	INTERCEPT a	CORREL COEFF.	STANDARD ERROR	SAMPLE SIZE
Female mass, g	Female wing length, mm	0.391	1.388	0.948	0.067	38
Male mass, g	Male wing length, mm	0.404	1.371	0.945	0.068	37
Female mass, g	Egg size index, mm	0.212	1.337	0.981	0.022	39
Female mass, g	Min. mean home range, ha	1.296	-1.235	0.748	0.604	28
Female mass, g	Mean (median) clutch size	-0.145	0.877	-0.430	0.157	39
Female mass, g	Incubation period, d	0.089	1.253	0.767	0.039	
Female mass, g	Nestling period, d	0.227	1.004	0.834	0.078	
Female mass, g	Total nesting cycle, d	0.171	1.403	0.848	0.056	
Female mass, g	Fledging period, d	0.405	0.632	0.621	0.247	
Female mass, g	Age at 1st breeding, y	0.335	-0.769	0.812	0.111	
Female mass, g	Longevity, m	0.453	1.200	0.872	0.132	

Ecological requirements: Owls have a basal metabolic rate (BMR) about 25% less than most other non-passerine birds (and slightly lower than diurnal raptors) (BMR = 1.435 M .759, r=.973, n=13, BMR in kJ, M in grams, Wijnandts 1984). They thus require proportionately less food and their daily requirements of metabolised energy (ME) can be estimated from their body mass (ME = 8.630 M .578, r=.958, n=13, ME in kJ/bird/day, M in grams, Wijnandts 1984). The daily requirements of an individual of a species can be extrapolated to estimate food needed for annual survival, and possibly also for breeding. Indications of diet can be obtained from stomach contents, analyses of pellets and prey records. This, together with an estimation of annual requirements, may allow some assessment of the prey base available.

Minimum mean home range is related theoretically to metabolic rate and food requirements (Calder 1984). It should be predictable, therefore, from its correlation with body size (r=.748, Table 2). It should also allow estimation of the maximum density which a species might attain in optimum habitat, depending on its breeding organisation, and thereby the population which might be expected in a conserved area.

Breeding season and reproductive capacity: Breeding season and reproductive capacity can often be inferred from museum specimens or the literature. Gonad size, incubation patches and oviduct eggs are all indicators of timing of breeding, besides more definite data from records of eggs, nestlings or fledglings. Furthermore, presence of moult indicates when a species is not likely to be breeding. Records of active follicles, clutch size and brood size provide information on the mean reproductive capacity. This can only be predicted poorly by allometry (r=.430, Table 2). Larger species tend to lay smaller clutches but there is much variation suggesting that this trait is readily adaptive.

Most owls raise only one brood per season (but for opportunists like some *Tyto, Asio* and *Otus* species) and this is especially likely to hold true for tropical species. Larger species can be expected to breed only every second or third year on average (Kemp in press, cf. Newton 1979 for diurnal raptors) but there are insufficient data from large owls, especially tropical species, to confirm this.

Growth and development: Knowledge of the duration of growth to fledging, independence and sexual maturity are important for timing of management activities and estimation of population dynamics. Incubation and nestling periods correlate well with body size (r=.767 and .834 respectively, r=.848 for the total nesting cycle, Table 2). Post-fledging period is more variable (r=.621, Table 2) and would be difficult to predict without knowing something about the biology of the species concerned. Age at first breeding is also well correlated with body size (r=.812, Table 2), with larger species tending to be older when starting to breed than smaller ones.

Longevity: Maximum recorded ages of owls correlate well with their body mass (r=.872, Table 2). Longevity is not the same as average life span or life expectancy for members of a wild population, but these parameters, of importance in assessing population dynamics, are correlated to longevity (Calder 1984).

DISCUSSION

The application of allometry to the understanding of animal design and function has received considerable attention recently (e.g. Western & Ssemakula 1982; Peters 1983; Calder 1983, 1984). The extent to which aspects of the form, physiology, mobility, reproduction, growth, ecology and population dynamics can be predicted by scaling to body size is encouraging. Even greater precision can be expected once the data used in regressions are improved and where additional scaling relationships, to independent variables other than body size, begin to explain variation around the allometric regression (Western & Ssemakula 1982; Kemp 1985).

