

BODY WEIGHT AND THE POSSESSION OF TERRITORY FOR MALE AMERICAN WOODCOCK

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ABSTRACT.—Body weights were obtained from 213 male American Woodcock (*Scolopax minor*) that displayed on their territories in coniferous forest in north-eastern New Brunswick, 1977 to 1982. Weights were not different between yearling and adult males, between the first males removed and new birds moving into their territories, or between males on territories rated as high-activity vs. low-activity. Weights differed by time of season only in certain years. We conclude that body weight does not influence the ability of male woodcock to occupy a territory.

American Woodcock (*Scolopax minor*) exhibit a male-dominance polygynous mating system (Oring 1982). Accordingly, there should be contests among males for possession of the territory to which females are attracted for mating purposes only. Males appear to compete for certain territories, and aggressive vocalizations are frequent between apparently intruding males and the resident male. Sheldon (1967) and Whitcomb (1974), among others, have reported that a male frequently replaces another that is removed from a territory. Consequently, circumstantial evidence suggests that some male woodcock do not possess a breeding territory. Apparently, some mechanisms work so that certain males acquire a territory but others do not, or at least certain males do so earlier than others.

In polygynous species, body size of males is presumed to respond to sexual selection, whereby large size confers an advantage in intrasexual competition for territories or in mate selection (e.g., Searcy 1979). In most polygynous species, males are larger than females, but the reverse is true in woodcocks.

Redmond (1983) enlarged upon the earlier incidental removals of male woodcock by designing a six-year removal study explicitly to learn the extent that territories in coniferous forest differed in use by males. Because replacement males were common at certain territories, with up to seven males in a year, we became curious as to why some males successfully obtained a territory before others.

Despite reversed size dimorphism, we therefore analyzed the removal study data to learn if body weight was associated with certain attributes of territorial males. Specifically, we analyzed body weight according to (1) age of male, (2) whether he was the first or a succeeding occupant of a territory, (3) the relative

attractiveness of the territory to males—whether many or few occupied the site, and (4) time of season.

METHODS

During 1977 to 1982, we weighed 213 freshly killed male woodcock that were taken during dawn and dusk display performances in coniferous forest within 15 km north and west of the junction of the Sevogle and Northwest Miramichi rivers in northeastern New Brunswick (47°N, 66°W). Males began to display about mid-April each year. Birds were taken as follows: 14 from nine territories, 22 April–15 June 1977; 27 from 18 territories, 1 May–8 June 1978; 33 from 20 territories, 28 April–30 May 1979; 45 from 25 territories, 26 April–23 May 1980; 45 from 27 territories, 26 April–6 June 1981; 49 from 31 territories, 30 April–7 June 1982. Males that displayed on territories following the removal of first occupants were removed continuously throughout display seasons each year. Males were aged as either yearling or adult according to the criteria of Martin (1964). Territories were categorized as either high- or low-activity sites. Criteria for this classification were the total number of males using the territory within a year, the number of days the territory was occupied within a year, and the proportion of total years monitored that the territory was occupied (Redmond 1983). Weights include the alimentary tract; birds did not contain enough food to seriously affect results.

Within most years (except 1980), body weights were distributed normally (Zar 1974: 82–84). Data were analyzed first for homoscedasticity, a requirement for parametric testing (*t*-test, ANOVA) that usually was satisfied. A Kruskal-Wallis ANOVA was substituted for analyzing weight differences among years. Our

TABLE 1. Body weight of male American Woodcock from territories in coniferous forest in spring, 1977 to 1982, northeast New Brunswick.

Dates	Mean weight \pm 1 SD (N)				
	Adult	Yearling	1st occupant ^a	Replacements ^a	Total males
1977	—	—	—	—	136.2 \pm 4.4 (14)
1978	137.5 \pm 9.5 (11)	133.9 \pm 7.0 (16)	131.7 \pm 6.9 (10)	135.8 \pm 8.5 (4)	135.4 \pm 8.1 (27)
1979	131.2 \pm 6.6 (11)	135.5 \pm 7.4 (22)	134.1 \pm 7.8 (14)	133.7 \pm 2.1 (3)	134.1 \pm 7.3 (33)
1980	133.1 \pm 6.8 (17)	135.2 \pm 9.2 (28)	135.3 \pm 8.8 (20)	123.3 \pm 6.0 (3)	134.4 \pm 8.4 (45)
1981	134.3 \pm 7.9 (20)	133.2 \pm 5.6 (25)	132.9 \pm 6.6 (16)	130.6 \pm 5.6 (7)	133.7 \pm 6.7 (45)
1982	135.6 \pm 9.2 (28)	136.2 \pm 9.5 (19)	133.7 \pm 8.5 (20)	136.6 \pm 13.0 (5)	136.1 \pm 9.5 (49)
\bar{x}^b	134.6 \pm 8.0 (94)	134.5 \pm 7.7 (117)	133.9 \pm 7.6 (86)	132.3 \pm 8.4 (23)	134.8 \pm 7.9 (213)

^a Birds collected early, before mid-point dates of season.

