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A NEW METHOD FOR ESTIMATING INDIVIDUAL SPEED OF MOLT[1]

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Abstract. We introduce a new method, Residual Raggedness Value (RRV), for estimating molt duration for individual birds captured only once during a molting period. The method is developed and tested using data from Willow Warblers (*Phylloscopus trochilus*) in prebasic (post-nuptial) molt collected in Swedish Lapland during 1983–1990. The wing raggedness value (RV) describes the amount of "missing" feather area in the wing of a molting bird. RV was positively correlated with stage of molt. The RRVs from this correlation were used to obtain an estimate of the size of the gap in the wing that was independent of stage of molt (i.e., RV controlled for stage of molt). Molt speed of recaptured birds was highly correlated with RRV at the first capture ($r^2 = 0.57$). Thus, an individual's future molt speed could be predicted at the first capture with a high degree of accuracy. Compared to other methods for estimating molt duration, the RRV method produced estimates close to those obtained from recaptured birds. The widely used regression method for estimating molt duration (regressing date of capture on molt score) gave estimates that deviated substantially from both those obtained from the recapture and RRV methods. Our new method is a potentially powerful tool for increasing sample sizes of individual molt speeds in a studied population. This will facilitate understanding how individual birds may adjust the timing and duration of molt in relation to breeding and migration. The RRV method is probably applicable to most species that molt feathers sequentially. However, slow-molting species with few simultaneously growing feathers might be problematic.

Key words: Molt duration; feather growth; wing raggedness; Phylloscopus trochilus; *Willow Warbler.*

INTRODUCTION

The most widespread technique used to estimate duration of molt is to regress date of examination (dependent variable) on molt score (independent variable) of captured individuals (Pimm 1976, Summers et al. 1983). This gives a statistical description of an average individual's onset and duration of molt which can be used for comparisons between populations of the same or other species. However, the method fails to reveal the molt duration of the individuals behind the population average. Although date is the dependent variable, data are often shown with the axis reversed. In such a graph, points above the regression line of capture date against molt score indicate either high speed or early onset of molt. Thus, despite an underlying variation of molt duration among individuals in a studied population, the regression method cannot disclose the basis of variation within the population. Individual duration of molt can be extrapolated from birds captured two or more times during the molting period. However, in most studies only a low proportion of the molting birds are captured twice or more. Thus, a large number of molting individuals must be processed before the sample size of recaptured and still molting individuals allows a meaningful analysis of the variation in individual molt duration.

Onset of molt probably limits reproductive performance because missing feathers impair the bird's maneuverability (Pennycuick 1975), making a molting bird a less efficient forager and parent (Lustick 1970, Payne 1972). There are several examples demonstrating that breeding phenology influences onset of molt (e.g., Orell and Ojanen 1980, Rimmer 1988, Zaias and Breitwisch 1990, Morton and Morton 1990). Moreover, onset (Bensch et al. 1985) and presumably duration of molt (Pietiäinen et al. 1984) seem to be influenced by the number of young the adult is attending. These results indicate important trade-offs between breeding and molting. Furthermore, once molt has started it probably must be completed before the start of fall migration, and among passerines there seem to be few exceptions to this rule (Summers et al. 1983). A late start of migration might be disadvanta-

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geous since the bird might face food shortage as the fall approaches, or if there is an intra-specific competition for territories along the migratory route (Rappole and Warner 1976, Lindström et al. 1990) or in winter quarters (Price 1981). When breeding activities delay the onset of molt there are two possibilities for the bird to keep up with the migratory time schedule. It can either increase the speed of molt or postpone the molt of some flight feathers until after the migration. To investigate the adaptive significance of different molt patterns, one needs a reliable measure of molt speed and molt duration of individual birds.

We developed a method for obtaining estimates of duration of molt for individuals captured only once during a molting period, exploring the idea of "wing raggedness" introduced by Haukioja (1971a, 1971b). We compare this method with estimates derived from the regression method and from recaptures using a data set of Willow Warblers (*Phylloscopus trochilus*).

MATERIALS AND METHODS

The study was carried out in subalpine birch forest at Lake Tjulträsk (520 m altitude) near Ammarnäs (65°58′N, 16°07′E) in Swedish Lapland, as a part of the LUVRE project (Enemar et al. 1984). From 15 July to 20 August each year 1983–1990, with small variation between years, 20 to 22 mist nets were used daily from 07:00 to 13:00, local summer time (GMT + 2 hours). The nets were set at the same places in all years.

The molt pattern of the Willow Warbler is exceptional in that adults annually undergo two complete molts. The prebasic (post-nuptial) molt occurs on breeding grounds and the prealternate (prenuptial) molt takes place in the African winter quarters (Salomonsen 1945, Williamson 1976, Ginn and Melville 1983, Svensson 1984). However, the molt of *Phylloscopus* warblers does not readily fit the Humphrey and Parkes (1959) terminology. The prebasic molt has been estimated to last 30 to 50 days (Evans 1971, Tiainen 1981, Ginn and Melville 1983, Norman 1990, Underhill et al. 1992), while the prealternate molt is slower (Pearson 1973, Ginn and Melville 1983, Underhill et al. 1992). Our population breeds at a high latitude with little time between termination of breeding and onset of fall migration (Högstedt and Persson 1982). Clutches are initiated from 10 June (Arvidson and Nilsson 1983) and at least the females do not commence molt until young fledge (Bensch et al. 1985). At Ammarnäs, temperatures regularly drop to 0°C in early September and few Willow Warblers remain by the end of August (Nilsson 1983). Although arrested secondary molt (Ginn and Melville 1983) is frequently found, very few, if any, seem to commence migration with unmolted primaries (Hedenström et al. 1989).

