

- and female age in the primary reproductive output of Pied Flycatchers. *Oecologia* 126:339–344.
- SHELDON, B. C., AND S. VERHULST. 1996. Ecological immunology: Costly parasite defenses and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution* 11:317–321.
- SIKKAMÄKI, P., O. RÄTTL, M. HOVI, AND G. F. BENNETT. 1997. Association between haematozoan infections and reproduction in the Pied Flycatcher. *Functional Ecology* 11:176–183.
- STEARNS, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- SVENSSON, L. 1992. *Identification Guide to European Passerines*. Fingraf AB, Stockholm, Sweden.
- THOMSON, D. L., P. MONAGHAN, AND R. W. FURNESS. 1998. The demands of incubation and avian clutch size. *Biological Review* 73:293–304.
- WIDEMO, F. 1989. Effect of blood parasites on the Col-lared Flycatcher *Ficedula albicollis*. Honors thesis, Department of Zoology, Uppsala University, Uppsala, Sweden.
- WIEHN, J., AND E. KORPIMÄKI. 1998. Resource levels, reproduction and resistance to haematozoan infections. *Proceedings of the Royal Society of London, Series B* 265:1197–1201.
- WIEHN, J., E. KORPIMÄKI, AND I. PEN. 1999. Haematozoan infections in the Eurasian Kestrel: Effects of fluctuating food supply and experimental manipulation of parental effort. *Oikos* 84:87–98.
- WILLIAMS, J. B. 1997. Energetics of avian incubation. Pages 375–415 in *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, New York.

Received 5 August 2000, accepted 25 January 2001.

Associate Editor: C. Blem

*The Auk* 118(3):755–759, 2001

## Diving Depths of Shearwaters

ALAN E. BURGER<sup>1</sup>

*BirdLife Seychelles, P.O. Box 1310, Mont Fleuri, Seychelles*

**ABSTRACT.**—Maximum diving depths were measured for shearwaters breeding on Cousin Island, Seychelles. Eighty-three percent of 23 Wedge-tailed Shearwaters (*Puffinus pacificus*) dived, and their mean maximum depth was 14 m (SD = 23 m, range 1–66 m,  $N = 19$ ). All Audubon's Shearwaters (*P. lherminieri*) dived, and their mean maximum depth was 15 m (SD = 12 m, range 6–35 m,  $N = 7$ ). These data contradict the hypothesis that tropical shearwaters should not specialize in underwater foraging. They are capable of exploiting deep prey unavailable to most other tropical seabirds. Five *Puffinus* species (temperate and tropical) attained allometrically scaled maximum depths comparable to those of penguins and alcid.

It has long been known that shearwaters dive beneath the ocean to forage, using their feet and wings for propulsion (Brown et al. 1978, 1981), and show anatomical adaptations for this mode of foraging (Kuroda 1954, Warham 1990). Simple depth gauges measuring the maximum depths indicate some remarkably deep dives attained by shearwaters (Wei-

merskirch and Sagar 1996, Weimerskirch and Chérel 1998, Keitt et al. 2000). More sophisticated time-depth-recorders (TDRs), which indicate time spent at various depths and trace individual dives, have revealed much of the underwater foraging behavior of penguins, alcid, and cormorants (Kooyman 1989, Croll et al. 1992, Wilson 1995, Watanuki et al. 1996), but have not been applied to shearwaters. I report maximum depths attained by two tropical shearwaters, Wedge-tailed (*Puffinus pacificus*) and Audubon's (*P. lherminieri*) shearwaters, breeding on Cousin Island, Seychelles (4°20'S; 55°40'E), and review data on diving depths of other shearwaters. I examine the hypothesis that tropical shearwaters should not specialize in underwater foraging (Brown et al. 1978), and discuss the role of diving in tropical shearwaters.

