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Reviewed work(s):

Source: *Proceedings: Biological Sciences*, Vol. 261, No. 1361 (Aug. 22, 1995), pp. 239-243

Published by: [The Royal Society](#)

Stable URL: <http://www.jstor.org/stable/50292>

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# Moult varies with parasites in Laysan Albatrosses

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## SUMMARY

In Laysan Albatrosses the extent of primary moult is severely constrained by time, and should be considered in the context of life history trade-offs between current and future reproduction. In this study we asked whether differences in moult patterns varied with levels of the nematode *Seuratia* spp., and whether any of the observed variation in moult patterns could be explained by condition differences as reflected by parasite levels. Laysans with more nematodes replace fewer primaries, grow fewer feathers at a time, begin their moult later, and are more likely to replace only their outermost feathers – indicating that an individual bird's condition may affect the extent of its primary moult – which, in turn, may have significant effects on future reproduction.

## 1. INTRODUCTION

Because the avian moult is demanding both of energy and time (Murphy & King 1991), factors – such as parasites – which affect a bird's condition may also affect its moult. This may be particularly important in birds where the extent of feather replacement during the annual moult is subject to variations occurring both in the external environment and in the bird's condition. Surprisingly, correlations between parasites and moult have been examined rarely.

Researchers have long recognized the pathogenic effects of parasites. However, it is only recently that they have begun to consider the more subtle effects parasites have on host condition and behaviour, which can have interesting evolutionary consequences (Anderson & May 1979; Hamilton & Zuk 1982; Toft 1991; Zuk 1994). Recent avian studies have found correlations between parasites and reproduction, condition, secondary sex characters and behaviour (see Hillgarth 1990; and two reviews Clayton 1991; Zuk 1992). Experimental work has shown a causal relation between parasites and reduced expression of secondary sex characters in jungle fowl (Zuk *et al.* 1990), and between parasites and decreased breeding success in swallows and other passerines (Brown & Brown 1986; Lope & Møller 1993; and two reviews Møller *et al.* 1990; Møller 1993). Experimental work has shown too that nematodes affect reproduction in red grouse (Hudson & Dobson 1991) and ring-necked pheasants (Robertson & Hillgarth 1995).

Like all albatrosses, Laysans have incomplete moults: single egg clutches and extremely long breeding seasons leave them little time for this. As they do not overlap moult with breeding, replacement of all the flight feathers is impossible in the short time that successful breeders have away from the breeding colonies. The costs of this incomplete moult can be substantial; worn feathers accumulate, eventually forcing adults to apparently skip a breeding season

altogether to undergo a complete primary moult. The more time a Laysan invests in current reproduction, the less time it has available to moult, which may affect future reproduction (Langston & Rohwer 1995*a*).

To minimize the number of years they must skip breeding to complete their moult, Laysans have evolved a complex set of rules for replacing their flight feathers (Langston & Rohwer 1995*b*). Within a population, individuals vary the number of primaries they moult in any year, which primaries they moult, how many primaries they grow simultaneously, and how long it takes them to moult (Langston & Rohwer 1995*b*). In this study, we asked whether differences in moult patterns, which potentially have serious consequences on fitness, correlated with levels of the nematode *Seuratia* spp.

## 2. METHODS

### (a) *Natural history*

Laysan Albatrosses breed in colonies in the North Pacific, on the leeward Hawaiian Islands (Rice & Kenyon 1962*a*). They arrive at the breeding colonies in early November and lay eggs in late November and early December, incubating them for 64 days. Eggs hatch in early February, and the nestling stage lasts approximately 165 days. After 8 months at the breeding colonies, they depart in mid-July for the North Pacific Ocean where they forage and moult (Rice & Kenyon 1962*b*). Laysans (like all albatrosses) do not moult while they breed, and the extended length of their breeding season leaves successful breeders only about 110 days to moult: a period which is not sufficient to replace all the flight feathers (Langston & Rohwer 1995*a*).

Laysans are known as annual breeders, but few successful breeders can breed every year in succession (Rice & Kenyon 1962*b*; Fisher 1976). Approximately 25% of surviving adults that successfully bred do not breed in the next year (Rice & Kenyon 1962*b*), there

is also variation in the frequency with which pairs can breed (Fisher 1976). A few birds begin nesting when they are 6 years old, but most wait until they are 9 (Rice & Kenyon 1962*b*). From the age of 3 years, subadults return to the breeding colony at the same time as adults; they court, mate, build and attend nests just as the adults do (Rice & Kenyon 1962*b*).