Willow Warblers were banded with aluminum bands and aged and sexed according to Svensson (1984). Molt in the bird's left wing was recorded according to Ginn and Melville (1983): old feathers were scored 0; new, full grown feathers were scored 5; growing feathers were scored on a scale from 1 to 4. The outermost reduced primary (P10) has been excluded in the analyses (Rimmer 1988, Underhill et al. 1992). Thus, the primary score (PS) is the sum of the molt scores for primaries 1–9 and likewise the secondary score (SS) is the sum for secondaries 1–6. Tertials were not included in the secondary score. Only PS was used to describe the progress of molt since the molt of secondaries, with few exceptions, is completed within that period. The length of growing feathers was measured (in mm) using a thin ruler. In five males and five females that were not molting we measured the length of each remex. These measurements were later used to calculate the length of growing feathers relative to full-grown length.

To estimate the size of the gap in the wing caused by missing or growing feathers, we used the measurement of wing raggedness introduced by Haukioja (1971a). This method corresponds to the molt score, where the sum of the molt score and the raggedness score is 5 for each new or growing feather. Thus, both an old and a new full grown feather would give zero in raggedness score, whereas, e.g., a feather in pin (molt score 1) scores 4 in raggedness (Fig. 1). Raggedness values can only increase as long as there are feathers left to be shed. The innermost secondaries are shed after the shedding of the outermost primaries (pers. observ.). Thus, incorporation of the secondaries extends the period during which raggedness values can vary between individuals (Haukioja 1971b). Therefore, we included secondaries together with primaries when calculating the raggedness score. Raggedness can thus vary between 0 and 60. At both very low (PS $<$ 3) and very high (PS $>$ 42) molt scores, the raggedness values (RV) are low with little individual variation (Haukioja 1971b). Hence, in the analyses of raggedness we only included birds with a primary score in the interval of 5–35 points. At the beginning of this interval Willow Warblers

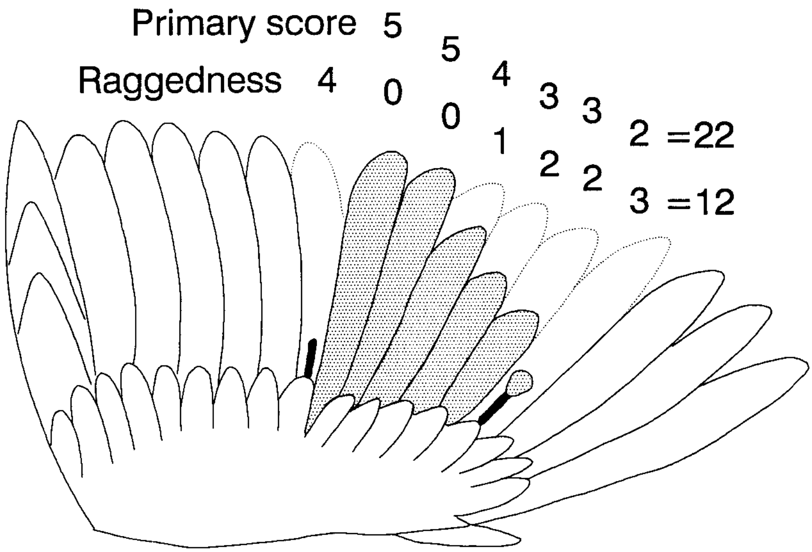

FIGURE 1. Description of the method for estimating the primary score and the corresponding raggedness value. Shading depicts the emerging new feathers.

have re-grown 7% of the remex mass, and at the end, 76% (Underhill et al. 1992). When estimating molt speed for individuals we excluded animals re-trapped in fewer than four days since the recapture method tends to produce estimates with very high variance when these are included (Ginn and Melville 1983). When estimating growth rates of a bird's flight feathers, we included all individuals that were re-trapped two to nine days apart. Throughout, each individual was only included once in a single year, the first time it fulfilled the criteria for the respective analysis. Furthermore, we will use the term "molt speed" to describe the rate at which molt progresses during short time intervals, whereas "duration of molt" will be used to describe the total number of days it takes to replace the primary flight feathers.

Parametric statistics are used throughout (unless otherwise stated) and all tests were performed according to SYSTAT. Residuals from regressions were tested for non-normality with the Lilliefors' test (Wilkinson 1990). Non-significant interaction terms have been excluded in analyses of variance (ANOVA) and covariance (ANCOVA) (Sokal and Rohlf 1981).

RESULTS

We captured 519 Willow Warblers in primary molt. Number examined per year varied from 28 in 1983 to 110 in 1987. When 31 individuals of unknown sex were excluded, the sample consisted of 240 females and 248 males. Of these, 38 females and 47 males were re-trapped and reexamined at least two days later in the same season. The frequency of recaptures did not differ between the sexes.

