from agricultural fields at the time of spring planting. Other studies have reported both faster (Crawford 1971) and much slower (Fowle 1965) removal rates in other habitats than I found in corn fields. Quantitative studies of avian mortality that depend on recovery of dead birds should monitor scavenger activity. Searches should follow immediately mortality events if a large proportion of the affected birds are to be detected.

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LITERATURE CITED

- AVERY, M. L., P. F. SPRINGER, & N. S. DAILEY. 1980. Avian mortality at man-made structures: an annotated bibliography (revised). U.S. Fish Wildl. Serv. Publ. FWS/OBS-80/54.
- BALCOMB, R. 1983. Secondary poisoning of Redshouldered Hawks with carbofuran. J. Wildl. Mgmt. 47: 1129-1132.
 - —, C. A. BOWEN, II, D. WRIGHT, & M. LAW. 1984. Effects on wildlife of at-planting corn applications of granular carbofuran. J. Wildl. Mgmt. 48: 1353–1359.
- BRESLOW, N. 1970. A generalized Kruskal-Wallis test for comparing k samples subject to unequal patterns of censorship. Biometrika 57: 579–594.
- BROWN, M. B. (Ed.). 1977. BMDP-77 biomedical computer programs, P-series. Los Angeles, Univ. California Press.
- BUNYAN, P. J., M. J. VAN DEN HEUVEL, P. I. STANLEY, & E. N. WRIGHT. 1981. An intensive field trial

and a multi-site surveillance exercise on the use of aldicarb to investigate methods for the assessment of possible environmental hazards presented by new pesticides. Agro Ecosystems 7: 239–262.

- CRAWFORD, R. L. 1971. Predation on birds at TV tower. Oriole 36: 33-35.
- DEWEESE, L. R., L. C. MCKWEN, L. A. SETTIMI, & R. D. DEBLINGER. 1983. Effects on birds of fenthion aerial application for mosquito control. J. Econ. Entomol. 76: 906-911.
- FINLEY, R. B., JR. 1965. Adverse effects on birds of phosphamidon applied to a Montana forest. J. Wildl. Mgmt. 29: 580-591.
- FLICKINGER, E. L., K. A. KING, W. F. STOUT, & M. M. MOHN. 1980. Wildlife hazards from Furadan 3G applications to rice in Texas. J. Wildl. Mgmt. 44: 190–197.
- FOWLE, D. C. 1965. A preliminary report on the effects of phosphamidon on the bird populations in central New Brunswick. Can. Wildl. Serv. Occ. Papers No. 7.
- GROSS, A. J., & V. A. CLARK. 1975. Survival distributions: reliability applications in the biomedical sciences. New York, John Wiley & Sons.
- MANTEL, N. 1966. Evaluation of survival data and two new rank order statistics arising in its consideration. Cancer Chemotherapy Repts. 50: 163– 170.
- MILLS, J. A. 1973. Some observations on the effects of field applications of fensulfothion and parathion on bird and mammal populations. Proc. New Zealand Ecol. Soc. 20: 65-71.
- OVERGAARD, N. A., D. F. WALSH, G. D. HERTEL, L. R. BARBER, R. E. MAJOR, & J. E. GATES. 1983. Evaluation of modified POWR-TILL seeder for soilincorporation to provide insect control and minimize bird mortality. U.S. Dept. Agr., Forest Serv. Tech. Publ. R8-TP3.

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Changes in Plasma Prolactin Associated With Laying and Hatch in the Spotted Sandpiper

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Among captive galliform and anseriform birds, plasma prolactin (Prl) levels tend to rise during laying, peak during incubation, and decline rapidly at hatch (Etches et al. 1979, Burke and Dennison 1980, Bedrak et al. 1981, Dittami 1981, Lea et al. 1981, Proudman and Opel 1981, Goldsmith 1982, Hall and Goldsmith 1983, Wentworth et al. 1983). While the role of Prl as a regulator of avian incubation has been discussed widely, it is not clear whether Prl induces incubation, incubation behavior causes a rise in Prl, both, or neither (reviewed in Goldsmith 1983). In Spotted Sandpipers (*Actitis macularia*), where incubation is biparental but males perform the greater share, Prl levels increase significantly in both sexes

Prelaying	1-egg	2-egg	3-egg	Midincubation	2-3 days post-hatch
87.8	149.4	130.2	178.0	182.5	156.5
±9.3	± 16.6	± 13.0	± 14.5	± 11.3	± 15.6
(n = 8)	(n = 4)	(n = 4)	(n = 3)	(n = 14)	(n = 9)

TABLE 1. Plasma prolactin levels (ng/ml) in male Spotted Sandpipers ($\bar{x} \pm SE$).

during incubation, but the rise is larger in males (Oring et al. 1986). Our earlier analyses, however, lacked information on Prl levels at two critical life history stages: egg laying and post-hatch.

