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SIZE OF THE BURSA OF FABRICIUS IN RELATION TO GONAD SIZE AND AGE IN LAYSAN AND BLACK-FOOTED ALBATROSSES[1]

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Age determination can be difficult for birds that undergo little or no plumage change during life. This is the case for Laysan and Black-footed Albatrosses (*Diomedea immutabilis* and *D. nigripes*). The juvenile plumage for both these North Pacific albatrosses is completely grown by about five to six months of age, just prior to their first flight, and is largely indistinguishable from the definitive basic plumage. Consequently, no well-documented methods of distinguishing newly fledged birds, older pre-breeders, or breeding-aged adults has been described for these species (Harrison 1985).

One potentially useful non-plumage-based technique of age determination involves the size of the bursa of Fabricius. The bursa is a dorsal diverticulum of the cloaca that performs an immunosuppressive function in immature birds (Glick 1983). In the few galliform birds in which the ontogeny of the bursa has been carefully described, the bursa begins to enlarge shortly after hatching and reaches a maximum size in four to six months. Soon after reaching peak size, the bursa decreases in size in a linear fashion. Involution is typically complete by the end of a bird's first year of life. The bursa is greatly reduced in size or absent in adult birds (Glick 1983, Mercer-Oltjen and Woodward 1987, Mase and Oishi 1991).

At least among galliforms, testosterone and progesterone have been demonstrated experimentally both to inhibit bursal development and stimulate bursa involution (e.g., Vujic et al. 1983, Mase and Oishi 1991). These findings may explain the inverse relationship between gonadal development and bursa size reported for a number of bird species (Kirkpatrick 1944, Davis 1947, Lewin 1963).

Since bursa size is correlated with age, it has long been used in wildlife management settings to separate birds-of-the-year from breeding-age birds (e.g., Davis 1947, Henny et al. 1981). In addition, because the decrease in bursa size appears to be nearly linear for most species examined (but see Siegel-Causey 1990), the size of the bursa should provide information on age on an even finer scale.

A series of banded known-age Laysan and Black-footed Albatrosses were salvaged from North Pacific driftnet fisheries in 1990–1991. With these specimens, I have examined the relationship between age, bursa size, and gonad size. This is the first chronological study of bursa involution for species that are long-lived and have delayed sexual maturity. This analysis has implications concerning the use of the bursa of Fabricius for age determination in albatrosses and for our understanding of the endocrine influences on the reproductive biology of these species.

MATERIALS AND METHODS

A sample of 340 Laysan and Black-footed Albatrosses was salvaged in the North Pacific Ocean (145°W to 175°E longitude and 30° to 46°N latitude) from high-seas squid and large-mesh driftnets by United States and Canadian scientific observers in 1990 and 1991 (see Shaw et al. 1993 for details of the salvage operation and mortality data). Of this sample, 10 Laysan Albatrosses (six females, four males) and eight Black-footed Albatrosses (five females, three males) had been banded with U.S. Fish and Wildlife Service metal bands.

Laysan and Black-footed Albatrosses are very closely related and are biologically quite similar. Based on PCR analysis, G. Nunn (pers. comm.) reports that Laysan and Black-footed Albatrosses are each other's closest relatives. Indeed, they occasionally hybridize and have nearly identical breeding cycles and ranges (Rice and Kenyon 1962b). Given this close relationship and the small sample of banded birds, the quantitative analyses were performed on the pooled sample of the two species.

The albatrosses were prepared as flat skin/spread wing/skeleton combination specimens and deposited in the collections of the University of Washington Burke Museum. Maximum length and width measurements were taken to the nearest millimeter on flattened bursas. Bursa size was calculated as the product of length and width measurements (mm^2). In addition to measurements, a five-step scale of involution was established based on the visible fleshiness of the bursa wall. On an increasing scale of involution (a decreasing scale of fleshiness), bursas were assigned to the following classes: fleshy, thin-walled, membranous, vestigial, or none. Fleshy bursas are characterized by an internal wall with deep deposits of spongy, gland-like tissue. The internal wall of thin-walled bursas exhibit little or no spongy, gland-like tissue. Membranous bursas exhibit see-thru walls and are very difficult to dissect from the intestine. Vestigial bursas have internal walls that can not be visibly differentiated from the cloaca wall.