**Methods.**—Maximum-depth gauges were made from flexible plastic tubing with internal diameter 0.8 mm, lined with a thin layer of icing sugar and sealed at one end. Gauges were 70–120 mm long on Wedge-tailed Shearwaters, and 70–90 mm long on Audubon's Shearwaters. As the gauge is submerged, the increasing pressure forces water into the tube, dissolving the sugar and leaving a record of the deepest dive (Kooyman et al. 1971, Burger and Wilson 1988, Hedd et al. 1997). The equation provided

<sup>1</sup> Present address: Department of Biology, University of Victoria, Victoria, British Columbia V8W 3N5, Canada. E-mail: aburger@uvic.ca

by Burger and Wilson (1988) was used to calculate maximum dive depths.

Cousin Island supports breeding populations of ~13,000 pairs of Wedge-tailed and 5,000–10,000 pairs of Audubon's shearwaters (Burger and Lawrence in press). At the time of this study (7–17 June 1999), Wedge-tailed Shearwaters were returning nightly to nest cavities for courtship, but did not have eggs or chicks. Audubon's Shearwaters breed all year round on Cousin Island and the status of those used in the study was not known. Adult shearwaters sitting in or near nest cavities were caught and banded at night. Each gauge was firmly tied to the base of a single tail feather with a thread (dental floss). Once attached the gauges were surrounded by feathers and created no impediments to the birds. Handling time was 10–15 min. Gauges not recovered would eventually work loose or be lost when the birds molted. Each bird was sampled once. I made no attempt to collect food samples, and none of the captured birds regurgitated food.

Prolonged deployment increases errors in these devices (Burger and Wilson 1988). I included gauges recovered within two days of deployment, and all except two (one for each species) were recovered after one day. I encountered an unusual problem in the form of tiny ants that crawled inside the tubes and removed the sugar. Ants removed sugar unevenly, in contrast to the sharp boundary created by water, and so with careful inspection I was able to reject gauges affected by ants.

**Results.**—Out of 23 undamaged gauges recovered from Wedge-tailed Shearwaters, 19 (83%) indicated some diving activity (Fig. 1) and their mean maximum depth was 14 m (SD = 23 m, range 1–66 m). All 7 gauges recovered from Audubon's Shearwaters indicated diving, and the mean maximum depth was 15 m (SD = 12 m, range 6–35 m). Most Wedge-tailed Shearwaters remained within 20 m and most Audubon's Shearwaters within 10 m of the surface (Fig. 1).

**Discussion.**—Many procellariiform species dive to capture prey, but most species remain within 1–5 m of the surface (Warham 1990, Prince et al. 1994, Hedd et al. 1997), with the exception of the specialised diving petrels, Pelecanoididae (Prince and Jones 1992, Chastel 1994, Zavalaga and Jahncke 1997). Some shearwaters of the genus *Puffinus* regularly use pursuit diving for foraging (Brown et al. 1978, 1981; Warham 1990). They show adaptations for underwater swimming, including flattened tarsi and humeri, and shorter wings and higher wing-loading than most other petrels (Kuroda 1954, Warham 1977, 1990). Maximum diving depths have been measured using gauges in five species of *Puffinus* (Table 1). Some published depth records unavoidably came from prolonged foraging trips. There is a greater chance that those gauges overestimate maximum depths with repeated submersion and prolonged de-

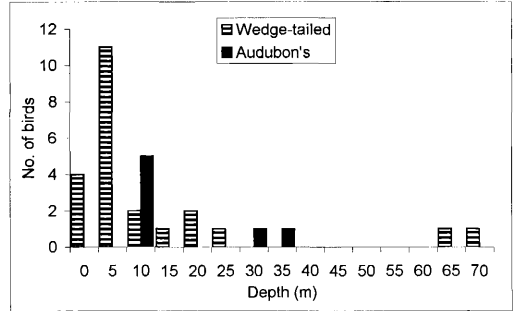


FIG. 1. Frequency distribution of maximum depths attained by Wedge-tailed and Audubon's shearwaters on Cousin Island, Seychelles. X-axis labels indicate the upper limit of each 5 m depth category.

ployment, although the error with dives >20 m was likely to be <10% (Burger and Wilson 1988). There is also a greater probability of recording an exceptionally deep dive during a long trip. Those data are compared with depths measured in Cory's Shearwater (*Calonectris diomedea*) and White-chinned Petrel (*Procellaria aequinoctialis*), which share many similarities with *Puffinus* but seem less morphologically adapted to diving (Warham 1977, 1990).

