

SEASONAL CHANGES IN DIET, DIGESTIVE MORPHOLOGY AND DIGESTIVE EFFICIENCY IN THE RUFOUS-COLLARED SPARROW (*ZONOTRICHIA CAPENSIS*) IN CENTRAL CHILE¹

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Seasonal changes in birds' energy requirements as well as in environmental food availability and quality, influence birds' capability to obtain and digest food (Karasov 1990). Increased metabolic rates, hypertrophy of the gastrointestinal tract, and increased absorption of nutrients may be viewed as responses of wintering birds to physical and biotic seasonal habitats (Sibly 1981, Dykstra and Karasov 1992).

In central Chile, the climate is seasonal with warm, dry summers and cool rainy winters; mean annual temperature is 22.1°C and mean annual minimum temperature is 7.7°C (di Castri and Hajek 1976). One of the most conspicuous resident birds of the mediterranean environments in central Chile is the Rufous-collared Sparrow *Zonotrichia capensis* (Emberizidae). This species is opportunistic, feeding on seeds and insects and showing seasonal dietary shifts according to food availability (López-Calleja 1995). Individuals of this species also exhibit seasonal changes in metabolic rates and thermal insulation (Novoa 1993). Consequently, *Z. capensis* lives under marked seasonal variations in energy availability and requirements. Specifically, when nutritional demands increase during winter, birds may respond to the seasonal environment through behavioral, anatomical and physiological changes that allow the maintenance of a positive energy budget and consequently permit survival. The aim of this work is to examine the relationship between seasonal changes in diet, digestive tract morphology, and digestive efficiency of Rufous-collared Sparrows in central Chile.

MATERIAL AND METHODS

Zonotrichia capensis were collected bimonthly from January to November 1992 in central Chile (33°17'S, 71°11'W) by shooting. Digestive tract contents were preserved in 70% alcohol for dietary analysis of gross items (proportion of seeds and insects) following López-Calleja (1995). After capture, the digestive tract was

removed and the dry mass of digesta determined. Digestive organs were washed with physiological saline solution. We measured the fresh length (L) (± 0.01 cm) and dry mass (DM) (± 0.001 g). The following organs were measured: crop, small intestine, large intestine, and cecum (see Bozinovic et al. 1990 for methodological details). Given the allometric relationship between body mass (mb) and L, digestive tract length values were standardized by $mb^{0.33}$, and digestive tract dry mass values standardized by $mb^{1.0}$ (see Karasov 1990).

To determine the effects of seasonal changes in diet and digestive tract morphology on digestive efficiency, birds were captured every two months in 1992 and transported to the laboratory. There we conducted feeding trials for five days, offering an equal amount of commercial bird seed (*Phalaris sp.*) to each animal and collecting their feces and remaining food. Feeding trials were begun immediately after the birds were captured. Collected feces and remaining food were weighed and stored, after drying them at 60°C to constant weight. Apparent digestibility was calculated as: $[(Q_i - Q_e)/Q_i] \times 100\%$, where Q_i = daily weight of dry matter consumption and Q_e = daily weight of dry feces production. Digestibility is apparent because this method underestimates digestive efficiency by the contribution of metabolic and urine wastes and nonreabsorbed secretions of the digestive system (see Karasov 1990).

The significance of the effects of seasons on diet, digestive tract morphology, and digestive efficiency was assessed by a one-way ANOVA. To determine significance of differences between variables after the ANOVA, we used the *a posteriori* Tukey test for multiple comparisons. Relationships between variables were established with a least-squares linear regression (Steel and Torrie 1985).

RESULTS AND DISCUSSION

Our seasonal dietary analyses showed that seeds account for about 80% of the diet. However, during July (winter) insects increased significantly, representing about 50% of the diet (see Table 1). On the other hand, mass of digesta contents increased significantly during winter (May–July) being between 40% to 58% higher than during spring-summer (November–January) (Table 1).

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TABLE 1. Seasonal body mass, length, dry mass of digestive organs and apparent digestibility of *Zonotrichia capensis* in different seasons. Values represent mean \pm 1 SD. *P*-values obtained after a one-way ANOVA are shown. Similar letters represent non-significant differences between seasons.

