ANATOMICAL ADAPTATION OF THE GUT TO DIET IN RED-WINGED BLACKBIRDS (*AGELAIUS PHOENICEUS*)

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ABSTRACT.—I examined gross and microscopic anatomical responses of the gastrointestinal tract of Red-winged Blackbirds (*Agelaius phoeniceus*) to experimental variation in diet quality. Birds fed an energy-dense diet had the smallest measures of gizzard, small intestine, and villi. Birds fed an energy-dilute diet had the largest villus length, lamina muscularis depth, and small-intestine outer diameter. These responses are consistent with observations in other birds and are related to increased intake. *Received 21 May 1990, accepted 22 December 1990.*

THE VERTEBRATE gastrointestinal tract is a dynamic and energetically expensive organ system. The small intestine is characterized by high rates of epithelial cell loss and cell production. For example, cell turnover occurs approximately every 2–5 days in chicks (*Gallus gallus*, Imondi and Bird 1966) and every 2–3 days in healthy laboratory rodents and humans (Johnson 1987). The energetic cost of maintaining a gut is unknown in birds, but may contribute up to 40% of basal metabolic rate in ruminant mammals (Webster 1981). Because birds have high metabolic rates and poor energy-storage capacities, conserving energy allocated to gut tissue may provide a means to temporarily reduce the cost of existence (Sibly 1981). Changes in both gross and microscopic gut anatomy may be important to a bird's ability to maintain energy balance.

Seasonal changes in the sizes of digestive organs occur in wild birds, but the proximate factors for such changes are poorly understood. The size of digestive organs can be greatest during times of year when intake is high, possibly due to low available energy of the food, rapid processing rates, or high metabolic demand. Such changes were documented for the gizzard, small intestine, or cecum in the Anseriformes (Miller 1975), Galliformes (Moss 1989; Savory and Gentle 1976a, b; Remington 1989), Columbiformes (Kenward and Sibly 1977), and Passeriformes (Davis 1961, Al-Joborae 1979, Al-Dabbagh et al. 1987, Ankney and Scott 1988). In contrast, captivity, and the associated increase in diet quality or decrease in activity, can produce reductions in gross measures of the gizzard, small intestine, or ceca (Moss 1972) as well as in the microanatomy of the small intestine and ceca (Hanssen 1979, Goldstein 1989).

I used Red-winged Blackbirds (*Agelaius phoeniceus*) to examine avian digestive responses to dietary manipulation because they have (1) a simple digestive anatomy and (2) seasonal fluctuations in factors that could influence cellular growth, such as food type, physiological status, and metabolic activity. Red-winged Blackbirds have an expandable esophagus but not a crop (McLelland 1979), a small proventriculus, enlarged gizzard, short intestines, and small ceca (Brugger 1989). Simplicity of the digestive tract limits the options for response of gut tissues to external or internal influences. However, seasonal variations in food quality (Beal 1900), coupled with variation in reproductive or migratory status (Payne 1969) and variation in energy requirements (Brenner 1966), could create asynchronous fluctuations in energy supply and demands. Thus, energy conservation by varying tissue allocated to the gut may be important to Red-winged Blackbirds. My objective was to determine how the gross and microscopic structures of the gastrointestinal tract varied in Red-winged Blackbirds in response to experimental manipulations in diet quality.

METHODS

I captured male Red-winged Blackbirds in decoy traps within 10 km of Gainesville, Florida. I weighed each bird and measured wing chord, bill length, and tarsus length (Baldwin et al. 1931). To reduce poten-

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TABLE 1. Nutrient composition of experimental diets fed to adult male Red-winged Blackbirds. Nutritional analyses are organic matter (OM) as percentage of fresh mass from the bag, metabolizable energy content of dry matter, and the proportions of nitrogen (N), ash-free neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin (Lig), reported as % dry matter.

			Metabolizable energy			Fiber		
Diet	Energy density	OM (%)	Mass (kJ/g)	Volume (kJ/cm³)	N (%)	NDF (%)	ADF (%)	Lig (%)
1	Dense	91.5	15.6	31.3	5.5	18.8	9.0	2.1
2	Dilute by volume	90.2	13.9	19.9	3.8	31.0	17.5	4.9
3	Dilute by mass	83.6	11.1	22.3	3.0	23.1	9.8	2.9

tial variance in responses associated with sex, age, or allometry, I selected only after-second year males of a standard body size for use in feeding trials. Adult males were selected by plumage and date of capture. All test birds had a body mass between 52 and 60 g, and wing chord between 112 and 118 mm.