All five *Puffinus* shearwaters demonstrated remarkable diving abilities (Fig. 2). Their maximum diving depths clustered close to the allometric equation derived from maximum diving depths of penguins and alcid (maximum depth (meters) =  $75.905 M^{0.316}$ , where M is body mass in kilograms; Burger 1991). Maximum depths of *Calonectris* and *Procellaria* fell well below that regression. The diving abilities of *Puffinus* shearwaters require more detailed study, using TDR and activity data-loggers, to confirm whether deep diving forms a significant part of their foraging routine. It will be fascinating to discover whether they show convergent anatomical, physiological, and behavioral adaptations for prolonged diving to those being revealed for penguins, alcid, and cormorants.

Kuroda (1954) regarded smaller species of *Puffinus* as morphologically more specialized for diving than most other shearwaters. Visual observations of small shearwaters (Brown et al. 1978), including Audubon's Shearwater (Harris 1969), confirmed that they dived, but this study is the first to confirm that diving occurs regularly (in all foraging trips made in my small sample), and that they are proficient, deep divers.

Keitt et al. (2000) speculated that shearwaters might be most efficient at diving during wing molt, when the reduced wing area would produce sufficient propulsion but less drag. None of the shearwaters in my sample showed any sign of primary

TABLE 1. Maximum diving depths in shearwaters and petrels measured with depth gauges.

Species	Body mass (g)	No. of depth records	Duration of gauge deployment (days)		Maximum depth (m) depth $\pm$ SD (m)	Mean maximum depth $\pm$ SD (m)	Reference
			Mean	Range			
Wedge-tailed Shearwater <i>Puffinus pacificus</i>	426	19	1.1	1-2	66.4	13 $\pm$ 19	This study
Audubon's Shearwater <i>Puffinus lherminieri</i>	168	7	1.4	1-2	35.4	15 $\pm$ 12	This study
Black-vented Shearwater <i>Puffinus opisthomelas</i>	406	30	3.4	1-5	52	21 $\pm$ 11	Keitt et al. 2000
Sooty Shearwater <i>Puffinus griseus</i>	850	35	4.1	1-14	67	39 $\pm$ 20	Weimerskirch and Sagar 1996
Short-tailed Shearwater <i>Puffinus tenuirostris</i>							
Long trips	569	8	12.1	9-17	70.6	58 $\pm$ 11	Weimerskirch and Cherel 1998
Short trips	595	14	1.3	1-3	30	13 $\pm$ 7	Weimerskirch and Cherel 1998
Cory's Shearwater <i>Calonectris diomedea</i>	840	19	No data		1.4	0.3 $\pm$ 0.3	Monteiro et al. 1996
White-chinned Petrel <i>Procellaria aequinoctialis</i>	1270	11	5.8	1-12	13	6 $\pm$ 3	Huin 1994

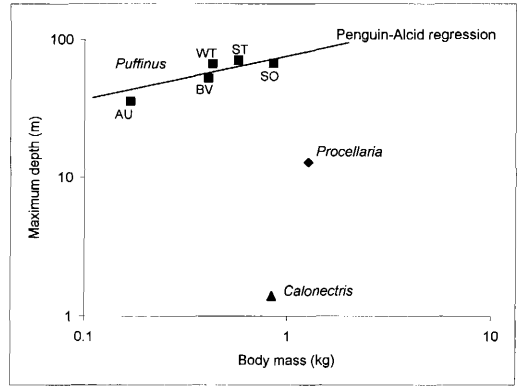


FIG. 2. *Puffinus* shearwaters had maximum diving depths similar to those of alcids and penguins. This log-log plot of maximum diving depths against body mass compares five species of *Puffinus* shearwaters (squares), including Audubon's (AU), Black-vented (BV), Sooty (SO), Short-tailed (ST), and Wedge-tailed (WT) shearwaters, with Cory's Shearwater (triangle) and White-chinned Petrel (diamond), and the allometric regression of maximum depths predicted for penguins and alcids (Burger 1991).

wing molt and all appeared to have recently replaced primaries.

