Ecología permit numbers 0492, 00987, and 11782. We thank the Secretaría de la Marina, Sexta Zona Naval, Guaymas, for transportation and food deliveries. For logistic support, we are indebted to the Instituto Tecnológico y de Estudios Superiores de Monterrey-Campus Guaymas, Rescue One, A. Robles, E. Velarde, J. Guzman, L. Gonzales, Prescott College, Baja Expeditions, Special Expeditions, H. and V. Ballance, and T. Pfiester. We are grateful to Eureka Tents, Ocean Kayaks, S. Emlen, J. Guzman, and E. Velarde, for use of research equipment. We especially thank D. Able, A. Angeles, S. Ashe, X. Basurto, G. Brabata, C. Carmona, M. Cervantes, D. Craig, G. Fernández, K. Mingo, C. Navaro, N. Nuñez, H. Pérez, and E. Tobón for excellent help and company in the field. We are grateful to D. Anderson, H. Drummond, and BRT's graduate committee members E. Adkins-Regan, S. Emlen, T. Gavin, P. Sherman, and D. Winkler for their excellent reviews of the manuscript.

LITERATURE CITED

ALVAREZ-BORREGO, S. 1983. Gulf of California. Pages 427–449 *in* Estuaries and enclosed seas (B. H. Ketchum, Ed.). Elsevier, Amsterdam, The Netherlands.

AMERSON, A. B., Jr., AND P. C. SHELTON. 1976. The natural history of Johnston Atoll, central Pacific Ocean. Atoll Research Bulletin No. 192.

ANDERSON, D. J. 1990a. Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis. American Naturalist 135:334–350.

ANDERSON, D. J. 1990b. Evolution of obligate siblicide in boobies. 2. Food limitation and parent-offspring conflict. Evolution 44:2069–2082.

DORWARD, D. F. 1962. Comparative biology of the white booby and the brown booby *Sula* spp. at Asension. Ibis 103b:174–234.

DRUMMOND, H. 1987. A review of parent-offspring conflict and brood reduction in Pelecaniformes. Colonial Waterbirds 10:1–15.

DRUMMOND, H., AND C. GARCIA CHAVELAS. 1989. Food shortage influences sibling aggression in the Blue-footed Booby. Animal Behaviour 37: 806–820.

FORBES, L. 1991. Insurance offspring and brood reduction in a variable environment: The costs and benefits of pessimism. Oikos 62:325–332.

KEPLER, C. B. 1969. Breeding biology of the Blue-faced Booby *Sula dactylatra personata* on Green Island, Kure Atoll. Publications of the Nuttall Ornithological Club No. 8.

MOCK, D. W., H. DRUMMOND, AND C. H. STINSON. 1990. Avian siblicide. American Scientist 78:438–449.

MOCK, D. W., AND L. S. FORBES. 1992. Parent-offspring conflict: A case of arrested development. Trends in Ecology and Evolution 7:409–413.

NELSON, J. B. 1978. The Sulidae: Gannets and boobies. Oxford University Press, Oxford.

SIMMONS, R. G. 1988. Offspring quality and the evolution of cainism. Ibis 130:339–357.

TERSHY, B. R. 1998. Sexual selection in the Brown Booby. Ph.D. thesis, Cornell University, Ithaca, New York.

TRIVERS, R. L. 1974. Parent-offspring conflict. American Zoologist 14:249–264.

WOODWARD, P. W. 1972. The natural history of Kure Atoll, Northwestern Hawaiian Islands. Atoll Research Bulletin No.164.

The 20-cm Spiny Penis of the Argentine Lake Duck (*Oxyura vittata*)

KEVIN G. MCCRACKEN[1]

School of Forestry, Wildlife, and Fisheries, Louisiana State University, Baton Rouge, Louisiana 70803, USA

The genitals of male birds generally are not noted for their size or extravagant ornamentation. For most species of birds, well-developed penes or intromittent organs are absent (e.g. King 1981, Briskie and Montgomerie 1997). Sperm transfer occurs via the mutual juxtaposition of the protruded cloacae, and there is relatively little contact between males and females compared with the process of coital penetration in mammals, reptiles, some species of fish, and most insects (Eckstein and Zuckerman 1956, Dowling and Savage 1960, Eberhard 1985). Several groups of birds, including ratites, screamers, waterfowl, and cracids, possess well-developed male copulatory organs (Forbes 1882, King 1981, Lake 1981). In these groups, the penis (or male intromittent organ) arises