An advantage of the scaling approach is that predictions can be made about the biology of a species that can later be measured directly. Predictions of some of the life-history parameters so far undescribed for African owls are given in Table 3, together with a few measured values for these estimates (from Kemp in press). Where deviations from the allometric predictions are found, these are likely to be important in alerting biologists to special adaptive features of a species that might be vital to its conservation (e.g. *Strix butleri*, Table 3).

A study of the relationship between design, habitat use and diet is necessary before any improvements can be made in prediction of habitat preference and food. A detailed analysis of proportions and external anatomy of well studied species, in relation to their exact use of the habitat, their hunting methods and their diet, would be an important contribution.

What constitutes optimum habitat for an owl species can only be determined by comparison of density, home range and productivity in different areas. Obviously, in suboptimum habitats, the species can exist with larger home ranges, and therefore at lower densities, than it does in optimum habitat. The relationship between home range or density recorded in an area and the predicted minimum home range (and maximum density) may serve as a measure of the quality of any habitat surveyed, with respect to the species concerned. This would be particularly useful for owls, where density, based on calling males, and territory size, based on response to playback (which in many tropical species is likely to be the same as home range), are among the more easily determined biological indices.

Mean clutch size, as an indication of reproductive capacity, should be confined to the mean for pairs existing in optimum habitat, as discussed above. Deviations from this figure might also be used as a measure of habitat quality in other areas and seasons.

Improved data are likely to permit greater accuracy in prediction of growth indices and population dynamics. Some form of standardisation of the start and finish of incubation, nestling and post-fledging periods, together with presentation of means and sample sizes rather than just ranges or median values, would go far to improve the data base. The same applies to determining whether age at first breeding refers to physiological maturity, or to when breeding is first attempted in the wild.

There appears to be a bias introduced into these analyses by the high proportion of species from high northern latitudes that have been included. This is evident in the frequency with which these species lie far off the regression lines, usually in a direction that suggests that they are more r-selected (smaller eggs, large clutch size, smaller home range, faster growth and development, short post-fledging period and low longevity) than sub-tropical and tropical owls. Additional data from more tropical owls would correct this bias or allow for separate analyses for owls from different latitudes.

It is worth noting that work done on owls in one part of the world, even common species, provided it documents the required indices necessary for scaling, might have direct application to the conservation of rare owls in other parts of the world. Workers, especially in museums and zoos, should be encouraged to make maximum use of specimens which come to hand in measuring, at least, aspects of body size, brain size and body temperature. Field and zoo workers should also plan to record these and other measures of the growth, development and ecology that have application in conservation planning and management. There is a role, therefore, for many people to contribute to conservation of rare owls, however remote they may be from these owls. Such a combined and theoretical approach may expedite the conservation of owls, especially those in tropical forests where many may have only a short future.

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Appendix. Common names of species mentioned in text.

Tyto alba Barn Owl
T. capensis Grass Owl
T. novaehollandiae Masked Owl
Speotyto cunicularia Burrowing Owl
Athene noctua Little Owl
Glaucidium perlatum Pearl-spotted Owlet
G. capense Barred Owlet
G. passerinum Eurasian Pygmy Owlet
G. gnoma American Pygmy Owlet
G. brazilianum Ferruginous Pygmy Owlet
G. tephronotum Red-chested Owlet
G. albertinum Albertine Owlet
G. sjostedti Chestnut-backed Owlet
Micrathene whitneyi Elf Owl
Surnia ulula Hawk Owl
Ninox rufa Rufous Owl
N. strenua Powerful Owl
N. connivens Barking Owl
N. novaeseelandiae Boobook Owl
Aegolius arcadius Saw-whet Owl
A.funereus Tengmalm's Owl
Otus senegalensis African Scops Owl
O. leucotis White-faced Scops Owl
O. asio Screech Owl
O. scops Eurasian Scops Owl
O. icterorhynchus Sandy Scops Owl
O. ireneae Sokoke Scops Owl
O. brucei Bruce's Scops Owl
O. hartlaubi Sao Tome Scops Owl
O. pembaensis Pemba Scops Owl
Asio flammeus Short-eared Owl
A. capensis African Marsh Owl
A. otus Long-eared Owl
Bubo bubo Eurasian Eagle Owl
B. capensis mackinderi Mackinder's Eagle Owl
B. c. capensis Cape Eagle Owl
B. africanus Spotted Eagle Owl
B. lacteus Milky Eagle Owl
B. virginianus Great Horned Owl
B. poensis Fraser's Eagle Owl
B. shelleyi Shelley's Eagle Owl
B. leucostictus Akun Eagle Owl
Nyctea scandiaca Snowy Owl
Scotopelia peli Pel's Fishing Owl
Scotopelia ussheri Rufous Fishing Owl
S. bouveri Vermiculated Fishing Owl
T. tenebricosa Sooty Owl
Strix woodfordii African Wood Owl
S. aluco Eurasian Tawny Owl
S. uralensis Ural Owl
S. nebulosa Great Grey Owl
S. varia Barred Owl
S. butleri Hume's Tawny Owl
Jubula lettii Maned Owl