Non-breeding, actively moulting Laysans have rarely been studied because they winter in the North Pacific (from 28°00'–45°00' N and 150°00'–175°00' W, see Langston & Rohwer 1995*b*). In 1990 and 1991, 191 Laysans were recovered as bycatches from squid driftnets, as part of an international investigation of the impact of the squid fishery on non-target species (for details of the salvage operation and mortality data, see Johnson *et al.* 1992). Laysans examined in this study were captured between June and November. Carcasses were frozen when the birds were removed from the squid nets, usually within 12 h of drowning. Birds were shipped to the University of Washington Burke Museum in Seattle, Washington, where bursas were measured for aging, and birds were prepared as pelted skin/extended wing/skeleton/tissue combination specimens.

Birds caught in the driftnets were either in active moult (64%), ready to begin moulting primaries (20%), or had recently completed their primary moult (16%). We divided Laysans into four age classes using a combination of moult and bursa data (Langston & Rohwer 1995). Hatch-year birds are those from 4–10 months of age. Juveniles, which range from 16–21 months, were born during the previous breeding season and are therefore undergoing their first moult of flight feathers. Subadults were born at least two breeding seasons earlier, but are not yet breeding age. Adults are birds of breeding age, at least 6 years old, with fully resorbed bursas.

#### (b) *Moult*

Primary moult was scored and analysed for another study (Langston & Rohwer 1995*b*), but because they are critical to understanding the parasite results, the results are also summarized here. Primary moult was scored on the entire sample of 191 Laysans, including the 109 Laysans examined for parasites in this study. Juveniles moulting their flight feathers for the first time replace only their distal three or four primaries. In older birds, the ten primaries are divided at their mid-point into two series, each with an independent set of rules for replacement. The primaries of the two series are replaced in opposite directions, with moult proceeding toward the wing tip in the outer series and toward the body in the inner series.

The outermost feathers of the distal series are replaced every year without fail; the time available to moult determines how many feathers of this series are replaced. For the inner series, feather replacement occurs only every second to third year. When moult does occur in the inner series it is normally incomplete, and it proceeds in a wrap-around pattern which ensures that the oldest and most worn feathers are always the first to be replaced.

This elaborate pattern of incomplete moult appears to be driven by a time constraint forced on Laysans by their extended breeding seasons (Langston & Rohwer 1995*a*). Birds moulting the minimum number of primaries take 110 days: almost exactly the amount of time the breeding population is away from the breeding colonies. To moult all ten primaries Laysans would need 130 days, but birds that breed successfully are not away from the breeding colonies for that long. Only failed breeders, which leave the colony soon after failure, appear to have the time required for a complete moult.

#### (c) *The parasite*

Before the frozen specimens had completely thawed, the digestive tract was removed from 109 birds and then examined for nematodes. Nematodes found in the oesophagus were well preserved, as the carcasses were frozen soon after capture. Cestodes found in the illium and duodenum were beginning to disintegrate and so were not included in this study. Several parasites were preserved in alcohol for identification, although insufficient numbers of males were preserved intact to identify past the genus level.

The nematode examined was identified as *Seuratia* spp., a genus which has a broad host-range including Procellariiformes, Laridae, and Alcidae. Not enough males were present in the parasite sample to identify past the genus level, so more than one species may have been present. As far as we know, *Seuratia* has not been reported in Laysans previously, although it has previously been found in the North Pacific basin. The nematode attaches to the lining of the oesophagus wall, often causing necrotic lesions which may become infected and leave scarring (N. Hillgarth & N. Langston, unpublished data). The life cycle of *Seuratia* is not known but the intermediate hosts are probably Crustacea. The paratenic hosts may be flying fish or squid, both major food items for Laysans (Harrison *et al.* 1983; P. Gould, unpublished data). However, it is possible that the nematodes are transmitted to the Laysans via incidental prey. Current evidence suggests seabirds become infected with parasites while feeding in areas near the breeding grounds (Rausch 1983).

Here we focus on parasite prevalence (i.e. presence or absence of the parasite) rather than intensity (i.e. numbers of parasites for infected birds) because intensities were low for all infected birds. In another paper, we report prevalences and intensities for the sex and age classes of Laysans from this sample (N. Hillgarth & N. Langston, unpublished data). Briefly, hatch year birds and juveniles have more parasites than adult birds, and males have more parasites than females. We excluded juvenile and hatch-year birds from this study as their moult patterns differ dramatically from the patterns of older birds. Hatch-year birds do not replace any of the primaries that were grown before they fledged, and juveniles replace only three to four primaries of their outer series. Unlike older birds, neither of these age classes exhibits any significant amount of interindividual variation in moult (Langston & Rohwer 1995*b*).