Ovary and testis size was determined as the product of length and width measurements (mm^2). Since none

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TABLE 1. Age, gonad, and bursa data for banded Laysan and Black-footed Albatrosses.

Species	U.S.F.W.S. band no.	Date collected	Location banded	Age† (years)	Age class	Sex	Gonad size (mm)	Bursa size (mm)	Bursa class
D. immutabilis	1307-27661	2 Aug 1991	Whale-Skate Is., FFS*	1.42	1.50	M	14 × 3	20 × 10	membranous
D. immutabilis	1137-89250	12 June 1991	Kilauea, Kauai	1.40	1.50	F	20 × 6	0	none
D. immutabilis	1307-32993	14 Aug 1991	Whale-Skate Is., FFS	0.53	0.50	F	24 × 7	32 × 22	fleshy
D. immutabilis	1307-28112	29 Oct 1991	Whale-Skate Is., FFS	1.80	1.50	F	18 × 10	10 × 6	membranous
D. immutabilis	1137-89980	1 Oct 1991	Sand Is., Midway	4.75	4.50	M	12 × 5	15 × 10	fleshy
D. immutabilis	1307-31929	2 Oct 1991	Whale-Skate Is., FFS	0.67	0.50	M	10 × 2	48 × 20	fleshy
D. immutabilis	1307-29686	5 Aug 1990	Whale-Skate Is., FFS	0.51	0.50	F	21 × 6	35 × 22	fleshy
D. immutabilis	1307-28179	25 July 1990	Whale-Skate Is., FFS	0.48	0.50	F	19 × 5	35 × 22	fleshy
D. immutabilis	1307-31828	10 Sept 1991	Whale-Skate Is., FFS	0.69	0.50	F	17 × 5	44 × 25	fleshy
D. immutabilis	0887-12273	22 June 1990	Eastern Is., Midway	23.64	B**	M	12 × 8	0	none
D. nigripes	1307-26744	16 June 1991	Whale-Skate Is., FFS	2.40	2.50	F	22 × 9	13 × 8	membranous
D. nigripes	1307-31726	31 July 1991	Whale-Skate Is., FFS	0.52	0.50	M	12 × 2	38 × 23	fleshy
D. nigripes	1307-26635	1 June 1991	Whale-Skate Is., FFS	2.35	2.50	M	9 × 3	22 × 8	membranous
D. nigripes	1307-31081	25 July 1991	Whale-Skate Is., FFS	0.50	0.50	F	18 × 7	35 × 18	fleshy
D. nigripes	1307-29861	19 June 1991	Whale-Skate Is., FFS	1.40	1.50	M	9 × 3	31 × 14	thin-walled
D. nigripes	0737-83803	8 Mar 1991	Eastern Is., Midway	22.12	B	F	20 × 12	10 × 4	vestigial
D. nigripes	1117-83728	6 April 1991	Sand Is., Midway	13.36+	B	F	23 × 12	10 × 4	vestigial
D. nigripes	1367-21841	29 Aug 1990	Sand Is., Midway	7.60+	B	F	20 × 15	0	none

* FFS = French Frigate Shoals.
† Age to 100ths in years.
** B = breeding-age.