Table 1. Mass, wing length, mean egg size, egg size index, minimum mean home range, mean (median) clutch size, median incubation period, median nestling period, total nesting cycle, median post-fledging period, minimum age at first breeding and maximum longevity recorded for owls.

SPECIES AND REFERENCES	MASS M(n)	MASS F(n)	WING LENGTH M(n)	WING LENGTH F(n)	MEAN EGG SIZE LxB (n)	EGG SIZE INDEX L+B	MIN. MEAN HOME RANGE (ha)	MEAN (MEDIAN) CLUTCH SIZE	INCUBATION PERIOD (d)	NESTLING PERIOD (d)	TOTAL NESTING CYCLE	POST-FLEDGING PERIOD (d)	AGE AT FIRST BREEDING (y)	LONGEVITY
Tyto alba 2	304(25)	323(31)	286(54)	287(66)	41x32 (57)	73	250	5.7	31	53	84	28	1-2	256
T. capensis 6,7	419(8)*		334(15)*		42x34 (32)	75		4	32	49	81	30		
T. novaehollandiae 4,15	545+	673+	302+	332+	45x36 (?)	81	500	2-3	35	42	77	30		
T. tenebricosa 15	600+	875+	286+	392+	48x39 (11)	87	200	2	36	54	90	120		
Speotyto cunicularia 3,5,12	159(31)	151(15)	169(67)	166(36)	31x26 (214)	57		8	28					132
Athene noctua 2	160(5)	176(5)	163(13)	166(13)	36x30 (100)	66	35	3.6	28	33	61	30	1	114
Glaucidium perlatum 1,14	69(12)	91(13)	105(15)	107(15)	31x26 (25)	57	58	3	29	31	60			
G. capense 1	117(3)	122(6)	139(15)	140(10)	32x27 (7)	59		2-3		32				
G. passerinum 2	59(11)	71(14)	98(11)	105(23)	29x23 (80)	52	125	5.2	29	30	59	28	1	
G. gnoma 3,5,10,12	62(42)	73(10)	91(112)	95(56)	27x23 (21)	50		3-4	28	23	51			
G. brazilianum 3,9,12	61(29)	75(69)	?	?	29x23 (50)	52		3-4	28	29	57			
Micrathene whitneyi 3,5,9,11,12	41(20)*	45(?)	106(35)	107(23)	27x23 (50)	50	>1	3	24	31	55			84
Surnia ulula 2	270(17)	320(17)	234(15)	238(15)	40x32 (100)	72		6.6	27	30	57	45	1	
Ninox rufa 8,15	1225+	860+	369+	350+	52x46 (6)	98	400	2	37	49	86	30		
N. strenua 8,15	1415+	1325+	405+	386+	55x46 (?)	101	800	2	37	49	86	120		360
N. connivens 8,15	468+	455+	300+	299+	47x39 (36)	86	200	2-3	36	35	71	90	2	
N. novaeseellandiae 8,15	234+	277+	235+	241+	43x34 (4)	77	8	2-3	34	41	75		1	348
Aegolius arcadicus 3,5,12	75(27)	91(18)	132(37)	139(20)	30x25 (52)	55		5-6	27	31	58			
A. funereus 3,5,12	102(5)	140(4)	162(10)	174(5)	32x27 (47)	59		5	28	31	59			
Otus senegalensis 1	63(26)*		127(23)	130(19)	29x25 (17)	54	16	2-3	22	27	49	25		
O. leucotis 1	202(6)	206(10)	194(24)	191(14)	39x35 (30)	74	250	2-3	30	30	60			
O. asio 3,5,12,13	160(38)	184(36)	163(53)	167(61)	36x30 (56)	66		4-5	26	28	54		1	156
O. scops 2	78(136)	92(169)	160(11)	161(10)	31x27 (100)	59	20	4.5	25	25	50	35	0.7	150
Asio flammeus 2	278(3)	312(5)	315(39)	319(28)	40x31 (100)	71	15	6	26	26	52	30	1	153
A. capensis 1	313(35)*		296(10)	288(9)	40x34 (55)	74	250	3	28	32	60			
A. otus 2	233(6)	278(8)	294(57)	299(64)	40x32 (100)	72	75	4.2	28	30	58	30	1	333
Bubo bubo 2	2403(20)	3049(18)	444(9)	482(12)	60x50 (56)	110	1600	2.6	35	55	90	98	2-3	816
B. c. mackinderi 1,16	1304(2)	1570(5)	393(6)	418(5)	58x47 (26)	105	2500	2.1	35	65	108	90		
c. capensis 1,14	929(4)	1347(3)	357(1)	377(4)	53x45 (9)	98	5800	2	38	73	111			
B. africanus 1	585+	685+	333(15)	339(15)	49x41 (80)	90	1933	2-3	31	41	72	42	1	120"
B. lacteus 1,14	1704(4)	2625(6)	448(18)	465(22)	63x51 (30)	114	7000	2	39	63	102	180	3-4	180"
B. virginianus 3,5,12	1142(94)	1507(94)	339(125)	357(118)	56x47 (53)	103		2-3	35	66	101		2	348
Nyctea scandiaca 2	1730(36)	2120(23)	412(31)	445(32)	57x45 (100)	102	400	5.4	32	45	77	25		113"
Scotopelia peli 1	?	2188(4)	431(7)	426(6)	63x52 (32)	115	100	2	32	69	101	300		
Strix woodfordii 1	252(5)	293(2)	249(13)	249(16)	43x38 (11)	81	70	2	31	35	66	90	1	
S. aluco 2	409(20)	533(22)	267(35)	278(30)	47x39 (100)	86	18	2.7	29	35	64	90	1-2	226
S. uralensis 2	590(12)	870(12)	358(14)	363(15)	50x42 (36)	92	400	2.8	32	35	65	60	1	168"
S. nebulosa 2	778(16)	1005(11)	446(8)	452(13)	53x43 (153)	96	260	4.4	29	63	92	80	2	83"
S. varia 3,5,12	632(20)	801(24)	312(6)	320(15)	49x42 (82)	91		2-3	28	42	70			276