[1] Present address: University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775, USA. E-mail: fnkgm@uaf.edu

from the ventral wall of the cloaca and generally is believed to facilitate sperm transfer via a series of longitudinal grooves (internal sperm ducts homologous to those in mammals are not present in birds). The penis of an Ostrich (*Struthio camelus*), for example, can measure as long as 20 cm when flaccid and is bright red in color (King 1981). The intromittent organs of various ducks, on the other hand, have been reported to vary in length between 50 and 90 mm, sometimes exceeding that range (Liebe 1914, Hochbaum 1942).

The presence of a well-developed penis in many dabbling and diving ducks may derive in part from their tendency to copulate in the water (Lake 1981). Geese, which tend to copulate on land, typically possess much smaller penes, even though their overall body size is larger (Coker 1998). Another probable, but not necessarily exclusive, explanation is that large ornamented penes have evolved in response to sperm competition within the female reproductive tract, such that males with larger penes achieve greater reproductive success than others (Waage 1979, Thornhill and Alcock 1983, Eberhard 1985). Species that experience greater sperm competition are expected to possess larger penes that may increase the probability of successful fertilization (Birkhead and Møller 1992, Briskie and Montgomerie 1997). Thus, sperm competition probably also explains the contrast between the larger penes of dabbling ducks and the smaller penes of geese. Dabbling ducks show some of the highest levels of forced and unforced extrapair copulations among waterfowl, whereas most geese show low frequencies of extrapair copulations (Mineau and Cooke 1979, McKinney et al. 1983; but see Dunn et al. 1999). An element of female choice also might play a role if changes in physiology and female behavior also affect the outcome of subsequent sperm competition. Teasing apart the two processes can be difficult, however, particularly when the contest occurs inside the female. Females also might choose among males in yet another manner, based on the size and appearance of the penis itself (Briskie and Montgomerie 1997).

I present here a description of the penis of the Argentine Lake Duck (*Oxyura vittata*). The use of the waterfowl penis as a means of sex and age identification of live birds is commonplace (e.g. Hochbaum 1942). What is novel and fascinating in this species is the relative size (ca. half the body length) and thorny, brush-like texture of its penis. Dissection and preparation of the Argentine Lake Duck's penis reveal a massive structure (approximately equal in length to the Ostrich penis) with a peculiar array of dense spines running the entire length of the organ. At the base of the penis, the spines are hardened and sharp. With the exception of a video sequence and numerous observations of copulating Australian Blue-billed Ducks (*Oxyura australis*) everting and preening (postcopulatory) similar-sized penes (E. Slater and P.

J. Fullagar pers. comm.; see also Marchant and Higgins 1990), and unpublished observations of similar intromittent organs in Ruddy Ducks (*Oxyura jamaicensis*; R. B. Brua pers. comm.), no records detailing the size, texture, or conformation of this structure within the abdomen are known to exist. Unusually large testes size, elaborate sexual display repertoires, and a putatively promiscuous mating system offer opportunities for speculation about the relationship between form and function of the unusual penis in this species.

Methods.—Seven adult male Argentine Lake Ducks were collected early in the breeding season on 22 November 1998 from a small wetland ($n = 2$) and irrigation canal ($n = 5$) adjacent to the Río Negro near General Conesa, Río Negro, Argentina (40°04'S, 64°16'W). Mass ($\pm$ 50 g) of each bird was measured at the time of collection. Carcasses subsequently were placed on ice, frozen, and exported to the Louisiana State University Museum of Natural Science (LSUMNS). Carcasses were thawed three months later and prepared as museum skins ($n = 6$) and a skeletal specimen ($n = 1$).