Maximum diving depths are generally determined by allometrically scaled physiological limits (Kooyman 1989), whereas the depths of most foraging dives are determined by distribution of prey. Typical foraging dives are much shallower than maximum limits (Kooyman 1989, Burger 1991, Wilson 1995). That applies to the *Puffinus* shearwaters; their mean maximum dives were generally far shallower than the overall maximum (Table 1). More accurate depth profiles will emerge with deployment of TDRs that show the depth distribution of all underwater activities, and not just the deepest dive per foraging trip.

Brown et al. (1978) speculated that shearwater species specialized for diving should be restricted to richer, cold, or cool-temperate seas. The sparse distribution of prey and presence of predatory fish in the tropics was believed to favor shearwaters with more efficient gliding flight rather than specialist divers. Shearwaters specialized for diving tend to have somewhat shorter wings and higher wing loading and hence rely more on flapping flight (Warham 1977, 1990), which is normally associated with highly productive temperate and polar seas.

My data do not support the hypothesis that tropical shearwaters avoid diving in preference for surface foraging. Both Wedge-tailed and Audubon's shearwaters were proficient, deep divers, and most (83%) Wedge-tailed and all Audubon's shearwaters employed diving on foraging trips. Diets of those

species in Seychelles have not been recorded, but Pacific Wedge-tailed Shearwaters primarily take small schooling fish and squid (Harrison et al. 1983), and Audubon's Shearwaters take planktonic fish larvae and crustaceans (Harris 1969). Depth distribution of likely prey in Seychelles is not known, nor is it known whether shearwaters were restricting their foraging to concentrated prey patches. Neither species was restricted to the most productive water masses in the tropical Indian Ocean (Bailey 1968, Pocklington 1979).

Both Wedge-tailed and Audubon's shearwaters regularly feed at the surface (Harris 1969, Harrison et al. 1983, Warham 1990), as do most tropical seabirds (Ashmole and Ashmole 1967, Harrison 1990, Ballance et al. 1997). The shearwaters' diving abilities give them access to additional, deeper prey inaccessible to most other tropical seabirds. Even plunge-diving boobies and tropicbirds seem restricted to the upper 13 m (Le Corre 1997). More intensive research is needed to elucidate foraging behavior of tropical shearwaters, to confirm whether they fill a similar pursuit-diving niche to that occupied by penguins, alcid, and cormorants in cool-temperate and polar seas.

*Acknowledgments.*—This study was funded by a grant from the Second Dutch Trust Fund to BirdLife Seychelles. Additional support came from National Sciences and Engineering Research Council Canada and the University of Victoria. I thank Andrea Lawrence and Ahtee Labonté for field assistance, Nirmal Jivan Shah and Steve Parr for support and discussion, and Harry Carter, David Lee, and Yutaka Watanuki for helpful comments.