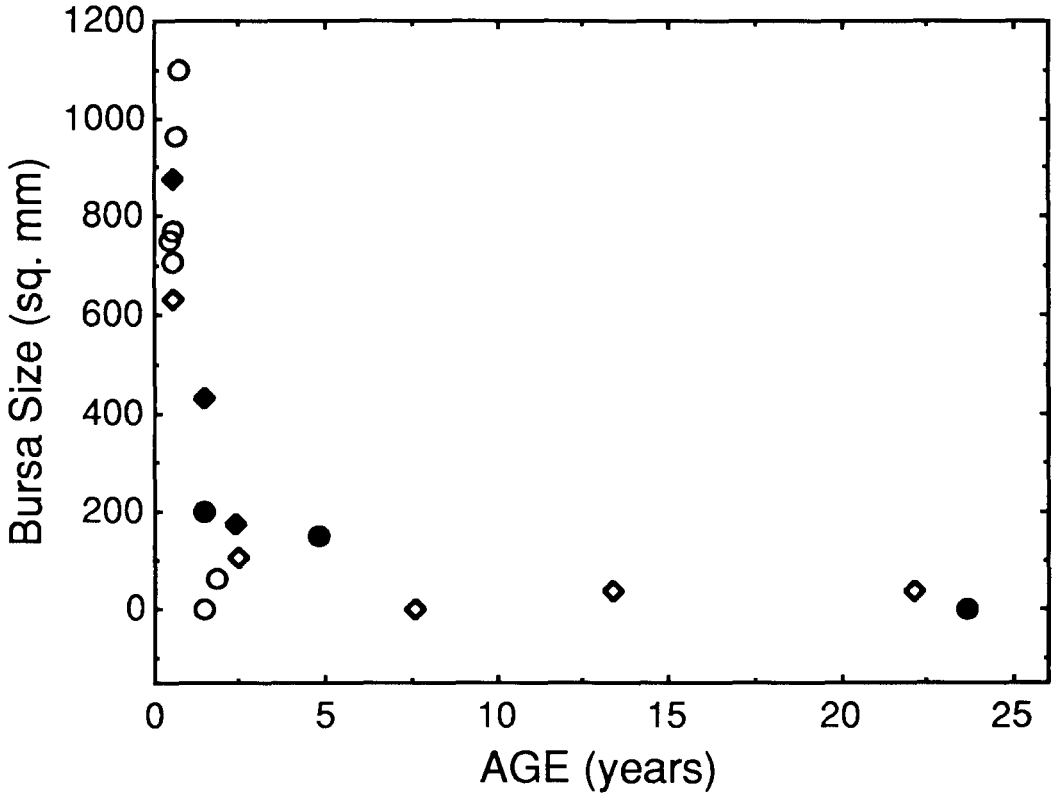

FIGURE 1. The relationship between bursa size and age (in years) in Laysan and Black-footed Albatrosses. Circles are laysans; diamonds are black-foots. Open symbols are females; solid symbols are males.

of the birds were in breeding condition, ovary measurements were not affected by extremes in follicle size that characterize females during laying.

All birds were banded on nesting colonies on the Hawaiian Island chain. Of the 18 banded birds, 16 were banded as flightless young. Two specimens were of unknown age when banded, hence, only time since banding can be determined. The time between banding and death for these two specimens was 13.36 and 7.60 years, respectively, putting them both into the breeding age class. It was necessary to estimate a hatching date in order to calculate age at death for the birds banded as flightless young. Time of hatching was estimated from mean hatching dates reported for 95 Laysan and 85 Black-footed Albatrosses on Midway Atoll (Rice and Kenyon 1962b).

RESULTS

Table 1 provides the age, location of banding, bursa size, bursa involution class, and gonad size, for the 18 banded albatrosses. Bursa size declines with age in Laysan and Black-footed Albatrosses in a curvilinear fashion (Fig. 1). A linear regression of bursa size on age is significant ($r^2 = -0.29$, $P < 0.02$, df = 1, 16) but a quadratic model significantly improves the fit ($P = 0.008$, df = 2, 15) with r^2 increasing to -0.48. The difference in bursa size between newly-fledged (0.5 year) birds and birds of the 1.5 and 2.5 year classes (pooled together) is significant (Mann-Whitney $U = 42.00$, $P = 0.003$). Bursa size decreases dramatically during a bird's second year of life.

