REPLY TO HOWELL ON PRIMARY MOLT IN ALBATROSSES

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In the Laysan and Black-footed Albatrosses the inner and outer primaries are replaced in opposite directions, making it clear that they are part of separate molt series. Howell (2006) argues that Langston and Rohwer (1995) were wrong about the location of the division between these molt series. While Langston and Rohwer interpreted this division as lying between primaries 5 and 6 (P5/6), Howell (2006) suggests that this divide lies between P7 and 8. Howell further posits that the mode of feather replacement in the inner primary series is stepwise, meaning that multiple waves of active feather replacement sometimes proceed simultaneously through the inner primaries.

There are four fundamental problems with Howell's (2006) arguments. First, he ignores previously published data on direction of feather replacement; second, he fails to take into account age-class differences in the number of primaries replaced, as well as year to year variation in the number of outer primaries that adults replace; third, he interprets feather replacement patterns in fields of new or old feathers, even though this is unhelpful because feather replacement in such wings can be interpreted in multiple ways; and fourth, he ignores published evidence that stepwise replacement does not occur in the inner series of primaries (Edwards and Rohwer 2005). We elaborate on each of these points below.

Previously published data on the direction of feather replacement fail to support Howell's proposal that the divide between the inner and outer primaries lies at P7/8. Howell recognizes that replacement of the outer primaries of Laysan and Black-footed Albatrosses proceeds distally, while replacement of the inner primaries proceeds proximally, and he cites Langston and Rohwer (1995) in support of this observation. But he fails to use the data presented by Langston and Rohwer to evaluate critically the very molt divide that he proposes. If P7/8 were a molt divide, then P7 and P8 would each be nodal feathers starting feather replacement in their respective molt series, at least when molts are extensive. Thus, under Howell's hypothesis of a P7/8 divide, any directionality between P7 and P8 would indicate only the sequence of activation between the inner and outer molt series in the primaries. But Howell's placement of the break at P7/8 makes the clear prediction that the direction of replacement between P6 and P7 should be distal to proximal. Yet, for cases where P7 is growing Langston and Rohwer (1995) showed the direction of replacement was proximal to distal in seven cases and distal to proximal in only one case (Langston and Rohwer 1995: table 6). These directionality data refute Howell's supposition that the divide between the inner and outer primaries in these albatrosses lies at P7/8.

The second problem with Howell's interpretation involves the fact that five of the eight birds in his table 1 are replacing only their outer two to four primaries. First-time molters usually replace just their three outer primaries (some replace just the outer two primaries, and a few replace the outer four primaries). This is analogous to the eccentric molts of primaries in many first-year passerines (Rohwer 1986, Pyle 1997). Furthermore, adults often replace only their three outer primaries in years when they undergo limited molts (Langston and Rohwer 1995). Two important implications follow from these facts. First, any effort to distinguish between molt divides at P7/8 versus P5/6 must exclude birds undergoing limited molts of just the outer two to four

primaries (molts starting at P7, P8, or P9) because such birds cannot help distinguish between alternative molt divides at P7/8 or P5/6. Further, if one examines mostly birds replacing just their outer primaries, without being critical about their age, it is easy to get the misimpression that the molt divide lies at P7/8 because almost all juveniles (as well as many adults) will be replacing only these outer three primaries.

Langston and Rohwer (1995) were able to identify first-time molters by their large bursas and by the absence of old feathers among their inner primaries and their many secondaries. North Pacific albatrosses retain their bursas for several years (Broughton 1994), so the presence of a bursa fails to distinguish between birds that are in their first, second, or third molt cycle. But birds that have (1) a large bursa, (2) outer primaries in molt, and (3) inner primaries and secondaries that are all the same age can be inferred to be undergoing their first molt of primaries, meaning that they are about a year old. This aging criterion works because the flight-feather molt of Laysan and Black-footed Albatrosses is essentially never complete, meaning that the 30 to 50 inner flight feathers of the wing will always contain two or more age classes of feathers in older birds (Langston and Rohwer 1995). Because most young birds replace only the outer three primaries in their first primary molt, and because adults often restrict replacement of outer primaries to these same three feathers, locating the molt divide between the inner and outer primaries requires examining adults undergoing extensive primary replacement, exactly the birds presented by Langston and Rohwer (1995) in their table 6. Howell offers only a single additional bird that is relevant to distinguishing between a P7/8 molt divide and a more proximal molt divide; this bird, number 710, supports a divide at either P7/8 or P6/7. Thus it contradicts Langston and Rohwer (1995) but offers only equivocal support for Howell (2006).

