PTERYLOSIS AND TIMING OF MOLT OF THE WATER PIPIT

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Dwight (1900) reports two annual molts in the adult Water Pipit (*Anthus spinoletta*), a complete postnuptial molt and an incomplete prenuptial molt. This has been confirmed by Williamson (1965). In a study of the breeding ecology of an alpine population of the Water Pipit (Verbeek 1970), it was of considerable interest to determine the timing of the post-nuptial molt in relation to the breeding cycle, because only a brief period is available for these two energy-demanding processes. The material collected during that study prompted me to undertake a more detailed analysis of molt and pterylography in this species. Nitzsch (1840) found the pterylosis of *Anthus* to be the same as *Motacilla* (shown in figures) and Verheyen (1953) gives a figure of the spinal tract of the Sandy Plain-backed Pipit (*Anthus vaalensis*). In addition, I want to provide more details of the sequence of plumage succession in some tracts in the postnuptial molt and the timing of this molt in relation to the breeding cycle.

METHODS AND MATERIALS

The distribution of natal down was determined from nine nestlings ranging in age from 1–5 days. For the definitive pterylosis, four breeding adults (3 males, 1 female) and two fledglings (13 and 14 days old) were used. All these specimens were preserved in alcohol. Pattern of molt was determined from 38 adult, molting birds collected in the summers of 1959–69 near Beartooth Pass, Park County, Wyoming. The stage of molt of the flight feathers of 23 of the 38 specimens was determined in the field before the birds were prepared as study skins.

RESULTS

NATAL DOWN

The number of nestling down feathers ranges from 123 to 214 (table 1). Figure 1 shows the distribution of the down feathers of one nestling, 1–2 days of age (in stage A of Wetherbee 1957).

The sample is too small for a definitive statement concerning maximum numbers of down feathers for all of the tracts. The two down feathers on the secondaries are located in the region where secondary seven and eight will emerge, being best developed on number seven. The data suggest a basic number of nine down feathers for the middle and greater secondary coverts. The spinal tract appears to have a basic number of 12 down feathers placed in two lines of six on either side of the midline in the dorsal region. In one specimen there is a seventh feather, placed anteriorly and in line with the six behind it (fig. 1). It has no counterpart on the other side of the midline and it is only one-fifth the length of the others. Numbers in the pelvic region of the spinal tract are more variable. In five specimens, this region had from zero to three down feathers in one line along the midline in the upper pelvic area, directly behind the dorsal ones. In four specimens (fig. 1, below), the pattern varied considerably. The basic plan probably consists of 16. The 11 abdominal down feathers in one of the 4–5-day-old specimens (table 1) are arranged in two single lines extending more anteriorly than shown in figure 1. Variability in natal pterylosis has also been reported in the Red-winged Blackbird (*Agelaius phoeniceus*) (Clark 1967).

PTERYLOSIS OF *ANTHUS SPINOLETTA*

In figures 2, 3, and 4, some feather tracts are shown as dotted areas. No attempt was made to count all feathers in these tracts as Clench (1970) did for the House Sparrow (*Passer domesticus*). The alar and caudal tracts, except for the anal circlet, are shown accurately. All other tracts are as accurate as the text indicates.

Alar tract. *Anthus spinoletta alticola* has nine well-developed primaries (fig. 2). A tenth primary is vestigial (Stegmann 1962), and is 5–7 mm long. The nine greater upper primary coverts are anterior and slightly distal to each corresponding primary. The vestigial primary has no covert and is obscured by the ninth greater primary covert. Six to eight upper middle primary coverts are anterior and dorsal to each corresponding primary. The first, and sometimes the second and third upper middle covert, is missing, and the presence of the last (10th) is impossible to determine because of the encroachment of the marginal coverts. A carpal remex occupies the position of the first primary covert. A small down feather at the very base of the first primary, proximal to the carpal remex, has been interpreted as a carpal remex covert (Boulton 1927; Pitelka 1945).