Here we focus on adults because subadults tended to have slightly more parasites than adults, and sample sizes were not large enough to analyse them separately. For the analysis comparing the timing of moult, we do include subadults because there were equal numbers of subadults and adults in the comparison groups. Because there were more adult females than males caught in the drift nets, our sample of adult moulting birds was dominated by females (27 out of 30). Therefore for each test we analyse females alone, and males and females combined to see if the trends hold for both sexes; we cannot analyse males alone. This is unfortunate because males have more parasites than females (N. Hillgarth & N. Langston, unpublished data), so we would expect them to show stronger effects of parasites on moult. All statistical tests are non-parametric because parasite distributions are skewed and sample sizes are small. Significance tests are two-tailed; means are reported  $\pm$  standard errors. StatView 4.01 was used to analyse data.

### 3. RESULTS

#### (a) Number of primaries replaced and parasites

If adult Laysans in better condition can replace more primaries and if condition and parasite levels are related, then parasitized birds should replace fewer primaries. Adults that were not infected replaced significantly more primaries by the end of their moult than infected adults (not infected  $n = 13$ , number of primaries replaced  $\bar{x} = 6.4 \pm 0.6$ ; infected  $n = 17$ , number of primaries replaced  $\bar{x} = 4.5 \pm 0.5$ , Mann-Whitney  $Z = -2.03$ ,  $p = 0.04$ ). Twenty-seven of the 30 birds in this sample were females, and when males were excluded means remained substantially the same, although the statistical test just missed significance with the smaller sample size (not infected,  $n = 13$ , primaries replaced  $\bar{x} = 6.4 \pm 0.6$ ; infected  $n = 14$ ,  $\bar{x} = 4.6 \pm 0.6$ , Mann-Whitney  $Z$  corrected for ties =  $-1.8$ ,  $p = 0.06$ ).

#### (b) Inner versus outer series moult and parasites

There are two distinct moult strategies among adult Laysan Albatrosses: some birds replace only primaries

of the outer series, whereas others replace primaries of the inner series as well. Replacing inner series primaries takes more time, and is likely to be energetically demanding as well because twice as many feathers must be grown simultaneously (Langston & Rohwer 1995*b*). If Laysans that replace only outer primaries are in worse condition than Laysans that also replace their inner primaries, we would expect them to have more parasites. As predicted, adults that skipped their inner primary moult had significantly higher parasite numbers than birds that underwent inner primary moult (see table 1). This result holds when females alone are analysed (see table 1).

For Laysans that do replace inner primaries, a critical variable is the number of primaries they can grow simultaneously. If infected Laysans are in poorer condition, we predicted that infected Laysans would not be able to grow as many feathers at once. As predicted, infected adults (males and females both) replacing inner primaries grow only an average of  $2.3 \pm 0.5$  primaries at once, whereas uninfected Laysans replacing inner primaries grow  $4.6 \pm 0.6$  feathers at once (Mann-Whitney U-test, infected  $n = 7$ , uninfected  $n = 9$ ;  $Z = -2.4$ ,  $p = 0.02$ ). Sample sizes are smaller than previous tests because only birds caught in active moult could be used.

At first we feared that this might be just an effect of sex, because all the uninfected birds were females, and only three of the seven infected birds were females (this sex difference is significant:  $\chi^2_{(1)}$  with continuity correction =  $4.1$ ,  $p = 0.04$ ). Therefore we repeated the test, this time with females only, and found that infected females ( $n = 3$ ) grew only  $2.0 \pm 1.0$  primaries simultaneously, whereas uninfected females ( $n = 9$ ) replaced  $4.6 \pm 0.6$  primaries at once. This difference is almost significant, even though the sample sizes are extremely small: Mann-Whitney,  $Z = -1.9$ ,  $p = 0.06$ .