After discovering unusually large cloacal swellings and correspondingly large penes in the first two specimens, I dissected and measured the intromittent organs and testes of the five birds collected on the canal (LSUMNS B34019, B34025, B34034, B34036, B34037). Genitalia subsequently were removed and further dissected to verify the extent of internal spine-like structures. I made a series of photographs from the second specimen to document both the position and conformation within the abdomen; dissection of the other four specimens revealed approximately identical features and no need for further photographs. Manually everting the organ in its erect conformation proved impossible given the absence of a vascular eversion mechanism (King 1981). In waterfowl, the eversion mechanism is lymphatic, and the unusual length of the structure relative to its width prohibited pulling the entire length of the organ inside out. However, longitudinal dissection and subsequent inversion of the outer surface to view the inner surface revealed what is believed to be a close approximation of the everted, but nonetheless flaccid conformation (see below). Genitalia and testes subsequently were fixed in 10% formaldehyde, preserved in 70% ethanol, and deposited at the Louisiana State University Museum of Natural Science.

Results.—Each of the five birds that I dissected appeared to be in breeding condition, as indicated by a bright blue bill, black head, and ruddy breeding plumage. Mean body mass was 630 $\pm$ SD of 24 g (range 600 to 650 g). Mean testes dimensions were 40.8 $\pm$ 3.6 $\times$ 17.8 $\pm$ 1.8 mm for the left testis and 41.0 $\pm$ 2.3 $\times$ 17.2 $\pm$ 3.1 mm for the right testis (left length testis range 37 to 45 mm, left testis width range 15 to 20 mm; right testis length range 37 to 43 mm, right testis width range 14 to 22 mm; Fig. 1A). Masses av-
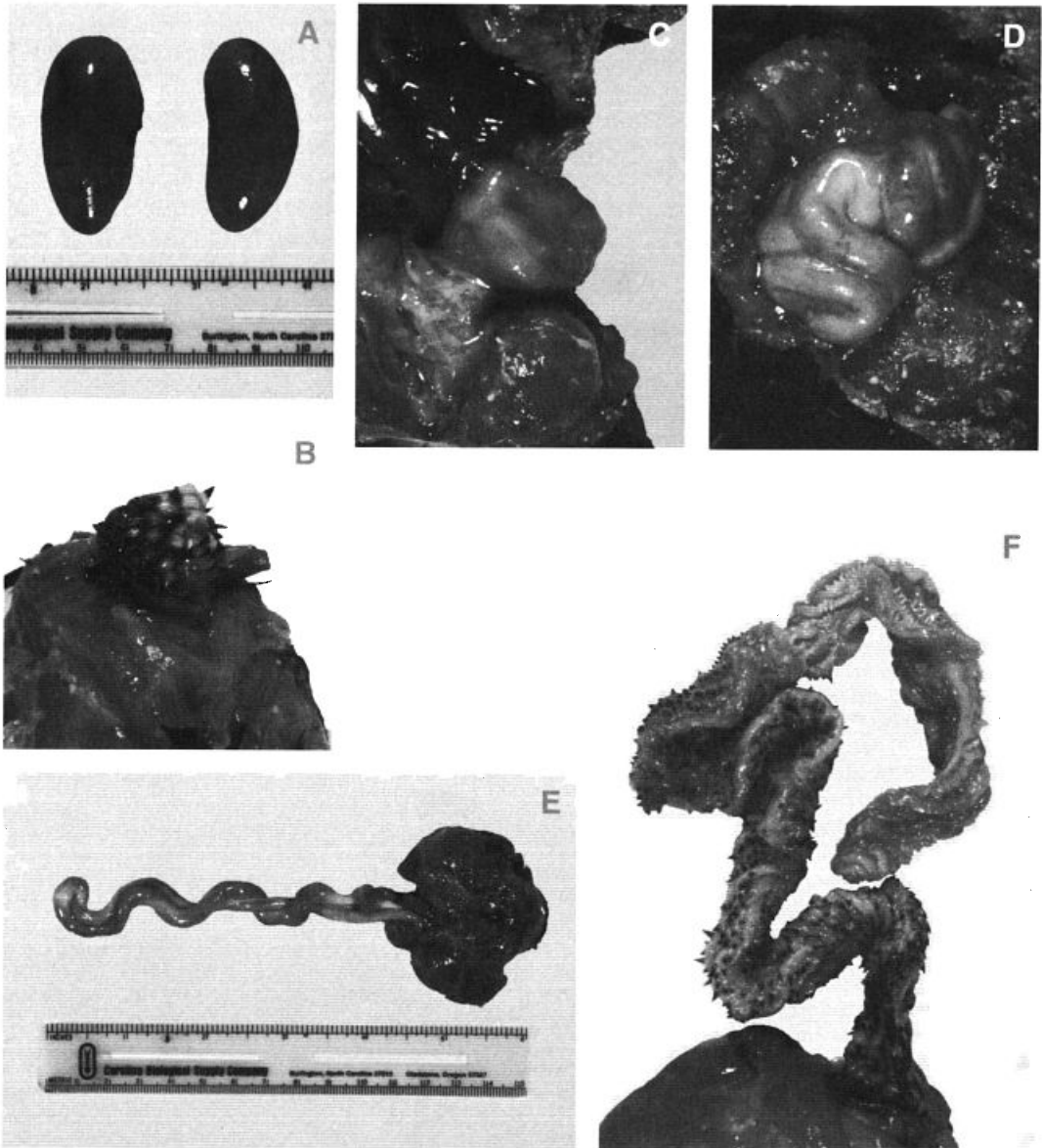
FIG. 1.   Photographs of the testes and genitalia of a male Argentine Lake Duck (LSUMNS B34025) col-
lected near General Conesa, Río Negro, Argentina, including (A) right and left testes as viewed from the
ventral surface of the abdomen, anterior margin at top; (B) cloacal area with skin removed to reveal cloacal
muscle ring, everted base of penis sheath, and foreskin, dorsal margin at right; (C) folded penis enclosed in
two-layered peritoneal membrane as viewed from the ventral surface of the abdomen, anterior margin at top;
(D) folded penis with membranes removed to reveal internal conformation, posterior margin at lower left;
(E) unraveled penis loop and dissected cloacal muscle ring as viewed from the ventral surface, posterior
margin at right; (F) outer surface of the penis sheath as it might appear in the everted but nonetheless flaccid
conformation arranged to reveal spines and ornamentation patterns, proximal margin at bottom.