The distribution of bursa involution categories varies markedly across age classes (Table 1). Prior to frequency analysis, I pooled both the bursa involution categories and age classes in order to reduce the proportion of cells with low or zero values. ("Membranous" and "thin-walled" bursas were pooled, as were the "vestigial" and "none" involution classes. The post first-year, pre-breeding-age classes [1.5 year, 2.5 year, 4.5 year] also were pooled as one group.) The differences are dramatically significant ($G = 23.55$, $P < 0.006$, df = 4), with fleshy bursas heavily represented in newly fledged (0.5 year) birds and vestigial or no bursas heavily represented in breeding-age birds. Thin-walled and membranous bursas are heavily represented in post-fledging-year (0.5 year), pre-breeding age birds (Table 1).

Figure 2 shows the relationship between gonad size and age for the sample of banded albatrosses all in non-breeding condition. Testis and ovary size both appear to increase in size in a linear fashion during the first five to seven years of life, leveling off somewhat for

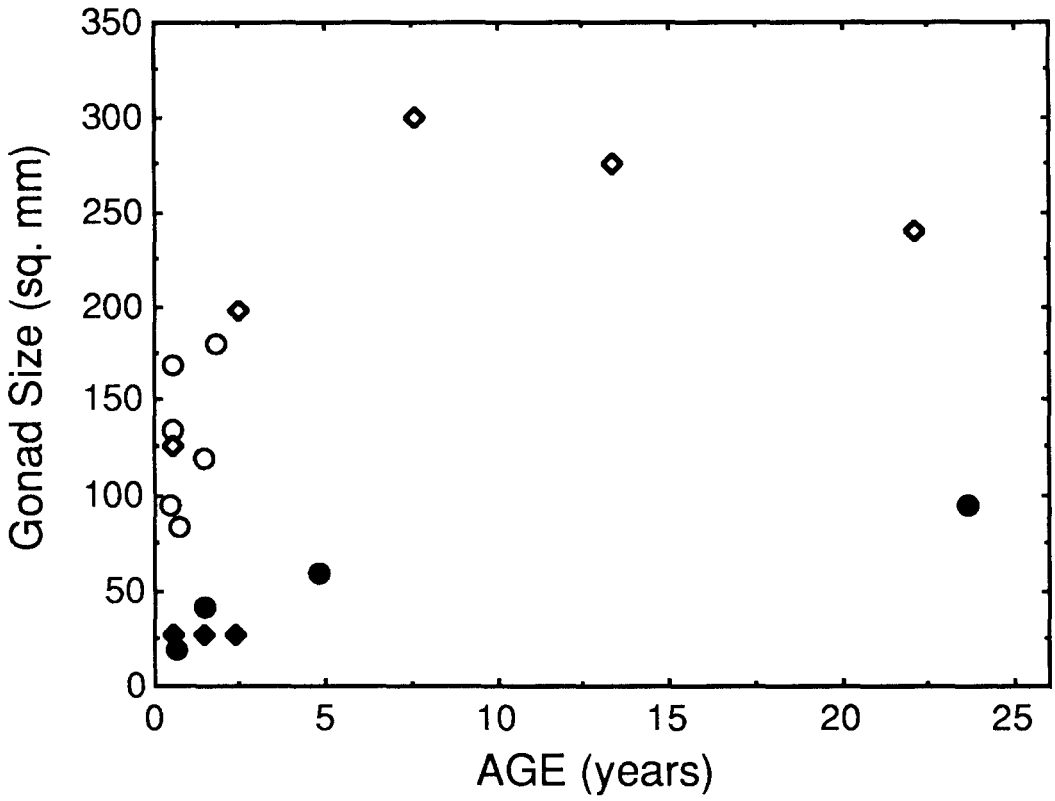

FIGURE 2. The relationship between gonad size and age (in years) in Laysan and Black-footed Albatrosses. Circles are laysans; diamonds are black-foots. Open symbols are females; solid symbols are males.

breeding age birds (7 to 10 years). The pattern in gonad size is approximately the inverse of bursa involution. Indeed, the relationship between gonad size and bursa size is negative and significant for both sexes (males: $r_s = -0.937$, $P < 0.01$; females $r_s = -0.672$, $P < 0.04$).