RAGGEDNESS PREDICTS SPEED OF MOLT

We used all birds with a primary score of 5–35 points when first examined, and recaptured at least four days later, provided that they still had growing primaries. Average speed of molt of primaries for 34 re-trapped males and 25 females was 1.06 ± 0.31 ($\bar{x} \pm$ SD) and 1.20 ± 0.52 points per day, respectively. Speed of molt was significantly correlated with wing raggedness (RV) at first capture ($r = 0.70$, $P < 0.001$, $n = 61$, including three unsexed birds). While speed of molt seemed constant during different stages of molt within the 5–35 PS interval ($r = 0.02$, $P = 0.87$, $n = 61$), wing raggedness increased significantly with stage of molt (Fig. 2, $r = 0.48$, $P < 0.001$, $n = 61$). Thus, a large RV indicates either a high speed or a later stage of molt. To make RV independent of stage of molt we used the residual of the regression in Figure 2, i.e., the deviation of each observation from the regression line of RV against PS. We will call this value the Residual Raggedness Value (RRV). The relationship between RRV and speed of molt was highly

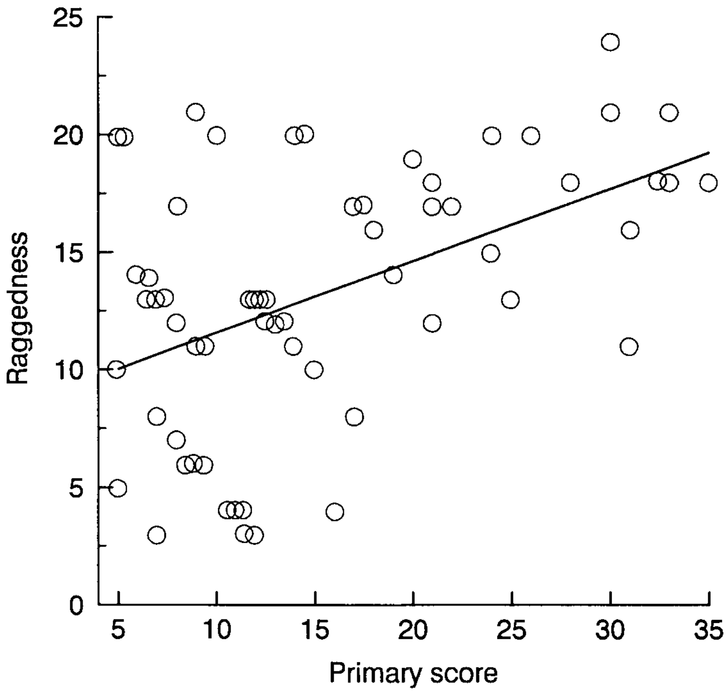

FIGURE 2. The relationship between raggedness value (RV, see methods) and primary score (PS) for recaptured male and female Willow Warblers (Y = 0.31X + 8.48, data from 1983–1990).

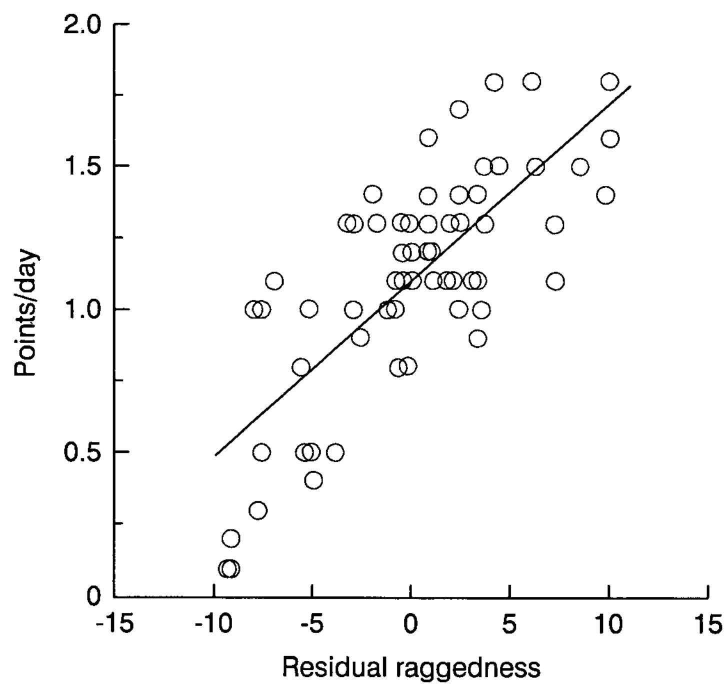

FIGURE 3. The relationship between residual raggedness value (RRV), when first examined, and speed of molt (points per day) for re-trapped male and female Willow Warblers (Y = 0.062X + 1.105, n = 61, data from 1983–1990).