eraged 5.4 ± 1.3 g for the left testis and 5.4 ± 1.9 g for the right testis (left testis range 4.3 to 7.0 g; right testis range 3.9 to 8.6 g). The left testis was the larger of the two in all but one individual. Mass of the two testes combined averaged 10.8 ± 3.1 g (range 8.2 to 15.6 g), or 1.7 ± 0.5% of total body mass (range 1.4 to 2.4%).

Each individual possessed a large, well-developed cloacal swelling ventral to the base of the tail (Fig. 1B). Dissection revealed that the cloacal swelling is composed primarily of a large ring of muscle; the base of the penis, seminal vesicles, and intestine are embedded within this muscle and constitute the remainder of the cloacal mass. Within the cloacal orifice, the base of the penis is clearly visible as an inverted blind-end tube arising from the ventral wall of the cloaca and penetrating well into the body cavity, not unlike the Mallard (*Anas platyrhynchos*) penis (King 1981). Manual eversion beyond a couple centimeters, however, was not possible. Eversion to a centimeter or so, nonetheless, revealed a dense array of black-tipped, white spines at the base of the penis. Spine density is highest on the ventral side of the penis, and their angles are such that I believe they embed into and clasp the wall of the female cloaca at the point of insertion, whereby the male may evert the remaining length of the penis. A small foreskin-like structure with no spines and measuring 7.2 ± 1.3 mm (range 6 to 9 mm) arises dorsally from the base of the penis (see Fig. 1B). No other notable traits were revealed by further manipulation of the cloaca.