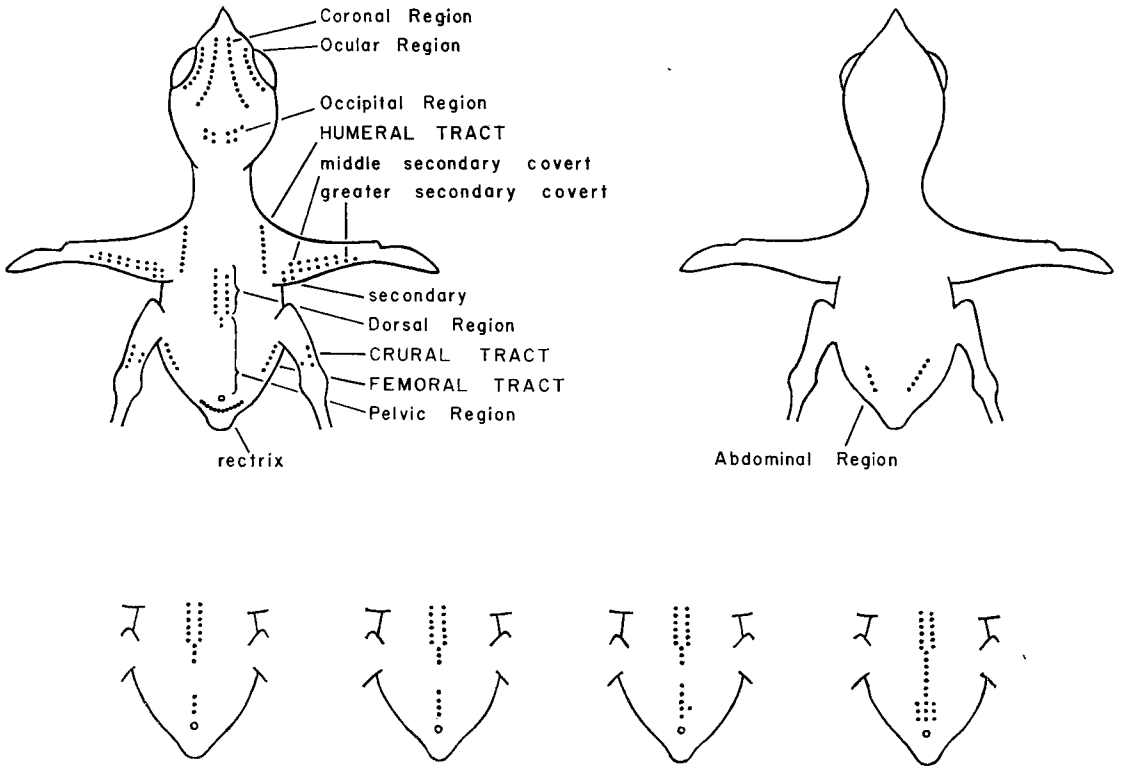The nine under greater primary coverts are

FIGURE 1.   Distribution of natal down in one nestling of *Anthus spinoletta* (above), and variation in the dorsal and pelvic region in four other specimens (below), showing a progressive series toward what may be the basic plan in the bottom right-hand diagram.
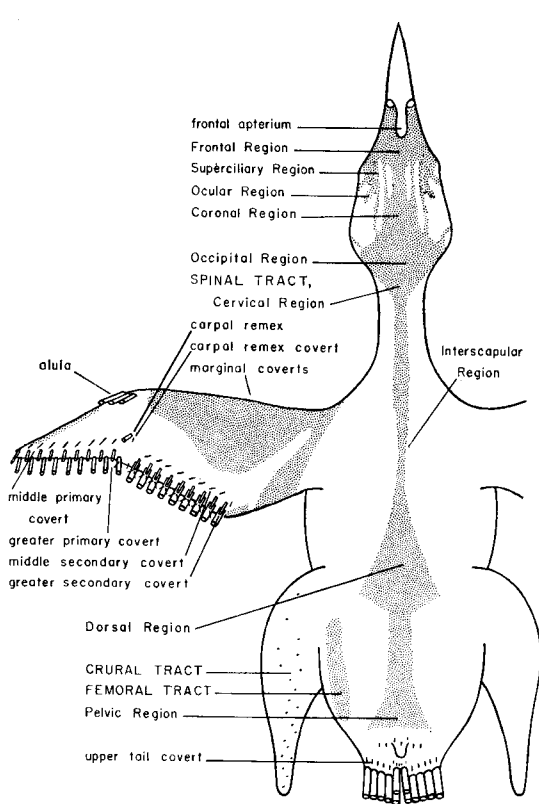