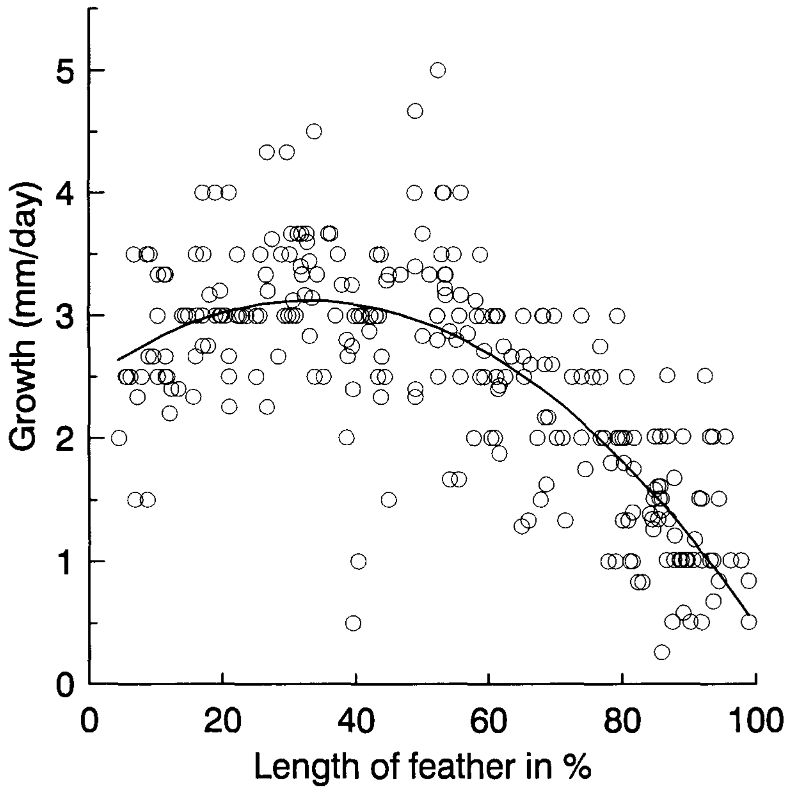

FIGURE 4. Growth rate of separate remiges in relation to percent of full-length. Line fitted by polynomial regression. Each data point represents one growing feather. Data from 48 birds re-examined two to nine days after first capture.

significant (Fig. 3, $r = 0.76$, $P < 0.001$, $n = 61$) and the RRV predicted 57% of the variation in speed of molt. In general terms, this is the partial correlation between estimated speed of molt and raggedness, controlling for the influence of stage of molt (primary score). Thus, unlike RV, RRV is independent of stage of molt. The data were pooled for both sexes since there was no significant difference between males and females (ANCOVA, effect of RRV; $F = 73.4$, $P < 0.001$, effect of sex; $F = 0.09$, $P = 0.76$).

One could expect that there is a trade-off between the number of growing feathers and the growth rate of individual feathers (GRF), so that a bird with a high RRV will have many feathers growing but with each feather growing at a slow rate. Feathers grow at different rates depending on how far they are from being complete (Newton 1967). Since there is a correlation between RRV and average feather length, we must control for the effect of feather growth stage on feather growth rate before searching for the relationship between RRV and feather growth rate. We plot the daily growth rate of the feather against its average length (i.e., the mid-point between the two captures) for each growing feather (Fig. 4). We have included all growing primaries and secondaries (in left wing) for every bird that was examined two to nine days apart, in total 275 feathers of 48 birds. All feather lengths were transformed to percent of full grown, making it possible to use feathers of different position in the wing in the same analysis. We present the rate of feather growth as mm/day, since actual growth rate seems independent of the feathers' final length (Newton 1967). A second-order equation described the relationship and both the first and second-order term contributed significantly ($Y = 2.482 + 0.0389X - 0.00059X^2$, $r = 0.76$, $n = 275$, $P \ll 0.001$). Growth rate was maximum at 3.1 mm per day when the feather was 33% of full length. To estimate the growth rate of feathers (GRF) of individual birds, we calculated the deviation in growth rate from the

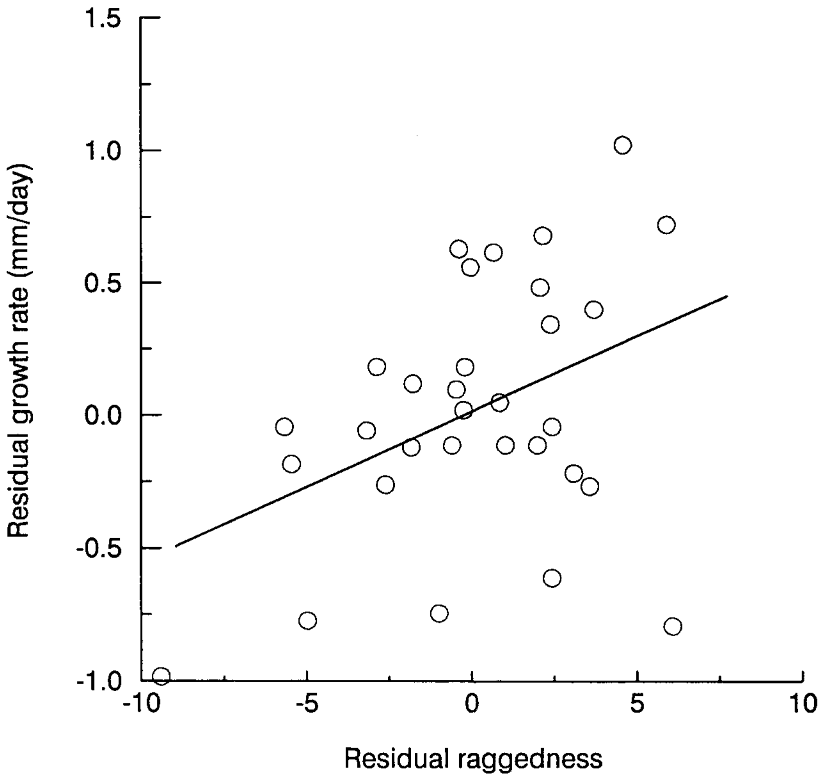

FIGURE 5. The relationship between an individual's mean growth rate of feathers (the average residual from Fig. 4) and its residual raggedness value at the first examination event (Y = 0.06X + 2.31).

curve in Figure 4 (residual GRF). The mean residual GRF of each of the 31 individuals with PS 5–35 was calculated as the average deviation of all of a bird's growing feathers from the expected GRF (i.e., average residual from the equation in Figure 4 for each individual). Mean residual GRF was positively correlated with residual raggedness (RRV) ($r = 0.41$, $n = 31$, $P = 0.02$, Fig. 5). Thus, a high RRV indicates both that many feathers are growing and that they are growing rapidly.