^b Includes birds collected in 1977.

criterion for statistical significance was the 0.05 level.

RESULTS

Mean body weights (Table 1) did not differ among years. All weights, therefore, were combined and averaged (\pm 1 SD) 134.8 \pm 7.9 g (n = 213) over all years. Weights ranged from 116 to 160 g, a 1.4-fold difference. A low coefficient of variation (0.059), however, indicated that weights generally were similar.

Within each year, 1978–1982 (data were insufficient in 1977), mean weight of adults did not differ from that of yearlings; the maximum difference within years was 4.3 g (Table 1). Weights were used for all males for whom we could assign an age, over the entire season.

Mean weight of the first males occupying territories did not differ from that of succeeding males on territories before the mid-point dates (9–20 May) of collections (Table 1). We conducted this analysis only during the first half of the season because weights increased over season in some years. Any effects upon weight that were associated with season must have been constant for the two cohorts of males (two-factor ANOVA, see below) because their mean weights also did not differ over the entire season (114 first occupant and 89 replacement males). Yearlings comprised 56% of first occupant and 64% of replacement males in early season.

Given that we did not mark individuals, we can only guess that many replacement males had not occupied a territory earlier, at least not a neighboring territory. We believe this to be the case because we were frequently successful in removing all males from a cluster of territories before new males replaced any sites (Redmond 1983). We did not begin removals until approximately two weeks after males first appeared on territories in spring; hence, it is possible that these males were not the first occupants of those sites. We have only indirect evidence that the first males removed were

indeed the first to occupy territories. We monitored territories an average of eight times before killing males each season; the mean interval between surveys was 1.4 days. Before initial removals, only 14% of territories were not occupied continuously. Once removals commenced, the median interval until males re-colonized territories was three days, and this did not change as the season progressed. Thus, it is likely that our monitoring effort before initial removals was sufficient to detect vacancies at sites if they occurred. We assumed that the pressure to occupy the territories before removals was not so much greater than it was after removals commenced so that it would have caused a much faster speed of replacement (one vs. three days). Several factors could account for the 14% of territories that showed inconsistent occupancy before first removals: (1) temporary occupancy by migrants, (2) predation of occupants, and (3) observers may have erred in not detecting the presence of displaying males. In contrast to our suspicion that most replacement males had not occupied a territory earlier, M. Ellingwood (pers. comm.) reported that marked individuals in West Virginia will move from a territory to a neighboring vacant territory.

Mean body weights did not differ between males that occupied high-activity territories (12 sites; 134.1 \pm 8.1 g, n = 119 males) and those that occupied low-activity territories (19 sites; 135.2 \pm 6.6 g, n = 43 males). Data from males collected on the same territory were combined over years (1977–1982) for this analysis because weights showed no difference among years.

The possibility remains that male weights differed among individual high- or low-activity territories. For example, did males weigh more on certain high-activity territories? We conducted a single-factor analysis of variance on 136 weights from 17 sites (H_0 : no difference in weights among geographic locations). Territories analyzed had males collected over at

least three years. Data were from yearlings and adults, and first occupant and replacement males over the entire season. Variances in weights among territories were homoscedastic, and were not greater than within territories ($F = 0.00$, $P > 0.50$). Thus, weights were not consistently heavy or light at specific territories.

Our analysis of body weight and time of season initially divided the season into three periods, pre-active, active (mid-season), and post-active display, determined largely by changes over time in the daily frequency that territories were occupied (Redmond 1983). Variances of weights did not differ between the active and post-active display periods (sample of weights too small during the pre-active period); hence, a regression line was fitted for weights plotted against date. Weights did not differ according to season date in 1978 and 1979 (slopes 0.14–0.15 g/day), but increased as the season progressed in 1980–1982 (slopes 0.24–0.93 g/day). This led us to question whether there was anything peculiar about weights in latter years. We found no significant difference among years in weights of the first 10 birds killed each season (Kruskal-Wallis ANOVA), but the lightest set of weights did occur in 1981 ($\bar{x} = 131.0$ g vs. 133.0–137.0 g). Further, rank tests on weights from the first 10 vs. the last 10 birds collected in each of 1980, 1981, and 1982 showed that the greatest difference occurred in 1981 ($P = 0.05$).