DISCUSSION

Bursa involution, as measured by both bursa size and thickness, appears to provide a good indicator of age for North Pacific albatrosses. Laysan and Black-footed Albatrosses with large (>600 mm^2) fleshy bursas indicate newly fledged birds (0.5 year). Birds with regressing bursas (intermediate-sized [<500 and >75 mm^2], thin-walled or membranous) may be considered young pre-breeders (1.5–4.5 years). Breeding-age birds invariably exhibit small (<50 mm^2) vestigial bursas or none at all.

While the bursa in Laysan and Black-footed Albatrosses clearly provides information on age beyond simply distinguishing juvenile from adult birds, the timing of involution is unlike that described for any other species. In other species in which the ontogeny of the bursa is well described, involution precedes initial breeding by no more than half a year and is associated with high plasma levels of gonadal steroids (Mase and Oishi 1991). Because Laysan and Black-footed Albatrosses do not breed until age six or seven, and bursas begin to involute during a bird's second year of life, involution occurs nearly half a decade prior to initial breeding. Bursa involution in albatrosses is, however, tightly correlated with gonad size during the pre-breeding period.

Given the strong inverse relationship between bursa size and gonad size in albatrosses, bursa involution in these birds may be controlled by sex steroids, produced in the gonads, as has been documented experimentally in other species. This suggests that steroid hormone levels may begin to be elevated in North Pacific albatrosses by their second year of life. Indeed, precocial gonadal/hormonal development has been documented empirically in the Wandering Albatross (*Diomedea exulans*) (Hector 1988, Hector et al. 1990).

Wandering Albatrosses typically do not breed before age seven years and 50% of individuals do not breed until they are 11 years old. Nonetheless, both juvenile males and females (age 4–10 years old) exhibit precociously developed gonads and elevated circulating levels of gonadal steroid hormones (Hector et al. 1990).

Bursa involution in young North Pacific albatrosses may be due to precocious gonadal development and consequent elevated sex steroid hormone levels. Indeed, behavioral and limited physiological data from

immature Laysan and Black-footed Albatrosses on the breeding colony suggest that circulating sex steroids may approach adult levels several years before breeding.

Young Laysan and Black-footed Albatrosses begin to spend considerable amounts of time at breeding colonies when they are between two and four years of age. Along with adult non-breeders, pre-breeding age birds associate in groups, establish territories, engage in aerial displays, copulate, and perform the well-known series of intricate courtship dances. Pre-breeders can even exhibit well developed brood patches and engage in nest building activities (Rice and Kenyon 1962a, 1962b; Fisher 1971; Robbins and Rice 1974). All of these features, which characterize breeding birds in most short-lived species, are consistent with high circulating levels of gonadal hormones in young albatrosses.

The size of the bursa of Fabricius has been used to separate birds-of-the-year from breeding-age birds in a number of species: large bursas signal pre-breeding age birds, while atrophied bursas indicate breeding adults. This simple dichotomy cannot be extrapolated to long-lived monogamous species, such as albatrosses, that exhibit a prolonged and hormonally dynamic pre-breeding period. In albatrosses, bursas commence involution up to half a decade prior to initial breeding. This is associated with a lengthy pre-breeding courtship period during which these birds may have high circulating levels of gonadal hormones. While the timing of bursa involution among North Pacific albatrosses is unusual compared to other birds that have been studied, the data presented here suggest that the bursa may be used to separate albatrosses into one of three age-classes: (1) birds during their first year after fledging, (2) young pre-breeders, and (3) older pre-breeders and breeding-age adults.

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