RAGGEDNESS PREDICTS DURATION OF MOLT

If a bird tended to change speed of molt during the molting period, then RRV cannot be used to estimate the duration of molt. One can test the constancy of RRV over time if the majority of the feathers that contributed to the raggedness value at time t were fully grown when the bird was re-examined. To keep the same residual raggedness value at two examination dates, a bird must shed a similar number of feathers at the same rate. We found a significant correlation ($r = 0.88$, $n = 12$, $P < 0.001$, Fig. 6) between the RRV at the first examination and the RRV at the second examination. (The two examinations were at least 10 days apart.) Thus, RRV at one capture was a good predictor of the bird's future RRV, indicating that Willow Warblers adopt an almost constant molt speed during most (5–35 PS) of the molting period. However, since the slope of the regression line Y = 0.69X − 0.439 (Fig. 6) was significantly less than 1 (F [1, 10] = 6.91, $P = 0.025$), birds with an initially low RRV slightly increased their RRV.

COMPARISONS OF METHODS

In Table 1 we summarize yearly estimates of molt duration, as revealed by three different methods: (1) linear regression of date against molt score, (2) recaptures of individuals caught at least four days apart, and (3) the RRV method applied to birds captured when showing molt score in the range of 5–35 points. Because the RRV method was developed from the recaptured individ-

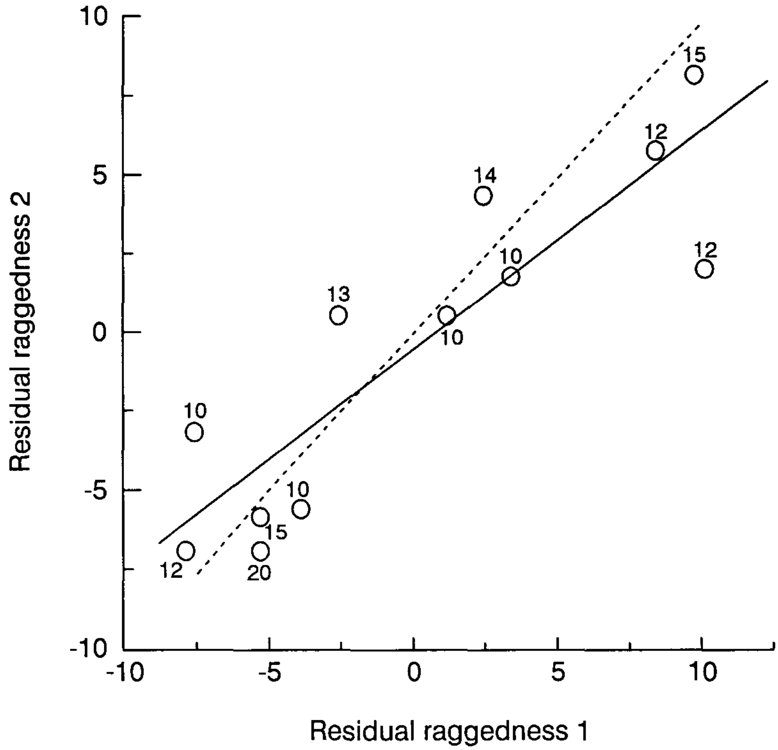

FIGURE 6. The correlation between residual raggedness values at the first and second examination event for Willow Warblers recaptured at least 10 days after first captured. The numbers at the data points give days between captures. The dotted line shows the expected 1:1 relationship.

uals included in method 2, these were excluded before we estimated molt duration by the RRV method. Although the three methods give different results, each method generated an estimate that varied consistently for the two sexes (Table 1). Linear regression produced the shortest durations, 28.6 days for males and 26.3 days for females (Fig. 7). The RRV method estimated molt duration as 42.2 days for males and 39.9 days for females, 1.8 days and 3.0 days shorter than the recapture method, respectively. For both males and females, the between-year variation

TABLE 1. Comparison between three different methods for the estimation of molt duration in Willow Warblers caught at Lake Tjulträsk during eight years. Sample sizes are given within parentheses. The coefficient of variance (CV) expresses the between-year variation as a percentage of the mean (SD × 100/$\bar{x}$).

	Males			Females		
	Regression	Recapture	RRV	Regression	Recapture	RRV
1983	29.6 (8)	52.5 (1)	40.5 (3)	20.4 (17)	72.9 (3)	43.9 (9)
1984	30.4 (24)	50.7 (3)	41.0 (12)	19.5 (30)	34.8 (3)	50.4 (15)
1985	28.3 (45)	44.8 (8)	41.8 (30)	16.5 (39)	71.4 (5)	35.6 (20)
1986	36.9 (37)	50.2 (5)	43.1 (18)	26.9 (43)	42.3 (5)	43.4 (19)
1987	28.2 (73)	40.1 (10)	42.4 (44)	30.7 (34)	48.6 (3)	37.9 (12)
1988	32.0 (22)	49.1 (2)	46.5 (15)	37.5 (22)	58.8 (3)	36.2 (8)
1989	25.8 (32)	37.3 (5)	40.3 (17)	27.1 (36)	30.7 (9)	36.0 (11)
1990	27.4 (7)	—	37.7 (5)	21.6 (17)	39.8 (1)	37.5 (8)
Mean	28.6 (248)	44.0 (35)	42.2 (144)	26.3 (238)	42.9 (32)	39.9 (102)
CV	11.5	12.5	6.1	27.5	32.4	13.2