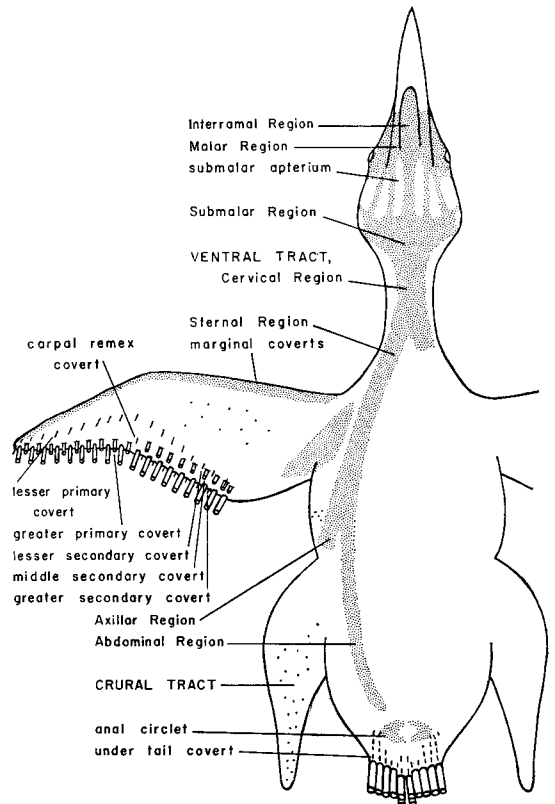FIGURE 2.   Distribution of feather tracts of *Anthus spinoletta* (dorsal view).

FIGURE 3.   Distribution of feather tracts of *Anthus spinoletta* (ventral view).

TABLE 1. Variation in natal pterylosis of nine nestlings of *Anthus spinoletta*.[a]

Tract	Age in days								
	1–2		2–3		4	4–5		5	
Ocular									
Right	8	3	12	10	12	11	8	8	5
Left	8	3	12	10	1	11	6	8	8
Occipital									
Right	5	4	5	6	6	4	5	5	6
Left	4	5	5	6	5	5	4	3	4
Coronal									
Right	12	12	12	13	15	14	15	15	12
Left	12	12	14	14	15	13	13	15	10
Humeral									
Right	8	3	2	9	8	9	9	6	8
Left	8	8	9	9	9	9	9	4	8
Middle s. c.									
Right	6	4	9	7	8	9	6	6	6
Left	7	3	9	7	8	9	6	6	5
Greater s. c.									
Right	9	9	9	9	9	9	8	9	9
Left	8	7	9	8	9	9	8	9	9
Secondary									
Right	2	2	2	2	2	2	2	2	2
Left	2	2	2	2	2	2	2	2	2
Spinal									
Dorsal									
Right	7	6	6	6	6	6	6	4	5
Left	6	5	6	6	6	6	6	6	5
Pelvic									
Right				1		3			
Left						3			
Middle	2	2	6	8	3	10	7	3	2
Rectrix									
Right	6	6	6	6	6	6	6	6	6
Left	6	6	6	6	6	6	6	6	6
Femoral									
Right	5	6	5	6	6	9	7	7	5
Left	5	6	8	5	6	8	7	6	7
Crural									
Right	6	4	13	7	6	9	4	11	12
Left	4	5	13	6	7	10	4	12	12
Abdominal									
Right	4	0	3	3	1	11	3	3	4
Left	6	0	4	7	2	11	5	2	7

a Each column of figures represents the down feathers of one nestling.

situated proximal to each corresponding primary (fig. 3). There are nine under lesser primary coverts, located dorsal and anterior to each under greater primary covert. A small down feather, distal to the ninth primary, close to the point of emergence of the latter, may represent the tenth under lesser primary covert. An under carpal remex covert is anterior and proximal to the first under greater primary covert.

Of the nine secondaries, the seventh is the longest and the ninth, most proximal, is the shortest. The nine upper greater secondary coverts originate directly over the base of each corresponding secondary (fig. 2). Upper middle secondary coverts one to eight are anterior and proximal to each greater secondary covert. The ninth upper middle secondary covert is situated at the same level as its corresponding middle secondary covert and proximal to it.

There are seven under greater secondary coverts, proximal to each of the first seven secondaries. Nine middle and eight under lesser secondary coverts originate progressively closer together going from the first to the eighth (fig. 3). The ninth secondary has no under lesser covert.