#### LITERATURE CITED

- ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. *Bulletin of the Peabody Museum of Natural History* 24:1–131.
- BAILEY, R. S. 1968. The pelagic distribution of seabirds in the western Indian Ocean. *Ibis* 110:493–519.
- BALLANCE, L. T., R. T. PITMAN, AND S. B. REILLY. 1997. Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. *Ecology* 78:1502–1518.
- BROWN, R. G. B., W. R. P. BOURNE, AND T. R. WAHL. 1978. Diving by shearwaters. *Condor* 80:123–125.
- BROWN, R. G. B., S. P. BARKER, D. E. GASKIN, AND M. R. SANDEMAN. 1981. The foods of Great and Sooty shearwaters *Puffinus gravis* and *P. griseus* in eastern Canadian waters. *Ibis* 123:19–30.
- BURGER, A. E. 1991. Maximum diving depths and underwater foraging in alcid and penguins. Pages 9–15 in *Studies of High-latitude Seabirds*. 1. Behavioural, Energetic and Oceanographic Aspects of Seabird Feeding Ecology (W. A. Montevecchi and A. J. Gaston, Eds.). Canadian Wildlife Service Occasional Paper 68.
- BURGER, A. E., AND A. D. LAWRENCE. 2001. Census of Wedge-tailed and Audubon's shearwaters on Cousin Island, Seychelles using call playback. *Marine Ornithology*. 29:in press.
- BURGER, A. E., AND R. P. WILSON. 1988. Capillary-tube depth gauges for diving animals: A review of their accuracy and applicability. *Journal of Field Ornithology* 59:345–354.
- CHASTEL, O. 1994. Maximum diving depths of Common Diving Petrels *Pelecanoides urinatrix* at Kerguelen Island. *Polar Biology* 14:211–213.
- CROLL, D. A., A. J. GASTON, A. E. BURGER, AND D. KONNOFF. 1992. Foraging behavior and physiological adaptation for diving in Thick-billed Murres. *Ecology* 73:344–356.
- HARRIS, M. P. 1969. Food as a factor controlling the breeding of *Puffinus lherminieri*. *Ibis* 111:139–156.
- HARRISON, C. S. 1990. *Seabirds of Hawaii: Natural History and Conservation*. Cornell University Press, Ithaca, New York.
- HARRISON, C. S., T. S. HIDA, AND M. P. SEKI. 1983. Hawaiian seabird feeding ecology. *Wildlife Monographs*, no. 85.
- HEDD, A., R. GALES, N. BROTHERS, AND G. ROBERTSON. 1997. Diving behaviour of the Shy Albatross *Diomedea cauta* in Tasmania: Initial findings and diver recorder assessment. *Ibis* 139:452–460.
- HUIN, N. 1994. Diving depths of White-chinned Petrels. *Condor* 96:1111–1113.
- KEITT, B. S., D. A. CROLL, AND B. R. TERSHY. 2000. Dive depth and diet of the Black-vented Shearwater (*Puffinus opisthomelas*). *Auk* 117:507–510.
- KOONYMAN, G. L. 1989. *Diverse Divers: Physiology and Behavior*. Springer-Verlag, Berlin.
- KOONYMAN, G. L., C. M. DRABECK, R. ELSNER, AND W. B. CAMPBELL. 1971. Diving behavior of the Emperor Penguin, *Aptenodytes forsteri*. *Auk* 88:775–795.
- KURODA, N. 1954. On the classification and phylogeny of the order Tubinares, particularly the shearwaters (*Puffinus*). Published by the author, Tokyo.
- LE CORRE, M. L. 1997. Diving depths of two tropical Pelecaniformes: The Red-tailed Tropicbird and the Red-footed Booby. *Condor* 99:1004–1007.
- MONTEIRO, L. R., J. A. RAMOS, R. W. FURNESS, AND A. J. DEL NEVO. 1996. Movements, morphology, breeding, molt, diet and feeding of seabirds in the Azores. *Colonial Waterbirds* 19:82–97.
- POCKLINGTON, R. 1979. An oceanographic interpretation of seabird distributions in the Indian Ocean. *Marine Biology* 51:9–21.
- PRINCE, P. A., N. HUIN, AND H. WEIMERSKIRCH. 1994. Diving depths of albatrosses. *Antarctic Science* 6:353–354.