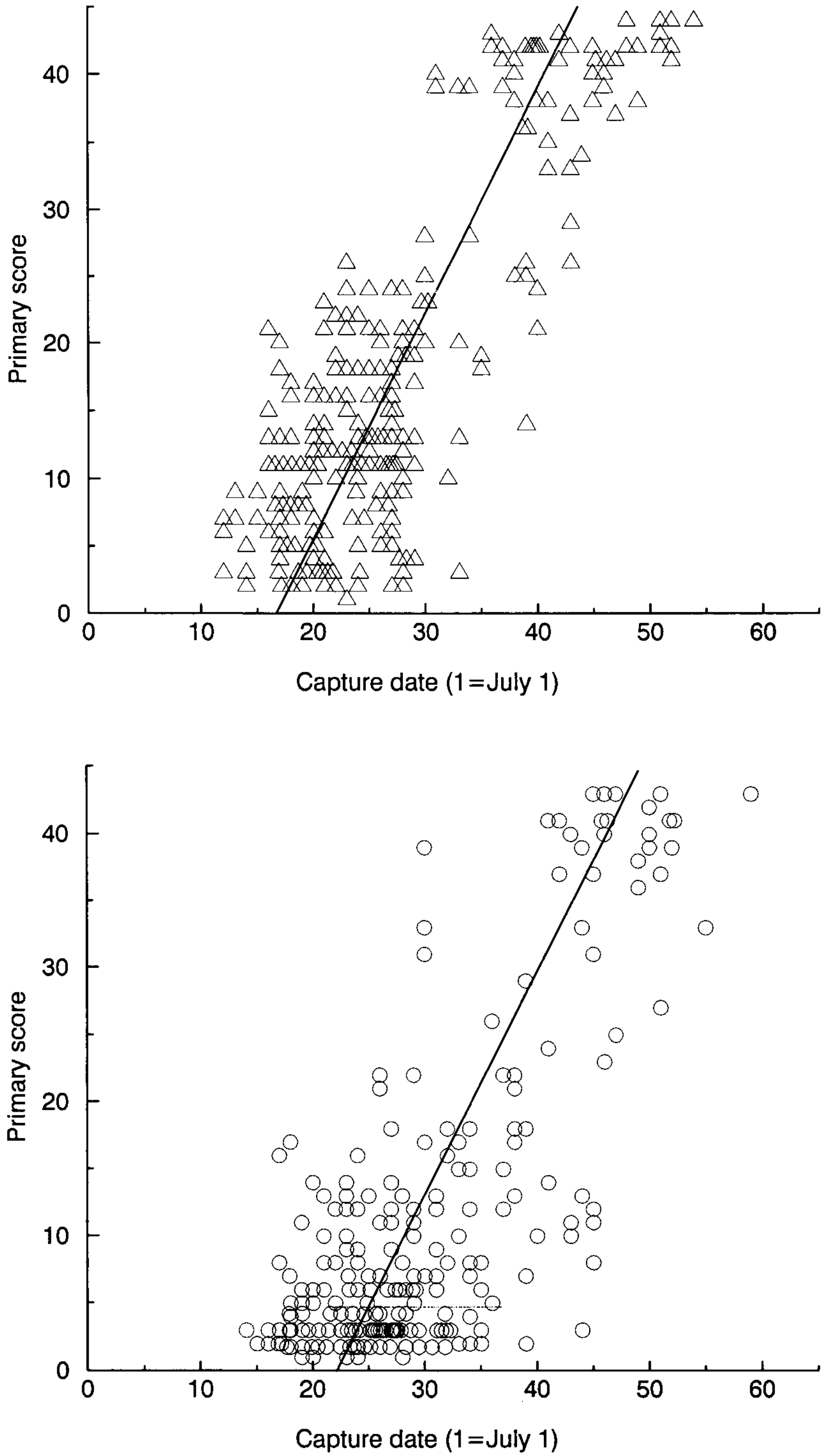

FIGURE 7 Primary scores of molting male (a) and female (b) Willow Warblers at Ammarnäs plotted against date of examination. Data from 1983–1990. Regression lines calculated with date as the dependent variable; (a) date = 1.62PS − 26.3, (b) date = 1.72PS − 39.2.

in estimated molt duration, calculated as coefficient of variance (CV), was highest for the linear regression method and lowest for the RRV method. For all three methods, females had a shorter molt duration and a higher between-year variation than had the males.

DISCUSSION

The linear regression method estimated molt duration as 26–29 days, which is shorter than the 31 days estimated for this Willow Warbler population by Underhill et al. (1992). However, this estimate may be too low. First, their analysis was based on a part of the data sample used in the present study and this is biased in favor of birds in the early stages of molt (Fig. 7). Underhill et al. (1992) note that their method is sensitive to such a bias. Our study period was shorter than the molting period of the population. This together with the few captures of birds in the middle stage of molt results in an underestimated duration of molt because early starting birds (mainly males) are under-represented in the sample at early molt stages and late starting birds (mainly females) at late stages. Second, Underhill et al. (1992) estimated molt duration to be 40 and 43 days for two other populations of *P. t. acredula*. These estimates are identical to the results obtained by the recapture method and RRV method in the present study (Table 1).