	January	March	May	July	September	November	<i>F</i>	<i>P</i> <
<i>n</i>	9	16	15	20	12	19		
Body mass (g)	21.4 \pm 0.4	22.8 \pm 0.5	22.6 \pm 0.4	22.1 \pm 0.3	22.1 \pm 0.3	22.2 \pm 0.4	1.20	0.32
Diet								
Insects (%)	12.2 \pm 2.8 ^{a,b}	6.2 \pm 1.4 ^a	17.9 \pm 4.4 ^{a,b}	53.2 \pm 14.3 ^c	29.2 \pm 5.6 ^{b,c}	24.7 \pm 6.9 ^{a,b}	6.10	0.001
Seeds (%)	87.8 \pm 2.8 ^{a,b}	93.8 \pm 1.4 ^a	82.1 \pm 4.4 ^{a,b}	46.8 \pm 13.3 ^c	70.8 \pm 5.5 ^{b,c}	75.3 \pm 6.8 ^{a,b}	6.10	0.001
Digesta mass (g)	0.065 \pm 0.008 ^{a,b}	0.096 \pm 0.008 ^{b,c}	0.108 \pm 0.017 ^{b,c}	0.125 \pm 0.002 ^c	0.065 \pm 0.009 ^{a,b}	0.053 \pm 0.008 ^a	5.63	0.002
Digestive tract length (cm/g ^{0.33})								
Crop	0.57 \pm 0.01 ^{a,b}	0.61 \pm 0.01 ^{b,c}	0.65 \pm 0.02 ^c	0.60 \pm 0.01 ^{a,b}	0.61 \pm 0.01 ^{a,b,c}	0.55 \pm 0.01 ^a	5.99	0.001
Small intestine	4.95 \pm 0.15 ^a	5.64 \pm 0.15 ^{b,c}	5.83 \pm 0.12 ^c	5.47 \pm 0.11 ^{a,b,c}	5.14 \pm 0.12 ^{a,b}	5.46 \pm 0.12 ^{a,b}	5.33	0.003
Large intestine	0.69 \pm 0.04 ^{a,b}	0.77 \pm 0.03 ^b	0.69 \pm 0.04 ^{a,b}	0.64 \pm 0.03 ^a	0.61 \pm 0.03 ^a	0.60 \pm 0.03 ^a	4.29	0.002
Caecum	0.13 \pm 0.01	0.14 \pm 0.01	0.13 \pm 0.01	0.12 \pm 0.01	0.12 \pm 0.01	0.12 \pm 0.01	0.64	0.68
Digestive tract mass (mg/g)								
Crop	9.0 \pm 0.6 ^{a,b}	11.6 \pm 0.3 ^{c,d}	13.0 \pm 0.4 ^d	11.7 \pm 0.5 ^{c,d}	10.9 \pm 0.4 ^{b,c}	9.0 \pm 0.56 ^a	14.61	0.001
Small intestine	2.83 \pm 0.40 ^a	4.09 \pm 0.34 ^{a,c,d}	5.2 \pm 0.21 ^{a,b,c}	5.35 \pm 0.24 ^c	5.15 \pm 0.44 ^{d,e}	2.90 \pm 0.16 ^{a,b}	14.72	0.001
Large intestine and caecum	0.38 \pm 0.07 ^{a,b}	0.54 \pm 0.04	0.43 \pm 0.03	0.47 \pm 0.04	0.41 \pm 0.06	0.35 \pm 0.07	2.21	0.06
Apparent digestibility (%)	83.4 \pm 1.2	80.9 \pm 1.3	77.3 \pm 8.1	77.7 \pm 3.1	77.0 \pm 1.0	79.7 \pm 1.6	0.68	0.64

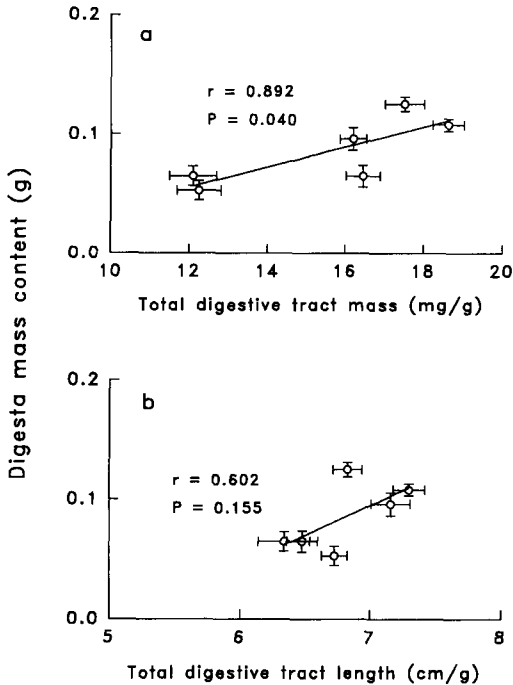


FIGURE 1. Relationships between: (a) total digestive tract mass and digesta mass content ($r = 0.89$, $P = 0.04$) and (b) total digestive tract length and digesta mass content ($r = 0.60$, $P = 0.15$) in *Zonotrichia capensis*. Each point represents bimonthly means \pm SD, r and P -values are from a linear regression.

Results of morphological analyses of digestive tract between seasons showed that both L and DM of the digestive tract changed seasonally (Table 1). During winter, crop L and DM increased by 9% and 27%, respectively. During winter, the small intestine L and DM also increased by 8% and 45%, respectively. Both large intestine and caecum L and DM did not exhibit significant seasonal changes (Table 1). Apparent digestibility was not significantly different between seasons, with an annual average of $79.8 \pm 1.0\%$ (Table 1).

A positive and significant regression was found between seasonal total digestive tract dry mass and digesta dry mass ($y = 0.0084x - 0.64$, $r = 0.892$, $P = 0.04$, Fig. 1a) but not between total digestive tract length and digesta dry mass ($y = 0.049x - 0.25$, $r = 0.602$, $P = 0.15$, Fig. 1b).