Spotted Sandpipers were studied at Leech Lake, Minnesota (47°07'N, 94°22'W). All birds were marked individually, and the precise breeding history of each was known. For details relative to the population, see Maxson and Oring (1980), Oring and Lank (1982, in press), and Oring et al. (1983). All birds were captured in mist nets and handled for a maximum of 10 min. Previously, we established that differences in Prl levels between individuals were not due to daily variation or to time of year independent of breeding cycle stage (Oring et al. 1986, unpubl. data). The limited number of birds in this study made assessment of the rhythmicity of hormone secretion impossible; hence, samples were taken between 0600 and 1000 whenever possible. Blood sampling procedures were as reported in Oring et al. (1986). Analyses were performed with the homologous turkey assay described by Burke and Papkoff (1980) and Burke and Dennison (1980), as validated for use with Spotted Sandpipers through comparison of serum dilution curves and molecular size (Oring et al. 1986).

In 1985, we obtained samples from males at the following stages: prelaying, 1-egg, 2-egg, 3-egg, midincubation (days 8–14 of 21-day incubation period), and 2–3 days post-hatch. There was a significant increase in plasma Prl from prelaying to the 1-egg stage (P < 0.05, Duncan's multiple range test). No further significant increases in Prl levels occurred; Prl remained high at least through the third day post-hatch. These data differ from the typical pattern of Prl levels in precocial birds in two ways: (1) Prl rose sharply with the laying of the first egg, 2 days before a high incubation constancy, and (2) Prl did not drop sharply at hatch.

Spotted Sandpiper males incubate sporadically after the laying of the first egg. The total incubation effort in any portion of the day involves less than 5% of the time. Once the third egg is laid, however, incubation constancy is high—63-86% at various times during daylight, and 100% at night (Maxson and Oring 1980). Here we have shown that Prl levels rise significantly an average of 2 days before full incubation. Previously, we showed that plasma Prl levels in males, but not females, continued to rise slightly, but significantly, from week 1 to week 3 of incubation (Oring et al. 1986). Thus, in Spotted Sandpipers, Prl may induce incubation, but incubation may result in further increases in Prl. These results suggest experiments in which eggs are added to fresh 1-egg nests to determine whether Prl must, in fact, prime birds for the normal incubation response to be expressed, or, alternatively, whether incubation is initiated solely through perception of 3 eggs.

Prl levels drop precipitously shortly before or within 2 days of hatch in turkeys (Meleagris gallopavo; Wentworth et al. 1983), Mallards (Anas platyrhynchos; Goldsmith and Williams 1980), and Black Swans (Cygnus atratus; Goldsmith 1982). This hatch-related decline in Prl may be characteristic of most precocial birds (Goldsmith 1983). By contrast, in Spotted Sandpipers, Prl remained high through at least 3 days post-hatch (Table 1). Because in central Minnesota Spotted Sandpiper males brood 1-3-day-old chicks an average of 36% of the time from 0500 to 2100, and nearly 100% of the time from 2100 to 0500, the high post-hatch levels of plasma Prl may be associated with brooding, as is the case in altricial birds. The percentage of time male Spotted Sandpipers spend brooding drops steadily from hatch to 10 days posthatch, but we have no data on post-hatch Prl levels beyond 3 days. Alternatively, the continued high Prl levels witnessed in Spotted Sandpipers may be due to phylogenetic factors. As with the incubation period, our post-hatch data suggest the need for experiments aimed at teasing apart cause and effect in behavioral-physiological interactions underlying parental behavior.

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LITERATURE CITED

- BEDRAK, E., S. HARVEY, & A. CHADWICK. 1981. Concentrations of pituitary, gonadal and adrenal hormones in serum of laying and broody white rock hens (*Gallus domesticus*). J. Endocrinol. 89: 197-204.
- BURKE, W. H., & P. T. DENNISON. 1980. Prolactin and luteinizing hormone levels in female turkeys (*Meleagris gallopavo*) during a photoinduced re-

productive cycle and broodiness. Gen. Comp. Endocrinol. 41: 92-110.