We found that the RRV predicted individual molt duration because it correlated with molt speed (Fig. 3) and because individuals seemed to maintain a nearly constant RRV over a considerable part of the molting episode (Fig. 6). Compared with the recapture method, the greatest advantage of the RRV method when estimating duration of molt is that sample sizes are increased, often ten-fold. The between-year variation in estimates of molt duration may be reduced with larger sample sizes (see Table 1). Also, the recapture method likely produces a more biased sample of individuals because the capture rate probably is influenced by the molt speed. Birds in heavy molt often are reluctant to fly and thus less often captured in mist-nets (see Dolnik and Blyumental 1967, Haukioja 1971b). This may result in a biased sample in favor of recapturing slow-molting individuals.

The residual raggedness values cannot be directly translated into speed of molt owing to its fluctuating pattern in a molting individual. RRV peaks the day when an old feather is shed, then slowly stabilizes until another feather is shed and a new peak appears. An individual that maintains a stable molt speed will regularly show both higher and lower RRV than its average RRV. Thus, if RRV is translated into points per day, the RRV method will undoubtedly exaggerate the variation in molt speed, indicating some individuals with extremely fast or slow molt. For example, an RRV of 25 corresponds to a speed of molt of 1.75 points per day (Fig. 3). This yields a duration of 26 days, probably a few days shorter than what is actually occurring. The relationship in Figure 6 deviates from the expected 1:1 ratio, indicating that individuals with a fast molt speed at the first examination had a slower molt speed when recaptured, and vice versa. However, this is a methodological artefact. Individuals with extreme values (e.g., high RRV) are probably examined when showing peak RRV. When later recaptured, they will by chance alone have an RRV closer to their average. This will lower the slope of the line in Figure 5. Despite this, the RRV method should be a useful tool to detect relative differences in speed and duration of molt between individuals.

The relation between length and growth of feathers (Fig. 4) shows that a recently shed feather will have a high growth rate, and therefore, will contribute to a high molt speed. Also, when a feather is recently shed the individual will have a high RRV. Thus, during the interval from the shedding of one feather prior to the shedding of the next, RRV and molt speed will be positively correlated and both will be declining. However, this correlation between RRV and molt speed cannot generate the correlation in Figure 3 because the time between examination events (>4 days) exceeds the average shedding interval of primaries (2.9 days). Because the RRV method relies on the assumption that it describes the rate by which feathers are shed, a test of the validity of the RRV method by using recaptured birds therefore requires that the time span between captures is at least one shedding interval.

In general, a bird can modulate molt speed by varying the rate at which old features are shed, and thus the size of the gap in the wing, or by varying the growth rate of individual feathers (GRF). By definition, wing raggedness is strongly correlated with the number of simultaneously growing feathers (Fig. 1). However, our data do not suggest a trade-off between the number of growing feathers and their growth rate. Instead there was a positive relationship; birds with many feathers growing also had a higher feather growth rate (Fig. 5).

USING THE RESIDUAL RAGGEDNESS TECHNIQUE

The RRV method is probably applicable to most species that molt feathers sequentially, shedding the next feather before the preceding is full-grown. However, slow-molting species with few simultaneously growing feathers might be problematic and the method is not suitable for some larger species (e.g., eagles and vultures) with stepwise molt.

When applying the RRV method, the first step is to plot raggedness values (RV) against primary score (PS), also including birds only caught once. From this relationship, the residual raggedness values (RRV) can be obtained. RRV is the deviation parallel to the y-axis of each data point from the regression line. This value estimates the raggedness independent of molt stage. A bird with a positive RRV thus has a larger "hole" in the wing and more growing feathers than expected from its molt stage. Likewise, a negative RRV value reflects a smaller "hole" and fewer growing feathers.

Not all individuals can be used when calculating molt duration by the RRV method because near the onset and completion of molt, raggedness values are close to zero and the between-individual variation in RRV is too minute to predict molt speed. Furthermore, raggedness can only decrease after shedding the last feather and the speed of this decrease will be determined by feather growth rate. In this study, we have arbitrarily selected individuals with a primary score between 5 and 35 points. These limits are probably conservative and should not be considered as fixed. However, expanding the interval may increase uncertainty in the data, whereas shrinking the interval will decrease the sample size, which may bias the sample.

Two relationships confirm that RRV predicts duration of molt: (1) the correlation between RRV and speed of molt (Fig. 3), and (2) the constancy of RRV over a major part of an individual's molting period. Before using the RRV method it is desirable to confirm these relationships. This requires a sufficiently large sample of recaptured birds ($n \geq 30$) and that the interval between captures is longer than the interval between the shedding of feathers. With enough recaptures, RRV can be translated into actual speed of molt by the same method as in the correlation in Figure 3. This allows comparison with studies using this or other methods. Nevertheless, even without extensive recapture data the RRV might prove useful as a relative measure of molt speed within or between populations. For example, molt speed may influence survival between years and this can be tested by comparing the survival of birds having high RRV with those having low RRV. Hence, our method may give important information without establishing how RRV translates into actual molt speed. Note that when molt is compared over a wide geographical range, RRV must be calculated in the pooled sample because it measures the relative deviation in raggedness (Fig. 2).

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LITERATURE CITED

ARVIDSON, B. E., AND NILSSON, L. 1983. Breeding biology of Willow Warbler, *Phylloscopus trochilus,* in Swedish Lapland. Vår Fågelvärld 42:81–88.