Seasonal changes in digestive tract morphology have been demonstrated in many small endotherms inhabiting seasonal environments (Gross et al. 1985, Al-Dabbagh et al. 1987, Green and Millar 1987, Bozinovic et al. 1990, Walsberg and Thompson 1990, Nagy and Negus 1993). Environmental conditions that generate an increase in avian nutritional or energetic requirements could be related to the observed increase in size of digestive chambers. Such changes may tend to maximize ingestion rate and the effectiveness of energy use.

According to Sibly's (1981) model of optimal digestion, one of the advantages of increasing digestive tract size is that it allows an increase in digesta mean retention time, which increases digestibility if food ingestion rate is constant, or it allows a constant digesta mean retention time which maintains digestive efficiency if food ingestion increases. Alternatively, if food ingestion rate increases, increased digestive tract size allows a constant digesta mean retention time, which maintains digestive efficiency. Coincident with the winter season, *Z. capensis* switched to a higher-energy diet (insects) and still had to increase their gut capacity and meal size. Ordinarily, under constant energy demand, the switch from seeds to insects would promote a decrease in gut size. Thus, they made at least two adjustments to the winter season. It is unclear whether the switch to insects is due to increased energy demands by low ambient temperatures or simply increased insect availability/decreased seed availability. Nevertheless, digestive tract increases may allow an increase in the amount of food carried while still maintaining the effectiveness of food processing and digestion.

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WINTERING SWAINSON'S HAWKS IN CALIFORNIA'S SACRAMENTO-SAN JOAQUIN RIVER DELTA¹

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Key words: Swainson's Hawk; *Buteo swainsoni*; natural history; winter distribution; Sacramento-San Joaquin River Delta.

The Swainson's Hawk (*Buteo swainsoni*) is considered a summer resident breeder on large parts of North America, leaving in winter to migrate south to South America (AOU 1983, Palmer 1988). Wintering Swainson's Hawks in North America had been confirmed only from southern Florida, where some juveniles were found during most winters, and from the southwestern United States as occasional migration dropouts (Palmer 1988).

Swainson's Hawks in California breed chiefly in the Central Valley and on the Northeastern Plateau (California Department of Fish and Game 1993), and the species is listed as threatened in the state. Until 1990, few credible winter records had been reported from the state (e.g., Browning 1974, McCaskie 1985, Morlan et al. 1987, McCaskie 1989), most of which were considered to represent very late or early migrants. Several reports from California's Sacramento-San Joaquin River Delta (LeValley and Rosenberg 1984, Campbell et al. 1986, Morlan et al. 1987, Campbell et al. 1988, Yee et al. 1989, Erickson et al. 1990) suggested some Swainson's Hawks were wintering locally. During the 1990/1991 winter, 28 hawks were confirmed in the Sacramento-San Joaquin River Delta, mostly consisting of adults (Yee et al. 1991). A population of comparable size was reconfirmed in the two subsequent winters (W. Holt and D. G. Yee, unpubl. data).

Holt and Yee (unpubl. data) observed the population irregularly during all three winters. They discovered a communal roost on Andrus Island (Fig. 1) and ob-

served foraging flocks of up to 16 Swainson's Hawks on five Delta islands preying on small rodents in close association with farming operations. The objective of the present study was to systematically monitor the population to determine wintering season chronology, size, composition, distribution, and foraging ecology.

STUDY AREA AND METHODS

The study area was in the Sacramento-San Joaquin River Delta in the Central Valley of California (38°05'N, 121°35'W) (Fig. 1). Historically, the Delta was an extensive freshwater marsh. Naturally deposited levees had been forming regularly flooded islands dominated by tule (*Scirpus* spp.), cattail (*Typha* spp.), and reeds (*Phragmites* spp.) (Herbold and Moyle 1989). Since the 1850s, > 80% of the Delta's wetlands were converted to mostly agricultural lands (California Department of Water Resources 1987). The area's main crops were corn, grain, and hay. Access was limited because most Delta islands were privately owned and few public roads led through the study area. Boats could not be used because high levees and elevations below sea level limited visibility of islands.

Swainson's Hawk population surveys were conducted by car on 23 islands from 25 September 1993 to 11 March 1994. I first surveyed areas where hawks were seen previously (Holt and Yee, unpubl. data). Surveys were extended to other accessible islands and conducted 4–6 times a week by mid-October and reduced to twice a week by late February. Survey frequency was determined by logistic factors such as accessibility and remoteness. I conducted from 51 to 92 surveys per island on Andrus, Brannan, Bouldin, and Terminous, from 31 to 50 surveys per island on Empire, King, Staten, and Twitchell, from 11 to 30 surveys per island on Sherman and Venice, and from one to ten surveys per island on Bacon, Bethel, Byron, Holland, Jersey, Lower Jones, Medford, Palm, Roberts, Upper Jones, Veale, Victoria, and Webb. Potential roost sites were located during initial surveys and visited regularly from mid-November to early February in late

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