Internal dissection of the abdominal cavity revealed a far more extensive coiled structure placed slightly to the left of the center axis of the body, anterior to the mass of muscle that encircles the cloaca and adjacent to the intestine. Here the inverted penis was folded and enclosed within a two-layered peritoneal membrane measuring 25.5 ± 1.7 mm × 19.3 ± 2.2 mm at its two widest dimensions (*n* = 4; length range 24 to 28 mm, width range 17 to 22 mm; Figs. 1C,D). Subsequent dissection and unraveling from the two membranes revealed the inverted penis to be an elongated, blind-end, tube-like structure attached to the cloaca at both ends. Total length of the penis tube as measured from the base of the cloaca to the bend of the loop was 22.3 ± 2.1 cm (range 19.0 to 24.5 cm; Fig. 1E). The width at the base (the end of the penis visible upon cloacal examination) was 6.5 ± 1.3 mm (range 4.5 to 8 mm). From this point distally, the penis tapered gradually to the opposite end where it inserted the cloaca ventral to the insertion point of the base of the penis. At this juncture, the width of the penis tube was 3.4 ± 0.5 mm (range 3 to 4 mm). A large blood vessel extended along the entire length of the organ. Black pigments in the spines on the external surface of the penis, likewise, were visible from the abdominal surface, thus imparting a mottled gray appearance to the basal half of the penis; the distal half of the penis was more flesh-colored.

Mechanical eversion of the penis in its erect conformation was not possible given its unusual length and narrow width. Geometric relationships of the loop structure, nonetheless, predict what the penis should look like in its erect conformation. At maximum extent, the everted penis can be no longer than one-half the circumference of the loop, or a distance equivalent to the distance from the base to the head of the loop (see Fig. 1E). When everted, the penis thus conforms to the topology of a two-layered sheath connected to the cloaca at both ends, contiguous at the distal end, with an orifice at the tip and hollow in the middle (see King 1981). The outer surface of the sheath (which appears inverted in the abdominal cavity) possesses the spines. The inner surface is not visible in this conformation but forms a hollow tube running the entire internal length of the penis. Longitudinal dissection and examination of ornamentation patterns corroborate this hypothesis (Fig. 1F). When viewed like this, spines are observed along the entire length of the outer sheath (22.3 ± 2.1 cm) but not on the inner sheath. At the base of the penis (outer sheath), the spines are numerous, large, well developed, and sharp. As one proceeds distally, however, the spines diminish in number, become soft and brush-like, and take on a more ochre color, until at the distal terminus they disappear altogether; at this point the outer sheath inverts to become the inner sheath that extends proximally toward the base of the penis. Spines also are arranged along a series of spiral grooves extending the entire length of the everted penis (Fig. 1F).

Discussion.—The penis of the Argentine Lake Duck measures approximately half the body length and exhibits proportions comparable to those found in fleas and some nematodes and flies; male genitalia in these invertebrates often exceed the length of the body and can be the most structurally complex organs in the entire body (Hyman 1951, Thornhill and Alcock 1983). Without regard to size, such structures are uncommon in birds but are present in nonavian groups including crocodiles and turtles (King 1981). As such, the presence of a penis in birds is a shared ancestral trait, and an explanation for multiple origins of the avian penis is not necessary. What needs to be explained is why birds have lost the penis repeatedly, and moreover, why it has been retained or more complexly developed in some groups like waterfowl. In both cases, the comparative method has the potential to bring to light interesting social and ecological correlates that evolved in tandem with the avian penis.

For the Argentine Lake Duck, a number of functional questions remain. First is the question of size and seasonal recrudescence. The testes of birds undergo substantial changes in size, often enlarging greatly during the breeding season and then shrinking to become almost invisible (Witschi 1935, Wingfield and Farner 1980). Does the Argentine Lake

Duck penis recrudesce after the breeding season in a similar fashion, and if so, do the same hormones that regulate the testes cycle control the seasonal development of the penis? Either scenario can be construed as energetically expensive (i.e. annual development vs. year-round maintenance). Year-round maintenance may be more probable because Argentine Lake Ducks are likely to be sexually active throughout most of the year, and like other Southern Hemisphere waterfowl, they lack the sharply defined seasons of breeding activity typical of ducks in the far north. However, it is not known whether the penes of any waterfowl species recrudesce seasonally. Is it a coincidence that such a large structure has evolved in a diving duck with high wing loading that rarely flies?