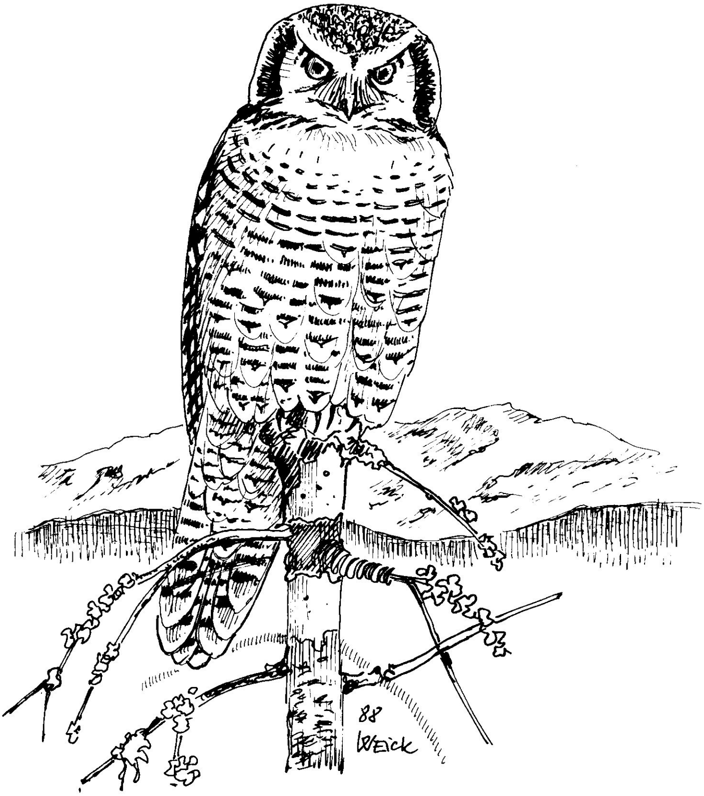
+ median value
* samples in which no marked dimorphism evident, measure used for both sexes in analyses.
" data considered inadequate for inclusion in analysis.