The above single-factor analyses do not show whether any of the variables in combination might affect body weight. We conducted 2 two-factor analyses of variance on what could have been possible interactions among variables and body weight: (1) age of male and whether it was a first or replacing occupant, and (2) age of male and time of season. For the first test, we used weights over the whole season, 1978–1982. To meet the requirement of equal replicates per cell (weights per category), weights of adult and yearling first occupants and yearling replacements were excluded at random so that the remainder of each equalled the smallest group, adult replacement males ($n = 30$). All three null hypotheses were not rejected ($P > 0.50$): no effect of age upon weight, no effect of occupancy status upon weight, no interaction of age and occupancy upon weight. The four categories of males (age and occupancy status) exhibited similar mean weights and similar coefficients of variation.

To evaluate a possible interaction between male age and time of season on body weight, the mid-point date was determined for each year's collection, ranging from 9 to 20 May. A procedure for unequal but proportional cell

sizes (Sokal and Rohlf 1981:360–363) was used: 38 weights for each age class in early season (< mid-point date) and 56 weights for each age class in late season. Data for first occupant and replacement males were combined over all years. As shown in certain earlier correlations, body weight was significantly associated with time of season. We found no interaction, however, between ages and season upon weight, that is, yearling and adult weights did not differ with respect to the intensity of effect from time of season.

DISCUSSION

We have been unable to identify any consistent way in which body weight of male woodcock was associated with age class, whether the male was a first or succeeding occupant at the territory, and whether the male occupied a territory that was classed as either a high- or low-activity site.

The lack of difference in weight between males taken from high- and low-activity territories is of special interest. High-activity territories attracted more males each year, were occupied more often within each year, and were occupied in more years than were low-activity territories (Redmond 1983). Because American Woodcock are polygynous, we would predict that there is considerable variance in male mating success, and that the more successful males exhibit some characteristic(s) that enhance(s) their ability to acquire a good territory or to directly attract mates. We are tempted to speculate that females are differentially attracted to males on high- and low-activity territories, but we have no data on female visitation. At least, body weight is an attribute that did not differ among males who might have differed in attractiveness to females or who possessed territories of potentially different quality. Sexual selection theory is most applicable for non-monogamous species (although see Price 1984), but virtually all empirical data are for species in which males are larger than females (e.g., Searcy 1979). American Woodcock present a unique opportunity to learn whether and how conventional concepts of sexual selection theory pertain to a polygynous species with reversed size dimorphism and no male parental care.

We have weights only from males found on territories. We believe, however, that many replacement males represented normally non-territorial individuals who would not have obtained a territory during the season if it had not been for our continuous removals. We know of no available mortality schedule for males in spring. Annual mortality rates from band recoveries of males vary but are high

(Dwyer and Nichols 1982). Yet, we speculate that, under normal circumstances, natural mortality is insufficient to induce such heavy replacement within years as we caused. Because first occupants weighed the same as their replacements, we infer that resident and normally non-territorial cohorts did not differ in weight.

However selection pressures act upon body weight of male American Woodcock, it is not apparent that they in turn proximally affect the ability to acquire a breeding territory. Intriguing questions nevertheless remain about male woodcock and body weight in spring. Woodcock migrate early in spring and breed relatively early in the display season (Sheldon 1967). Earthworms are their principal food (Reynolds 1977), but might be scarce for males arriving early in the north (Rabe et al. 1983). If food becomes more available as the spring progresses, do males become heavier or does territorial display demand so much energy that it counters any possible weight increase from increasingly abundant food? If display is energetically taxing and the food supply improves over season, non-territorial males should gain weight differentially over males that possess territories, unless the act of searching for and acquiring a territory in mid- to late season demands much energy. Our observations at territories and the weight data lead us to speculate that display is not energetically demanding and that food does not improve much over the season. We are led to this view because first occupants were removed earlier and had displayed longer than most replacement males (medians = 11 and 3 days, respectively) yet body weights were similar. These questions will be answered best by repetitive measurements, coupled with monitoring of activity of individuals, not by correlation approaches with individuals weighed only once, as in our study.

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