Another question that comes to mind concerns sperm flow and ejaculation. Other birds lack sperm ducts in their penes, and instead rely on spiral grooves to channel the flow of sperm. Does sperm proceed via a longitudinal sulcus in the Argentine Lake Duck as it does in other species? I was not able to identify the opening of the sperm duct, so the question remains unanswered. One last functional question concerns the topic of sperm displacement. The base of the penis in this species is generously ornamented with coarse spines, but the distal half is soft and brush-like. Do male Argentine Lake Ducks use the coarse spines at the base of their penis to clasp the female as morphology would predict, and does the softer brush-like distal half of the penis remove sperm deposited by other males? Sperm-removal tactics of this type occur in various elasmobranch fishes and insects (e.g. Leigh-Sharpe 1922, Simmons and Siva-Jothy 1998).

Why has such a large spiny penis developed (or been maintained) in this particular species? Limited information about the social behavior and mating habits of Argentine Lake Ducks suggests that peculiarities of size, ornamentation, and the potential for sperm displacement have evolved in conjunction with a promiscuous, group-display mating system. Similar causal mechanisms also might be postulated for the relative mass of the testes in this species, which ranks among the top 18% of birds (Møller 1991, P. Dunn unpubl. data). Like other stifftails (*Nomonyx* and *Oxyura*), the Argentine Lake Duck is nested within a clade of promiscuous, dichromatic congeners that share many derived social and morphological characters (McCracken et al. 1999; see also Livezey 1995, Johnsgard and Carbonell 1996). The most notable of these includes a series of shared stereotyped sexual displays that collectively set *Oxyura* (and probably *Nomonyx*) apart from all other waterfowl (Carbonell 1983, Marchant and Higgins 1990, McCracken et al. 1999). These displays, which can be quite vigorous and prolonged, typically are performed in the presence of many males and often in arena-like contexts. Other sources of information,

likewise, suggest that conventional pair bonds do not exist in this group (Matthews and Evans 1974, Siegfried 1976, Ladhams 1977, Gray 1980, Marchant and Higgins 1990). Pair bonds that have been observed probably reflect nothing more than short-term relationships for copulation or mate guarding. Copulation in Ruddy Ducks and Australian Blue-billed Ducks usually is tumultuous and boisterous and generally is preceded by prolonged pursuits across or under the surface of the water (Wheeler 1953, Gray 1980). In most instances, the everted penis is clearly visible prior to and after copulation (D. K. Rushton and P. J. Fullagar pers. obs., R. B Brau pers. comm.; see Marchant and Higgins 1990). Postcopulatory preening of the penis, likewise, appears to be common in both species (P. J. Fullagar and B. Brua pers. comm.).

Observations of these three *Oxyura* species suggest that well-developed intromittent organs are present in other members of the group. In this respect, a large ornamented penis appears to be a synapomorphic character that sets stifftail ducks apart from other waterfowl. The probability that the complexity of this organ developed in response to male competition for limited access to females also seems high given the obvious social and phylogenetic correlates (Birkhead and Møller 1992, Briskie and Montgomerie 1997). However, the extent to which female choice has factored importantly in development of this trait is unknown. Excellent potential certainly exists for a comparative study of penis morphology across waterfowl species and the investigation of other potentially correlated traits such as mating system, testes size, and the incidence of forced or extrapair copulations.

LITERATURE CITED

BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Sperm competition in birds: Evolutionary causes and consequences. Academic Press, London.

BRISKIE, J. V., AND R. MONTGOMERIE. 1997. Sexual selection and the intromittent organs of birds. Journal of Avian Biology 28:73–86.

CARBONELL, M. 1983. Comparative studies of stiff-tailed ducks (tribe Oxyurini: Anatidae). Ph.D. dissertation, University College, Cardiff, Wales.

COKER, C. R. 1998. The effects of sperm competition on testes size and intromittent organ morphology in waterfowl. M.S. thesis, University of British Columbia, Vancouver.

DOWLING, H. G., AND J. M. SAVAGE. 1960. A guide to the snake hemipenis: A survey of basic structure and systematic characteristics. Zoologica 45:17–28.

DUNN, P. O., A. D. AFTON, M. L. GLOUTNEY, AND R. T. ALISAUSKAS. 1999. Forced copulation results in few extrapair fertilizations in Ross's and Lesser Snow geese. Animal Behaviour 57:1071–1081.