BENSCH, S., L. GEZELIUS, M. GRAHN, D. HASSELQUIST, Å. LINDSTRÖM, AND U. OTTOSSON. 1985. Influence of brood size on moult in female Willow Warblers. Ornis Scand. 16:151–152.

DOLNIK, V. R., AND T. I. BLYUMENTAL. 1967. Autumnal premigratory and migratory periods in the Chaffinch (*Fringilla coelebs coelebs*) and some other temperate-zone passerine birds. Condor 69:435–468.

ENEMAR, A., L. NILSSON, AND B. SJÖSTRAND. 1984. The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland: a 20-year study. Ann. Zool. Fenn. 21: 321–338.

EVANS, P. 1971. Molting seasons of Willow Warblers and bramblings in Norwegian Lapland. Ornis Fenn. 48:131–132.

GINN, H. B., AND D. S. MELVILLE. 1983. Moult in birds. BTO guide No. 19. British Trust for Ornithology, Tring.

HAUKIOJA, E. 1971a. Processing moult card data with references to the Chaffinch *Fringilla coelebs.* Ornis Fenn. 48:25–32.

HAUKIOJA, E. 1971b. Flightlessness in some moulting passerines in Northern Europe. Ornis Fenn. 48: 101–116.

HEDENSTRÖM, A., Å. LINDSTRÖM, AND J. PETTERSSON. 1989. (The Willow Warbler project: a cooperation between Swedish bird observatories.) In Swedish. Vår Fågelvärld 48:87–90.

HÖGSTEDT, G., AND C. PERSSON. 1982. Do Willow Warblers *Phylloscopus trochilus* of northern origin start their autumn migration at an earlier age than their southern conspecifics? Holarct. Ecol. 5:76–80.

HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. Auk 76:1–31.

LINDSTRÖM, Å., D. HASSELQUIST, S. BENSCH, AND M. GRAHN. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. Anim. Behav. 40:453–461.

LUSTICK, S. 1970. Energy requirements of moult in cowbirds. Auk 87:742–746.

MORTON, G. A., AND M. L. MORTON. 1990. Dynamics of post-nuptial moult in free-living mountain White-crowned Sparrows. Condor 92:813–828.

NEWTON, I. 1967. Feather growth and moult in some captive finches. Bird Study 14:10–24.

NILSSON, L. 1983. Laying of replacement clutches in the Willow Warbler *Phylloscopus trochilus* in Lapland, Sweden. Ornis Scand. 14:48–50.

NORMAN, S. C. 1990. Factors influencing the onset of post-nuptial moult in Willow Warblers *Phylloscopus trochilus*. Ring. & Migr. 11:90–100.

ORELL, M., AND M. OJANEN. 1980. Overlap between breeding and moulting in the Great Tit *Parus major* and Willow Tit *P. montanus* in northern Finland. Ornis Scand. 11:43–49.

PAYNE, R. B. 1972. Mechanism and control of moult, p. 103–155. *In* D. S. Farner and J. R. King [eds.], Avian biology, Vol. 2. Academic Press, London.

PEARSON, D. J. 1973. Moult of some Palaearctic warblers wintering in Uganda. Bird Study 20:24–36.

PENNYCUICK, C. J. 1975. Mechanics of flight, p. 1–75. *In* D. S. Farner and J. R. King [eds.], Avian Biology, Vol. 5. Academic Press, New York.

PIETIÄINEN, H., P. SAUROLA, AND H. KOLUNEN. 1984. The reproductive constraints on moult in the Ural Owl *Strix uralensis*. Ann. Zool. Fenn. 21:277–281.

PIMM, S. L. 1976. Estimation of the duration of bird molt. Condor 78:5–50.

PRICE, T. 1981. The ecology of the Greenish Warbler *Phylloscopus trochiloides* in its winter quarters. Ibis 123:131–144.

RAPPOLE, J. H., AND D. W. WARNER. 1976. Relationships between behavior, physiology and weather in avian transients at a migratory stopover site. Oecologia 26:193–212.

RIMMER, C. C. 1988. Timing of the definitive prebasic moult in Yellow Warblers at James Bay, Ontario. Condor 90:141–156.

SALOMONSEN, F. 1945. Notes on the variation and moult in the Willow Warbler (*Phylloscopus trochilus* (L.)). Arkiv für Zoologi 36A(17):1–13.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. Freeman, New York.

SUMMERS, R. W., R. L. SWANN, AND M. NICOLL. 1983. The effects of methods on the estimates of primary moult duration in the Redshank *Tringa totanus*. Bird Study 30:149–156.

SVENSSON, L. 1984. Identification guide to European passerines. 3rd ed. Stockholm.

TIAINEN, J. 1981. Timing of the onset of post-nuptial moult in the Willow Warbler *Phylloscopus trochilus* in southern Finland. Ornis Scand. 14:1–15.

UNDERHILL, L. G., R. P. PRYS-JONES, R. J. DOWSETT, P. HERROELEN, D. N. JOHNSON, M. R. LAWN, S. C. NORMAN, D. J. PEARSON, AND A. J. TREE. 1992. The biannual primary moult of Willow Warblers *Phylloscopus trochilus* in Europe and Africa. Ibis 134:286–297.

WILKINSON, L. 1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.

WILLIAMSON, K. 1976. Identification for ringers: the genus *Phylloscopus*. 3rd ed. BTO guide No. 8. British Trust for Ornithology, Tring.

ZAIAS, J., AND R. BREITWISCH. 1990. Molt-breeding overlap in northern mockingbirds. Auk 107:414–416.