Arising at the upper dorso-lateral proximal base of the first primary is a small down feather (fig. 2). Two such small down feathers are located on each of the first six secondaries, one dorso-lateral and distal, the other proximal and lateral in position. The seventh secondary may have one or two such down feathers, the eighth, one or none, and the ninth secondary has no down feather associated with it. In addition, there is a small down feather located between the first primary and the first secondary. Similar down feathers are reported for the genus *Aphelocoma* (Pitelka 1945) and the Orange-crowned Warbler (*Vermivora celata*) (Foster 1967a).

The alula consists of three feathers. The longest feather is anterior and distal to the other two, which are progressively shorter proximally. The alular coverts merge with the marginal coverts of the patagium, which in turn merge with the humeral tract.

Capital tract. A frontal apterium is present as in *Lanius* (Miller 1931). The eye is surrounded by two concentric circles of small feathers (fig. 4). In the ocular region a single row of feathers surrounds the eye, leaving a definite gap posterior to the eye. The situation anterior to the eye is obscured by the encroachment of the loral feathers. The superciliary region consists of a single line of feathers that encircles the superciliary apterium. The feathers of the superciliary region merge anteriorly with the densely feathered loral region and posteriorly with the coronal region. The ear has two lines of feathers along its posterior margin. Dorsal to the ear is a well-developed temporal apterium, which is isolated from the postauricular apterium by the encroachment of feathers of the occipital region. The postauricular apterium is continuous with the lateral neck apterium. Both the temporal and postauricular apteria have scattered down feathers. A rictal apterium extends from the corner of the bill to slightly anterior-ventral to the ear.

Spinal tract. Directly behind the occipital region, the spinal tract is four feathers wide.
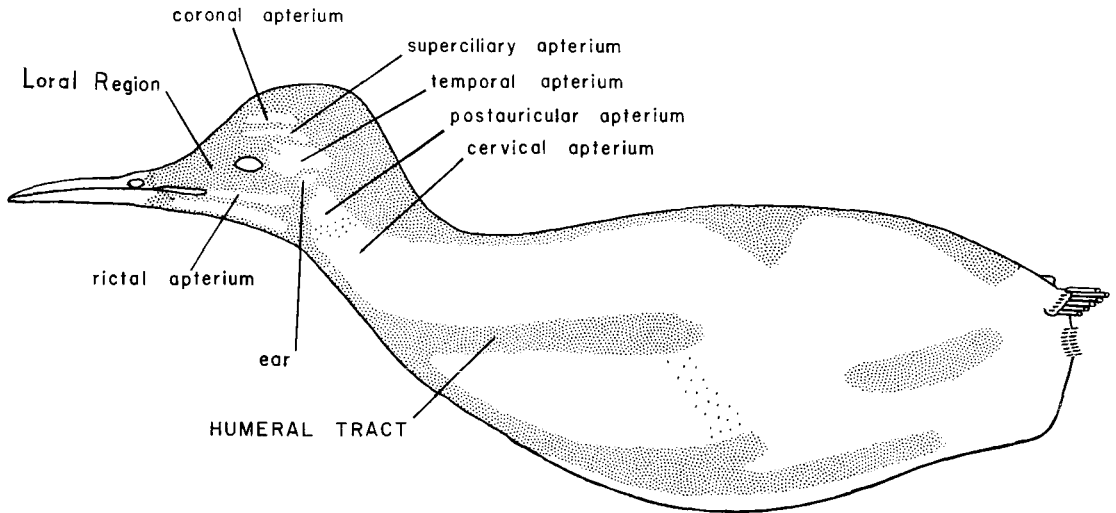
FIGURE 4. Distribution of feather tracts of *Anthus spinoletta* (lateral view).

The band narrows to one or two feathers in the interscapular region, just before it widens again into the dorsal region, which is about 15 feathers wide along its posterior margin (fig. 2). The feathers are arranged in chevron-shaped rows as described for *Passer d. domesticus* (Clench 1970). The shape of the "saddle" in *Anthus spinoletta* is similar to that shown by Nitzsch (1840) for *Motacilla* but quite different from those shown in figures of these genera by Verheyen (1953). The dorsal region has no apterium. Posterior to the dorsal region, the spinal tract is about six feathers wide. The outer feathers of this region are directed postero-laterally. The tract widens again just anterior to the oil gland. The configuration of the spinal tract shows great similarity to that found in *Lanius* (Miller 1931).