#### (c) Timing of moult and parasites

In a system characterized by severe time constraints, a crucial parameter is the date when birds can begin their moult. If birds in poorer condition are constrained in their moult, we would expect infected birds to begin moulting later than uninfected birds. The date on

Table 1. Comparisons between birds which followed different moult strategies and the mean number of parasites present, as well as the mean number of primaries replaced

(Comparisons between means are two-tailed Mann-Whitney tests, means are reported  $\pm 1$  s.e.)

moult strategy	<i>n</i>	mean primaries replaced	mean number of parasites
males and females			
replaced outer primaries only	16	$3.4 \pm 0.2$	$3.3 \pm 0.9$
replaced inner primaries too	14	$7.5 \pm 0.3$	$1.2 \pm 0.5$
Mann-Whitney test		$Z = -4.8$ $p = 0.001$	$Z = -1.99$ $p = 0.045$
females only			
replaced outer primaries only	14	$3.5 \pm 0.3$	$3.4 \pm 1.0$
replaced inner primaries too		$137.6 \pm 0.4$	$1.0 \pm 0.5$
Mann-Whitney test		$Z = -4.5$ $p = 0.001$	$Z = -2.06$ $p = 0.04$

which birds began their moult is a difficult parameter to obtain on birds killed by drift nets, so our measure of moult initiation is necessarily indirect. For the subset of birds captured early in the moult season (in June and July), individuals that had already begun their moult were less likely to be infected with parasites than birds that had not yet begun their moult. Of 25 actively moulting birds caught early in the season, 28% were infected; while of 8 premouling birds, 88% were infected (d.f. = 1,  $\chi^2_{(1)}$  with continuity correction = 6.5,  $p = 0.01$ ). Infected Laysans appear to delay their moult.

#### 4. DISCUSSION

Parasitized Laysans replaced fewer primaries, were less likely to undergo the demanding moult of the inner primaries, grew fewer primaries simultaneously, and began their moult later than uninfected birds. Although sample sizes are small, the correlations support the hypothesis that some of the variance in Laysan moult patterns can be explained by variance in individual condition, as measured by parasite loads. This is the first evidence we can find of a relation between parasites and moult, a relation which is probably widespread, especially in large seabirds with incomplete moults.

Because more adult females than males were caught in the drift nets, females dominated our sample. Because males have higher parasite levels than females, we expect that males would show stronger trends, but unfortunately we could not test this. Males and females might possibly show quite different patterns, even though they are similar in size and behaviour.

Because these birds were captured while foraging at squid driftnets, one possible concern is that the parasite levels reported in these birds are unnatural artifacts of the squid driftnets. We have no evidence, however, that infection is from squid.

Without experimental tests, it is not possible to distinguish between cause and effect. Individuals infected with parasites may be poor quality individuals, and moulting patterns may be a function of another variable associated with poor quality, such as foraging efficiency. A bird in poor condition may have both less energy available for moulting but also have less ability to resist parasitic infection. Alternatively, parasites may directly lower the condition of a bird and therefore lessen its ability to put energy into moult. Either way, our results suggest that the extent and patterns of moult are affected by individual condition, as measured by parasite levels.

Other studies have also suggested that individual condition can affect the extent and timing of avian moult. Underhill *et al.* (1994) found two dead knots (*Calidris canutus*) that had been parasitized by the trematode *Cyclocoelum mutabile* and which seemed to have delayed their moult. White-crowned sparrows in poorer condition slowed the rate of their moult (Murphy & King 1991). When nutritional conditions are severe, feathers replaced are shorter, lighter and deformed (Murphy & King 1991). Few other studies of the effects of malnutrition on moult have been

conducted. Gosler (1991) showed that in juvenile Great Tits, protein stress during feather replacement arrested the moult of outer coverts. Meijer (1991) restricted food availability to startlings and found a delay in the onset of moult.

For large birds (such as seabirds, diurnal raptors, and herons) with time limitations that prevent complete moults, if parasites affect moult, this may be one additional avenue through which parasites can have important life history and evolutionary consequences. If albatrosses in poorer condition replace fewer primaries, this may give them more time for the next breeding season. However, this comes with costs attached: birds that replace fewer primaries accumulate old primaries and eventually may be forced to skip breeding to undergo a complete moult (Langston & Rohwer 1995*a*). Fisher (1976) showed that there is a great deal of variance in the frequency with which adult Laysans must skip breeding. Our results suggest that this variance may, at least in part, be due to differences in parasite levels which affect the extent of their moult *and* which, in turn, may affect future reproduction.

We thank Eric Hoberg, Bob Rausch, Pat Gould, Gary Shugart, Brian Schmidt, Carol Spaw and Jack Broughton for technical assistance, and Sievert Rohwer for comments on the paper. N.L. was funded by NOAA grant 43ABNF202931, the Burke Museum's endowment for Ornithology and the Burke Museum's Eddy Postdoctoral Fellowship in Ornithology. N.H. was supported by a NATO Postdoctoral Fellowship. This work was additionally funded by NSF SGER grant (BSR-9121879), and The University of Washington.

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Received 28 April 1995; accepted 17 May 1995