- PRINCE, P. A., AND M. JONES. 1992. Maximum dive depths attained by South Georgia Diving Petrel *Pelecanoides georgicus* at Bird Island, South Georgia. *Antarctic Science* 4:433–434.
- WARHAM, J. 1977. Wing loadings, wing shapes, and flight capabilities of Procellariiformes. *New Zealand Journal of Zoology* 4:73–83.
- WARHAM, J. 1990. The Petrels: Their Ecology and Breeding Systems. Academic Press, London.
- WATANUKI, Y., A. KATO, AND Y. NAITO. 1996. Diving performance of male and female Japanese Cormorants. *Canadian Journal of Zoology* 74:1098–1109.
- WEIMERSKIRCH, H., AND Y. CHEREL. 1998. Feeding ecology of Short-tailed Shearwaters: Breeding in Tasmania and foraging in the Antarctic? *Marine Ecology Progress Series* 167:261–274.
- WEIMERSKIRCH, H., AND P. M. SAGAR. 1996. Diving depths of Sooty Shearwaters *Puffinus griseus*. *Ibis* 138:786–794.
- WILSON, R. P. 1995. Foraging ecology. Pages 81–106 in *The Penguins Spheniscidae* (T. D. Williams, Ed.). Oxford University Press, Oxford.
- ZAVALAGA, C. B., AND J. JAHNCKE. 1997. Maximum dive depths of the Peruvian Diving-petrel. *Condor* 99:1002–1004.

Received 3 August 2000, accepted 20 January 2001.

Associate Editor: D. Nettleship

*The Auk* 118(3):759–765, 2001

## Visual Signals for Individual Identification: The Silent “Song” of Ruffs

DAVID B. LANK<sup>1,3</sup> AND JAMES DALE<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada; and

<sup>2</sup>Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853-2702, USA

**ABSTRACT.**—Breeding male Ruffs (*Philomachus pugnax*) appear to communicate individual identity through extreme variation in coloration and pattern of their plumages. If plumage variation evolved to provide sufficient information to signal individual identity, we might expect different plumage components to vary independently. We find that variation in four plumage characteristics is largely independent. Previous studies produced conflicting answers about plumage-component independence, perhaps because they failed to separate two genetically distinct behavioral categories of males, which differ in plumage types, in their analysis. We propose that using plumage variation to signal individual identity, rather than voice (used by most other bird species) was favored by lengthy daytime male display in open habitats in close proximity to receivers. However, signaling associated with the unique dimorphism in this species' male mating behavior might also have influenced the evolution of extraordinary plumage diversity in this species.

Breeding male Ruffs (*Philomachus pugnax*) have the most variably colored and patterned feather tracts of any species of nondomesticated bird. This extraordinary variation facilitated study of sexual selection by allowing an early student to follow mating success of individuals at leks using natural markings

alone (Selous 1906–1907), and it has long been assumed to function as a cue for individual identity for Ruffs themselves (Hogan-Warburg 1966, van Rhijn 1983, 1991). Individual identification based on plumage variation has been demonstrated experimentally for just a few species of birds (Whitfield 1986, Watt 1986), including Ruffs (experiments by A. Segre Terkel in van Rhijn 1991; D. B. Lank et al. unpubl. data). Whereas many species of birds identify individuals by voice (Stoddard 1996, Wiley 2000), male Ruff courtship and aggressive displays are completely silent.

Did plumage variation in Ruffs specifically evolve to facilitate individual variation? Is the functional design of plumage variation consistent with that adaptive hypothesis? Characters specifically evolved to facilitate individual identification should have certain properties (Beecher 1982, Dale 2000, Dale et al. 2001). The most fundamental is sufficient phenotypic variation among individuals to facilitate discrimination by receivers. One simple and powerful way to generate such variation is to have independently varying signal components, each with high variance, that combine to produce many different phenotypes.

We examine to what extent the most prominent plumage characteristics of breeding male Ruffs vary independently. Previous analyses have produced conflicting results (Table 1; van Rhijn 1991). We revisit that question using automated and quantitative measurements of plumage characteristics, and by

<sup>3</sup> E-mail: dlank@sfu.ca