Caudal tract. There are 12 rectrices; the central pair is displaced dorsally. Ten upper tail coverts are present. The central pair corresponding to the central rectrices is absent. The principal row of under tail coverts consists of 12 feathers; the central pair is displaced dorso-laterally to the second pair. A second row of under tail coverts is incomplete and includes pairs 1, 4, 5, and 6.

The anal "circlet" consists of a double row of feathers grouped into two concentric semicircles that leave a small gap anterior and posterior to the cloaca. Scattered feathers connect the anal circlet with the outer under tail coverts.

There are about six filoplumes dorsal and anterior to the central, displaced rectrices, and about six more filoplumes are located ventrally in the space between the second pair of rectrices (2–2) and their under tail coverts. These were the only filoplumes seen in the pterylosis.

Ventral tract. The submalar apterium, enclosed by the malar and the submalar regions, extends back to almost the ear opening and is separated from the postauricular apterium. The cervical region extends back in chevron-shaped rows containing seven to nine feathers and splits into two sternal regions. In the anterior part of each sternal region, the feathers are arranged in single rows. Closely posterior to where the humeral tract approaches the ventral tract, the feathers are grouped in chevron-shaped rows. This continues posteriorly until the tract again bifurcates into a short axillary region, and into an abdominal region that continues posteriorly in oblique rows of three feathers. The two abdominal regions curve slightly inward and diminish in tract width toward the cloaca. Clench (1970) showed that in *Passer domesticus* the abdominal region (the main element by Clench) extends forward along the inside of the sternal region (flank element). The area where the main element separated from the flank element was indicated by irregularities in the row pattern. My material does not show these subtle irregularities in this area. The forward extension of the main element in *Anthus* is indicated by the proximity of the two most median feathers in each of eight rows. These feathers are arranged much closer to each other than the other feathers in the rows. Anterior to these eight rows, the forward extension of the main element consists of one feather in each of two rows. Posterior to the eight rows, the main element consists of three regularly spaced feathers in three or four rows anterior to the point of separation of the axillar from the abdominal region.

Humeral tract. This tract starts at the lead-

ing edge of the wing where it is confluent with the marginals of the wing, and it extends backward to the trailing edge of the wing. It is one to two feathers wide in front and widens to four or five feathers posteriorly. Scattered feathers indicate a connection between the posterior end of the humeral tract and the ventral tract (fig. 4).

Femoral tract. The tract is two to four feathers wide. It begins in the region of the femur and extends posteriorly to a level anterior to the oil gland.

Crural tract. The ventral and dorsal surfaces of the tibia are well feathered. The feathers are densest at the distal end. The lateral surfaces are very sparsely feathered.

POSTNUPTIAL MOLT

Figure 5 shows the sequence of feather replacement in the remiges and rectrices and the approximate date of inception and completion of growth in each feather. The figure was prepared from a molt chart on which the stage of molt of each rectrix and remex was recorded, allowing comparison among them in one bird and among all birds in the sample ($N = 38$).

The earliest sign of molt occurs in the interscapular region of the spinal tract and simultaneously (or very shortly afterward) in the sternal region of the ventral tract. This is soon followed by the first (innermost) primaries. Williamson (1965) suggests that body molt in *A. s. kleinschmidti* does not begin before primaries one and two are being replaced. The primaries are replaced in sequence from one to ten. The vestigial tenth primary drops independently of the ninth, in contrast to the findings of Foster (1967b) for the Orange-crowned Warbler.

The eighth secondary drops at about the same time as the third primary. When the three innermost secondaries are fully grown, the first five primaries are also new, and all other primaries, except the ninth and tenth, are being replaced. Secondaries 1–6 are replaced in sequence from one to six. The first secondary (outermost) drops at about the same time as the sixth primary, at which time secondaries 7–9 are growing, and secondary 8 is fully grown. The sixth secondary is the last feather to be replaced. The rectrices molt rapidly and in regular sequence from one to six.

