tree, however, may be later eaten by a nonvolant seed disperser. *B. jugularis* may therefore not only kill fig seeds but alter the nature of the seed shadow by directing seeds into a different portion of the disperser coterie than would have swallowed them had the ripe figs been left in the crown for arboreal and volant vertebrates to eat.

This study was supported by NSF DEB 80-11558 and the Servicio de Parques Nacionales de Costa Rica. The manuscript was constructively reviewed by G. Stevens and W. Hallwachs. It is dedicated to the surviving mate of the parakeet that was sacrificed.

Received 15 September 1980, accepted 7 April 1981.

Rete Mirabile Ophthalmicum in Hawaiian Seabirds

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The central role of the rete mirabile ophthalmicum (RMO) of birds in maintenance of a body-to-brain temperature difference has been well documented in several recent reports (Kilgore et al. 1979, Bernstein et al. 1979a, 1979b). The anatomical arrangement for counter-current heat exchange between the cerebral arterial supply of blood and cooler venous blood from evaporative respiratory membranes and the cornea has been reported for a number of species (Richards and Sykes 1967, Lucas 1970, Kilgore et al. 1976, Crowe and Crowe 1979), but no anatomical studies of the RMO in tropical seabirds have been reported. This study was undertaken to examine the anatomy of the RMO in some Hawaiian seabirds in view of the demanding and stressful environmental conditions encountered in the tropics.

The species, number of specimens examined, and collection points are listed in Table 1. Dissections were performed on fresh specimens in most cases. A binocular dissection microscope was used and annotated drawings made as the dissection progressed. The procedure involved the removal of the cranial skin and feathers with careful manipulation of the ventral intrasphenoid segment of the cerebral carotid arteries to expose the intercarotid anastomosis and external ophthalmic, external carotid, and internal carotid branches of the common carotid artery. After noting the configuration of the carotid segments, the dissection was extended to the temporal and orbital regions to expose the ophthalmic rete and rami of the external ophthalmic artery.

In all species examined, a RMO was found in a shallow depression in the temporal region of the head, lying in close contact with the skull between the otic process of the quadrate and the orbital ridge. A diagram of the arterial RMO for six species of Hawaiian seabirds is presented in Fig. 1. The RMO is composed of an arterial rete supplied by the external ophthalmic branch of the common carotid and a medial venous rete composed of branches of ophthalmic veins supplying venous blood to the cavernous sinus. The external ophthalmic artery crosses the middle ear in a canal dorsomedial to the oval window and emerges to subdivide into four rami: temporal, supraorbital, ophthalmic, and infraorbital. All rami and the inferior alveolar artery contribute vessels to the arterial component of the RMO.

The common carotid arterial supply to the RMO is derived from a unique intercarotid anastomosis characteristic of avian species (Baumel and Gerchman 1968). Two of the three principal patterns described by Baumel and Gerchman were observed (Table 1). The functional differences in the patterns of intercarotid anastomosis are not clear, but they may reflect differences in the amount of blood available for circulation to the RMO. Birds do not possess a cerebral arterial circle of Willis comparable to mammals, but the intercarotid anastomosis may serve as an effective substitute with the potential for shunting blood from one side to the other.

The existence of common morphologies for the RMO of these Hawaiian seabirds suggests that counter-current heat exchange is the common underlying mechanism for cooling the brain, as it is in most avian species. The advantages of tolerating an increase in body temperature while maintaining brain temperature below body temperature enhances a bird's tolerance of environmental heat stress. These advantages have been stated previously (Kilgore et al. 1976). In addition, the advantage of protecting brain tissue from thermal extremes during heat-stress associated with flight (Bernstein et al. 1979b) must be considerable for pelagic, migratory species. Based on morphology alone, the effectiveness of heat exchange

TABLE 1. List of species and number of specimens dissected. Type of intercarotid anastomosis is indicated.

Avian order and species	Pattern of anastomosis[a] H	X	X-H	Location of collection
Procellariiformes				
Oceanodroma markhami (Sooty Storm-Petrel)			1	Sand Island, Midway Atoll
Pterodroma hypoleuca hypoleuca (Bonin Petrel)	2		7	Sand Island, Midway Atoll
Puffinus pacificus chlororhynchus (Wedge-tailed Shearwater)			4	Manana Island, Oahu
Diomedea nigripes (Black-footed Albatross)		1	2	Sand Island, Midway Atoll
Diomedea immutabilis (Laysan Albatross)		4	1	Sand Island, Midway Atoll
Charadriiformes				
Anous tenuirostris (White-capped Noddy)	4			Sand Islands, Midway Atoll
Anous stolidus pileatus (Brown Noddy)	1		2	Manana Island, Oahu
Gygis alba (White Tern)	5			Sand Island, Midway Atoll
Sterna fuscata oahuensis (Sooty Tern)	2			Manana Island, Oahu
Pelecaniformes				
Sula sula rubripes (Red-footed Booby)		2		Ulupau Head, Oahu
Sula leucogaster plotus (Brown Booby)		1		Kewalo Basin, Oahu

[a] H-type is defined as having a lengthy transverse anastomosis connecting the cerebral carotids, X-type has cerebral carotids anastomosing side-to-side, and X-H type has a short transverse anastomosis and is borderline between the H- and X-types (after Baumel and Gerchman 1968).