EBERHARD, W. G. 1985. Sexual selection and animal genitalia. Harvard University Press, Cambridge, Massachusetts.

ECKSTEIN, P., AND S. ZUCKERMAN. 1956. Morphology of the reproductive tract. Pages 43–155 *in* Marshall's physiology of reproduction, vol. 1 (A. S. Parkes, Ed.). Longman's Green and Co., New York.

FORBES, W. A. 1882. Note on some points in the anatomy of an Australian Duck (*Biziura lobata*). Proceedings of the Zoological Society of London 31: 455–458.

GRAY, B. J. 1980. Reproduction, energetics, and social structure of the Ruddy Duck. Ph.D. dissertation, University of California, Davis.

HOCHBAUM, H. A. 1942. Sex and age determination of waterfowl by cloacal examination. Transactions of the North American Wildlife Conference 7:299–307.

HYMAN, L. H. 1951. The invertebrates: Platyhelminthes and Rhynchocoela. McGraw-Hill, New York.

JOHNSGARD, P. A., AND M. CARBONELL. 1996. Ruddy Ducks and other stifftails: Their biology and behavior. University of Oklahoma Press, Norman.

KING, A. S. 1981. Phallus. Pages 107–147 *in* Form and function in birds (A. S. King and J. McClelland, Eds.). Academic Press, New York.

LADHAMS, D. E. 1977. Behavior of the Ruddy Duck in Avon. British Birds 70:137–146.

LAKE, P. E. 1981. Male genital organs. Pages 1–61 *in* Form and function in birds (A. S. King and J. McClelland, Eds.). Academic Press, New York.

LEIGH-SHARPE, W. H. 1922. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Journal of Morphology 36: 191–243.

LIEBE, W. 1914. Die männliches Begattungsorgane der Hausente. Jenaische Zeitschrift für Naturwissenschaften 51:627–696.

LIVEZEY, B. C. 1995. Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini). Wilson Bulletin 107:214–234.

MARCHANT, S., AND P. HIGGINS. 1990. Handbook of Australia, New Zealand, and Antarctic birds. Oxford University Press, Melbourne.

MATTHEWS, G. V. T., AND M. E. EVANS. 1974. On the behaviour of the White-headed Duck with special reference to breeding. Wildfowl 25:55–66.

McCRACKEN, K. G., J. HARSHMAN, D. A. McCLELLAN, AND A. D. AFTON. 1999. Data set incongruence and correlated character evolution: An example of functional convergence in the hindlimbs of stifftail diving ducks. Systematic Biology 48:683–714.

McKINNEY, F., S. R. DERRICKSON, AND P. MINEAU. 1983. Forced copulation in waterfowl. Behaviour 86:250–294.

MINEAU, P., AND F. COOKE. 1979. Rape in the Lesser Snow Goose. Behaviour 70:280–291.

MØLLER, A. P. 1991. Sperm competition, sperm depletion, paternal care, and relative testis size in birds. American Naturalist 137:882–906.

SIEGFRIED, W. R. 1976. Social organization in Ruddy and Maccoa ducks. Auk 93:560–570.

SIMMONS, L. W., AND M. T. SIVA-JOTHY. 1998. Sperm competition in insects: Mechanisms and the potential for selection. Pages 341–434 *in* Sperm competition and sexual selection (T. R. Birkhead and A. P. Møller, Eds.). Academic Press, London.

THORNHILL, R., AND J. ALCOCK. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts.

WAAGE, J. K. 1979. Dual function of the damselfly penis: Sperm removal and transfer. Science 203: 916–918.

WHEELER, J. R. 1953. Notes on the Blue-billed Ducks at Lake Wendouree, Ballarat. Emu 53:280–282.

WINGFIELD, J. C., AND D. S. FARNER. 1980. Control of seasonal reproduction in temperate zone birds. Pages 62–101 *in* Progress in reproductive biology (R. J. Reiter and B. K. Follet, Eds.). S. Karger, Basel, Switzerland.

WITSCHI, E. 1935. Seasonal sex characters in birds and their hormonal control. Wilson Bulletin 47: 177–188.