TIMING OF MOLT

Figure 6 shows the timing of the postnuptial molt. The scoring scheme of Pitelka (1958), based on selected flight feathers, was used.
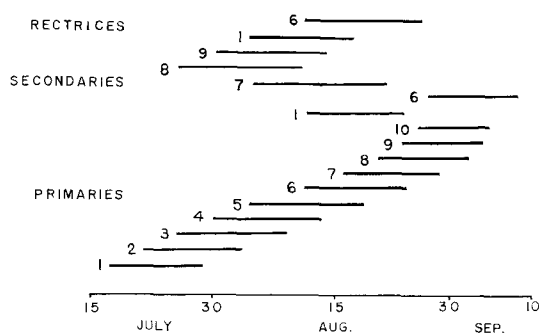

FIGURE 5. Approximate temporal sequence of inception and completion of molt in the rectrices and remiges of *Anthus spinoletta*, and the duration of molt in the population as a whole, based on 25 males and 13 females.

Although molt begins and ends on the body, this scheme was used because collectively the remiges and rectrices span most of the period of molt. Whatever body molt occurs before and after the replacement of the remiges is considered insignificant in relation to the total feather replacement.

Within the whole population, molt requires a little over 2 months. During this period males ($N = 34$) molt earlier than females ($N = 18$, fig. 6). In this species only the female incubates, and both parents feed the young (Verbeek 1970). Although the male feeds the incubating female, she obtains about half of her own food requirements during this time. Also, it is possible that the female cares for the young longer than does the male, but this could not be ascertained in the field. Thus the female's delay in molt could result from a greater energy expenditure in the reproductive effort.

Molt of the individual requires little more than a month (fig. 6), an unusually short
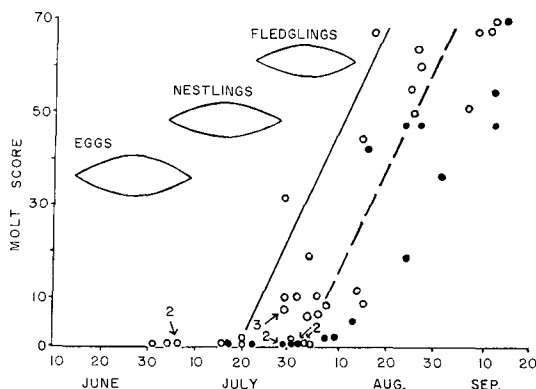

FIGURE 6. The period of the postnuptial molt in relation to the reproductive cycle. Molt in the males (circles and solid line) is about 14 days ahead of the females (dots and broken line).

period. During this time the birds remain inconspicuous, perhaps because of impaired flying ability. Similar short periods of molt are reported for the Snow Bunting (*Plectrophenax nivalis*) (Stresemann and Stresemann 1970) and the Thrush Nightingale (*Luscinia luscinia*) (Berger 1967). Figure 6 also shows the period when the eggs, nestlings, and fledglings are present. Considering the population as a whole, molt of the flight feathers overlaps with the end of the nestling period. On an individual basis, however, it probably does not begin until the young have fledged.

Earlier (Verbeek 1970:444), I noted that pipits appear to move away from their breeding ground when the fledglings become independent. It appears, though, that they remain in the alpine zone in their southward migration. Specimens in advanced stages of molt as well as birds that have completed their molt are present until the middle of September, at which time they are forced to lower elevations by snows. Migration during molt has been reported for the Tawny Pipit (*Anthus campestris*) and Richard's Pipit (*Anthus richardi*) (Stresemann and Stresemann 1968).

The alpine regions of Montana and elsewhere show an abundant and varied insect fauna (Chapman 1954a, b; Mani 1968). Preliminary insect-censusing on the Beartooth Plateau indicates that most insects are present in August (A. Eaton, unpubl. data). Indirect evidence for this abundance is the influx of bird species to the alpine zone in August and September (Pattie and Verbeek 1966). Such a rich food supply is not presumed to be present at this latitude in the more arid lower altitudes at this time of the year. It thus appears to be advantageous for the pipits to stay in the alpine in late summer.

CONCLUSION

In the Water Pipit, then, breeding and molt partly overlap. The birds breed early in the short alpine summer at relatively low temperatures (Verbeek 1970). Although the food supply steadily increases, nestlings are present prior to the greatest food abundance. In August, fledglings and adults exploit the same large food supply, which is plentiful enough to provide energy for a rapid molt as well.

ACKNOWLEDGMENTS

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