(and the magnitude of the brain-body temperature difference) can only be evaluated by the area and structural contact between arterial and venous components of the RMO. The Wedge-tailed Shearwater and Bonin Petrel utilize burrow habitats and behavioral inactivity to escape much of the heat stress encountered in the tropics. The shearwater pants in response to heat stress (Whittow and Pettit, unpubl. data), and the petrel is presumed to do so. In both species, the evaporative area drained by the rete is limited. Nevertheless, the rete in these two procellariiforms is well developed. The boobies, on the other hand, are typically exposed to high air temperatures and intense radiant heat from the sun and surroundings on a daily basis. These birds display efficient gular fluttering, which provides extensive evaporative cooling over the buccal membranes, which are drained by the RMO for heat exchange. The Brown Booby and the Red-footed Booby have a large RMO measuring approximately 20 × 5 mm, with close opposition of the arterial venous components, extending into the posterior border of the orbit. Venous drainage from the cornea may provide another significant source of evaporative cooling, as demonstrated in the pigeon (Bernstein et al. 1979a).

In addition to the anatomical relationship of the RMO, several behaviors observed in the course of fieldwork may affect the efficiency of heat exchange across the rete. As noted by Shallenberger et al. (1974), a characteristic posture of the Red-footed Booby in response to heat stress begins with the cessation of gular flutter; then the body is tilted with the head down, generally in the shade of the bird's body. Thus, the shaded head encounters a lowered radiant heat load, and respiratory water loss may be economized by this head-down behavior. If the head-down position does not trigger a blood shunt away from the RMO, it may be argued that cerebral vasodilation with increased blood flow across the RMO (i.e. increased heat exchange and brain cooling) may be promoted as the result of gravitational hydrostatic forces. Although not reported by Bartholomew (1966) in his study of the role of behavior in the Masked

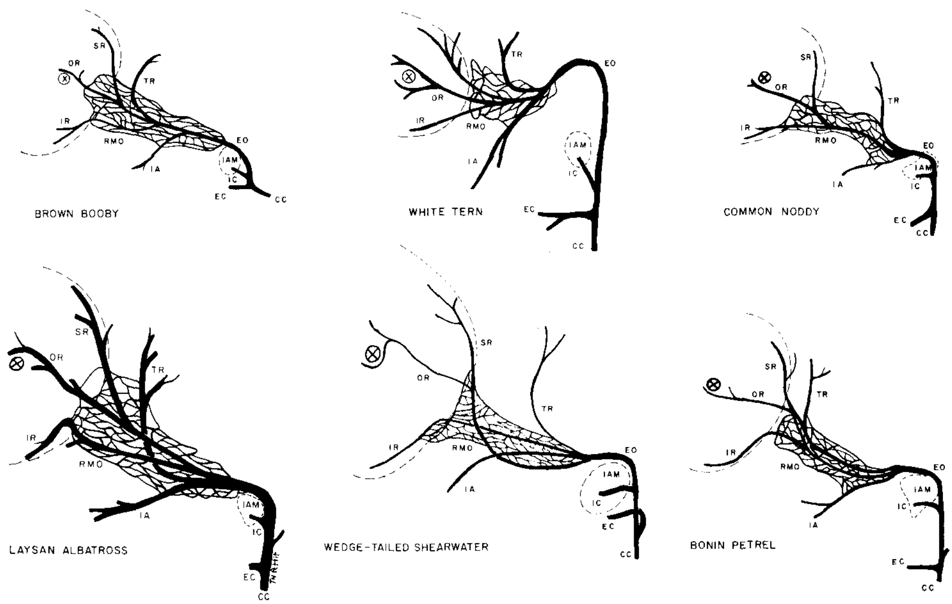

Fig. 1. Diagram of the arterial rete mirabile ophthalmicum in six species of Hawaiian seabirds. Dashed lines represent the border of the orbit and of the IAM. Vascular terminology follows that of Lucas (1970) and Kilgore et al. (1976): CC, Common Carotid; EC, External Carotid; EO, External Ophthalmic; IA, Inferior Alveolar; IAM, Internal Auditory Meatus; IC, Internal Carotid; IR, Infraorbital Ramus; OR, Ophthalmic Ramus; RMO, Rete Mirabile Ophthalmicum; SR, Supraorbital Ramus; TR, Temporal Ramus; X, Optic Nerve.

Booby (*Sula dactylatra*), head drooping is also a particularly prominent behavior in young Masked Boobies exposed to heat (Nelson 1978 and pers. obs.). Other avian behaviors that may act in concert with the RMO to lower brain temperature have not been described.

We thank the U.S. Fish and Wildlife Service and the State of Hawaii Department of Land and Natural Resources for granting permits to conduct this study. Our stay on Midway Islands was supported by a National Science Foundation grant (PCM-12351-A01).

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Received 26 June 1980, accepted 21 April 1981.