The third problem with Howell's (2006) critique is that he interprets feather-replacement patterns in fields of new or old feathers, even though feather replacement in such wings can be interpreted in multiple ways and is unhelpful, a point that Howell acknowledges. Thus he interprets his bird 711 as consistent with both of our hypotheses, meaning that it fails to distinguish between the hypotheses and is unhelpful. He considers as potentially informative San Diego Natural History Museum 38861, which was starting its molt at P7, but this bird could be consistent with a break at P7/8, P6/7, or P5/6, given the frequency with which middle primaries are skipped (Langston and Rohwer (1995). Howell reinterprets all 11 of the Black-footed Albatrosses reported in table 6 of Langston and Rohwer (1995), but only a single specimen contradicts our hypothesis of a P5/6 divide and supports Howell's P7/8 divide. All others fail clearly to support his hypothesis that the divide lies at P7/8.

Finally, many wings in Langston and Rohwer's (1995) table 6 are incompatible with Howell's (2006) proposed P7/8 divide without additional suppositions. To explain these birds Howell (2006) suggests that the mode of replacement in the inner primaries is stepwise. With this added complexity, Howell's paper joins a long history of speculation about stepwise replacement of primaries in albatrosses that seems based exclusively on intermixed blocks of old and new primaries (e.g., Prince et al. 1993, Furness 1988, Brooke 1981, Harris 1973). Stepwise feather replacement simply cannot be assessed without first defining the molt series to which this mode of replacement applies (Shugart and Rohwer 1996, Rohwer 1999). Once the molt series is defined, documenting stepwise molting further requires demonstrating that two or more waves of feather replacement are proceeding simultaneously through the series. Using the term "stepwise molting" in the absence of such data amounts to diluting its definition to meaning nothing more than the presence of at least three intermixed blocks of old and new primaries in a wing. Unfortunately, it is not particularly helpful to interpret exceptional birds as undergoing stepwise replacement of their inner primaries if the molt series itself is not clearly defined; pointing out doubt about this later point was exactly the purpose of Howell's (2006) paper.

As Edwards and Rohwer (2005) showed, the abundance of feather skipping within

molt series in these North Pacific albatrosses means that stepwise molting can be assessed without error only by using birds in active molt. Intermixed blocks of new and old feathers may arise (1) because the feathers being examined are really part of two separate molt series, or (2) because of feather skipping (no temporal overlap between groups of growing feathers in the same series), or (3) because of stepwise replacement. Assuming a P5/6 break between the inner and outer primaries of Laysan and Black-footed Albatrosses, Edwards and Rohwer (2005) found no case of multiple simultaneous waves of active replacement in the primaries. Further, there is still no case of this in our data (Langston and Rohwer 1995: table 6) if we assume the boundary is moved to P6/7, which we cannot distinguish from P5/6 (see below). In contrast, there is good evidence of two waves of primary replacement if the series boundary were at P7/8, but we have already shown that directionality data refute this divide. Thus Howell's (2006) stepwise replacement is an artifact of having the series boundary in the wrong place. So far as we know, there remains no proof for any albatross that stepwise molting occurs in any subset of the primaries. In contrast, stepwise feather replacement does appear to be the case for the two inner molt series that include only secondary feathers (Edwards and Rohwer 2005).

In spite of its problems, Howell's (2006) paper convinced us that past versions of the molt-summary tables advocated by Rohwer and his collaborators have been so complicated that they were inaccessible to most readers (see examples in Langston and Rohwer 1995, Shugart and Rohwer 1996, Yuri and Rohwer 1997). Thus, in a separate paper, we propose a far simpler method of scoring the direction of feather replacement; this new method limits directionality scoring to adjacent pairs of feathers, thus eliminating the "ambiguous direction" category of earlier papers (Rohwer and Edwards unpubl.). The surprise of this innovation is that we have discovered that there are two alternative locations for the divide between the inner and outer molt series in the primaries of Laysan and Black-footed Albatrosses and that these alternatives cannot be distinguished with present data. One possibility is a divide at P5/6 (slightly less plausible); the other possibility is a divide at P6/7 (slightly more plausible). In light of this discovery it is interesting to note that most of the potentially contradictory specimens cited by Howell become consistent with a divide lying at P6/7, without invoking stepwise replacement in the inner primaries. Thus bird 710, the upper on this issue's back cover, represents an exception to Langston and Rohwer's placement of the divide between P5/6. But this bird is consistent with the alternative P6/7 divide recognized in our new analysis (Rohwer and Edwards unpubl.), as well as with the P7/8 divide hypothesized by Howell (2006).

As much as we were frustrated by the need to reply to Howell, we would not have discovered this simpler method of summarizing molt data had Howell not written his paper. For that we are grateful. Hopefully this simpler method will inspire others to publish quantitative molt-summary tables that illustrate and support their conclusions about the rules of flight feather replacement.

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