- , & H. PAPKOFF. 1980. Purification of turkey prolactin and the development of a homologous radioimmunoassay for its measurement. Gen. Comp. Endocrinol. 40: 297-307.
- DITTAMI, J. P. 1981. Seasonal changes in the behavior and plasma titres of various hormones in Barheaded Geese, *Anser indicus*. Z. Tierpsychol. 55: 289-324.
- ETCHES, R. J., A. GARBUTT, & A. L. MIDDLETON. 1979. Plasma concentrations of prolactin during egglaying and incubation in the Ruffed Grouse (Bonasa umbellus). Can. J. Zool. 57: 1624–1627.
- GOLDSMITH, A. R. 1982. The Australian Black Swan: prolactin and gonadotropin secretion during breeding including incubation. Gen. Comp. Endocrinol. 50: 458-462.
 - —. 1983. Prolactin in avian reproductive cycles. Pp. 375–387 in Hormones and behavior in higher vertebrates (R. Gilles, Ed.). Berlin, Springer-Verlag.
 - ——, & D. M. WILLIAMS. 1980. Incubation in Mallards (*Anas platyrhynchos*): changes in plasma prolactin and luteinizing hormone. J. Endocrinol. 86: 371–379.
- HALL, M. R., & A. R. GOLDSMITH. 1983. Factors affecting prolactin secretion during breeding and incubation in the domestic duck (*Anas platyrhynchos*). Gen. Comp. Endocrinol. 49: 270–276.
- LEA, R. W., A. S. M. DODS, P. J. SHARP, & A. CHAD-WICK. 1981. The possible role of prolactin in the regulation of nesting behaviour and the secre-

tion of luteinizing hormone in broody bantams. J. Endocrinol. 91: 88–97.

- MAXSON, S. J., & L. W. ORING. 1980. Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. Behaviour 74: 200-263.
- ORING, L. W., A. J. FIVIZZANI, M. E. EL HALAWANI, & A. GOLDSMITH. 1986. Seasonal changes in prolactin and luteinizing hormone in the polyandrous Spotted Sandpiper, Actitis macularia. Gen. Comp. Endocrinol. 62: 137-144.
- , & D. B. LANK. 1982. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. Behav. Ecol. Sociobiol. 10: 185–191.
- , & _____, Kontext, In press. Environment and experience: impact on a polyandrous population of Spotted Sandpipers. *In* Ecological aspects of social evolution (D. Rubenstein and P. Wrangham, Eds.). Princeton, New Jersey, Princeton Univ. Press.
- , , , & S. J. MAXSON. 1983. Population studies of the polyandrous Spotted Sandpiper. Auk 100: 272–285.
- PROUDMAN, J. A., & H. OPEL. 1981. Turkey prolactin: validation of a radioimmunoassay and measurement of changes associated with broodiness. Biol. Reprod. 25: 573–580.
- WENTWORTH, B. C., J. A. PROUDMAN, H. OPEL, M. J. WINELAND, N. G. ZIMMERMAN, & A. LAPP. 1983. Endocrine changes in the incubating and broody turkey hen. Biol. Reprod. 29: 87–92.

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Composition and Quantity of Feather Sheaths Produced by White-crowned Sparrows During the Postnuptial Molt

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Measures of nitrogen balance and sulfur balance in molting White-crowned Sparrows (Zonotrichia leucophrys gambelii) revealed that the new plumage mass accounted for only about 50% of the nitrogen, and only about 80% of the sulfur, retained above the maintenance level during the molt (Murphy and King 1984a, b; corrected to a regenerated plumage mass of 2.1 g). These discrepancies result from undetected sites of nitrogen and sulfur deposition during molt or from nonquantified losses from the body. Included among the potential routes of deposition and undetected loss of nitrogen and sulfur are the sheaths that temporarily encase the growing feathers (Murphy and King 1984a). A sheath is a keratinized epithelial tube (Lucas and Jamroz 1961) that protects the pulp and growing feather from desiccation. It may help initially to retain the feather in its follicle, and function in the elongation of feather barbs (Lillie 1940). Sheaths are ephemeral. They rupture when the growing feather reaches about 20% of its final length, and soon thereafter begin to disintegrate from the tip into small flakes. Probably because they are short-lived and difficult to collect, sheaths have been essentially disregarded in analyses of the nutritional requirements of molt. To help remedy this lapse, we analyzed sheath chemical composition and attempted to estimate the mass of sheaths produced during the complete postnuptial molt of White-crowned Sparrows.

We captured White-crowned Sparrows during their spring migration through eastern Washington and kept them in an outdoor aviary where chick-starter mash and fresh water were freely available. During the postnuptial (late summer) molt, we plucked samples of growing feathers from the alar (primaries, secondaries, greater coverts), caudal (rectrices), and