Literature consulted: 1. Kemp (in press); 2. Cramp 1985; 3. Terres 1980; 4. Pettigrew et al. 1986; 5. Snyder & Wiley 1976; 6. Maclean 1985; 7. Steyn 1982; 8. Frith 1982; 9. Dunning 1985; 10. Holt & Norton 1986; 11. Ligon 1968; 12. Bent 1938; 13. Vancamp & Henny 1975; 14. Kemp et al. 1985; 15. Schodde & Manson 1980; 16. Benson & Irwin 1967.

SPECIES	RECORDED MASS M(n)	RECORDED MASS F(n)	ESTIMATED FEMALE MASS BASED ON WING LENGTH	ESTIMATED FEMALE MASS BASED ON EGG INDEX	WING LENGTH M(n)	WING LENGTH F(n)	RECORDED EGG SIZE LxB (n)	EGG SIZE INDEX L+B	FEMALE MASS USED IN CALCU-LATIONS	MIN. MEAN HOME RANGE (ha)	MEAN (MEDIAN) CLUTCH SIZE	INCUBATION PERIOD (d)	NESTLING PERIOD (d)	TOTAL NESTING PERIOD (d)	FLEDGING PERIOD (d)	AGE AT 1ST BREEDING (y)	LONGEVITY (m)
Glaucidium tephronotum	87(8)	89(2)	41		105(5)	104(2)			89	20	3.9	26	28	55	26	0.8	121
G. capense	117(3)	122(6)	87	111	139(15)	140(10)	32x27 (7)	59	122	29	3.8(2-3)+	27	30(32)+	58	30	0.9	140
G. albertinum			73		131(1)*				73	15	4.0	26	27	53	24	0.7	111
G. sjostedti			139	141	160(8)	168(2)	34x28 (?)	62	141	36	3.7	28	31	59	32	0.9	149
Otus icterorhynchus	75(3)	72(4)	70		129(8)*				72	15	4.1	26	27	53	24	0.7	110
O. irenea	48(2)		51		114(2)*				51	10	4.3	25	25	50	21	0.6	94
O. brucei	100(1)		107	103	153(9)	152(10)	31x27 (?)	58	103	24	3.8	27	29	56	28	0.8	129
O. hartlaubi			79		131(5)	135(3)			79	17	4.0	26	27	53	25	0.7	115
O. pembaensis			102		151(5)	149(2)			102	23	3.9	27	29	56	28	0.8	129
Bubo poensis	575(1)	746(4)	720		301(10)	320(10)			746	308(500)+	2.9	32	45	78	61	1.6	317
B. shelleyi		1257(1)	1771		466(1)	455(2)			1257	605	2.7	34	51	86	77	1.9	402
B. leucostictus	511(2)	555(3)	731		318(6)	322(7)			555	210	3.0	31	42	75	55	1.4	277
Scotopelia ussheri	743(1)		834		339(3)*				834	355	2.8	33	46	80	65	1.6	334
S. bouveri			637		311(4)	305(1)			637	251	3.0	32	44	76	59	1.5	295
Jubula lettii		183(1)	423		268(3)	206(7)			183	50	3.5	28	33	62	35	1.0	168
Strix butleri	?	220(3)	379		249(4)*				220	63	3.4(5)+	29(35)+	34(37)+	64(72)+	38	1.0	182

* measurements only available for males or for both sexes combined.
+ recorded value for index
Literature consulted: Kemp in press; Schönwetter 1984.

Table 3. Predicted values of life history indices for some African strigid owls (+), from regressions calculated from data in Table 1. and listed in Table 2.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