I used a completely randomized design, with one factor (diet) tested in 3 treatments and 10 birds per diet. I categorized diet quality by available energy density (Van Soest 1982), which I measured by mass (kJ/g) or volume (kJ/cm³). I measured diet volume (cm³) by water displacement of 10-g samples (Tarpey 1965). Flint River Mills Game Bird Starter served as the energy-dense test diet (Diet 1; Table 1). I created a diet that was energy-dilute by volume (Diet 2) by diluting Diet 1 with lignin fiber. I used mahogany sawdust in a ratio of 1:6 sawdust:feed as the diluent because of its high lignin content (26%). I assumed that lignin was indigestible by Red-winged Blackbirds, which have small ceca, because lignin is not digestible by gallinaceous birds with large, fiber-digesting ceca (Savory and Gentle 1976b). Purina Layena was the diet that was energy-dilute by mass (Diet 3).

I held birds separately in small cages (45 × 45 × 90 cm) and fed them the same batch of Diet 3 for a 2-week acclimation period. Then, I gave birds assigned to treatment groups 1 and 2 the new diets, while birds in treatment group 3 continued on Diet 3. Birds ate these diets for 5 weeks, a period which should ensure digestive adaptation to the new diets (Levey and Karasov 1989). I have no evidence that birds selectively fed (or "high-graded") from these diets, based on analysis of diets and orts (Brugger 1989). I sacrificed each bird by CO_2 overdose between 1200 and 1600 (6–10 h after sunrise), weighed it (±0.01 g), and removed its gastrointestinal tract. Birds had access to feed the day they were sacrificed, thus the influence of recent feeding activity on digestive organ size should be similar among treatment groups (Robel et al. 1990). I measured empty, rinsed organs as follows: fresh mass (mg) of gizzard (patted dry of excess moisture with a paper towel), small-intestine length (mm), and combined lengths of ceca (mm). To measure the length of the small intestine, I slipped it over a 2-mm diameter metal rod and allowed it to recoil to a relaxed shape. This is a variation of Leopold's (1953) method of simply laying the straightened intestine on a flat surface and measuring its relaxed length. It is in contrast to the technique of stretching the intestine with a standard 10-g tension recommended by Freehling and Moore (1987). The standard tension method yields higher mean values for intestine length, but 1.2–4.9% lower coefficients of variation than Leopold's method. Thus my method could yield variance in measurement that might obscure actual differences among treatments in small-intestine length.

Transverse sections of tissue were excised from the first 2 cm of the duodenum of each bird and immediately preserved in neutral buffered formalin. Sections were stained with Harris hematoxylin, Biebrich scarlet/orange II, and fast green. I measured in 5 sections per bird the lengths of the duodenal villi from submucosa to tip, depth of the lamina propria from base of the villi to the muscularis mucosa, depth of the lamina muscularis, inner diameter of the small intestine (from villus tip to villus tip, also called the lumen), and outer diameter of the small intestine. To determine a mechanism for increase in villus length, I counted the number and types of cells per 100 μm in the middle of 5 villi per bird.

I used a standard software package, Systat® (Wilkinson 1987) for statistical analysis. The variances among the 3 diet treatment groups for each of the parameters did not differ, thus analyses of variance could be used to test for differences in responses among diets. I used an ANCOVA, with body mass as the covariate, to test for allometric effects on dependent variables. I used a nested ANOVA to test for differences among fixed diet treatment groups in intestinal histology, with data from the 5 sections per bird as random repeated measures within the random variable of an individual bird. The nested repeated-measures ANOVA was used to allow for variability in the measurement of villus length within replicates (a single bird). I performed multiple comparisons with t-tests, adjusted with Bonferroni's α/k to preserve experiment-wise α levels, where k is the number of comparisons made (Day and Quinn 1989).

TABLE 2. Measures ($\bar{x} \pm$ SE) of body mass, intake, and gut anatomy for 10 adult male Red-winged Blackbirds fed 1 of 3 diets for 5 weeks. Diet 1 is energy dense, Diet 2 is energy-dilute by volume, and Diet 3 is energy-dilute by mass. Results of one-way ANOVA are presented. Values followed by different letters within a row are significantly different as determined by multiple comparisons.

Dependent variable	Diet 1	Diet 2	Diet 3	$F_{2,27}$	P
Body mass (g)	56.5 ± 1.5 A	53.6 ± 1.8 A	59.4 ± 1.2 B	3.5	0.04
Intake (g dry matter)	10.1 ± 0.4 A	13.5 ± 0.3 B	14.5 ± 0.3 B	48.0	<0.01
Gizzard mass (mg)	1,023.0 ± 47.0 A	1,287.0 ± 77.0 B	1,338.0 ± 53.0 B	7.7	<0.01
Small-intestine length (mm)	201.1 ± 4.1 A	214.5 ± 4.3 B	211.1 ± 5.0 B	3.8	0.03
Combined ceca lengths (mm)	5.0 ± 0.2	4.5 ± 0.4	4.7 ± 0.3	0.7	0.51

RESULTS

I found significant among-diet differences in body mass ($P = 0.04$), intake ($P = 0.001$), gizzard mass ($P = 0.001$), and small-intestine length ($P = 0.03$) after 5 weeks (Table 2). I found an allometric relationship for gizzard mass. Thus, the mean values of gizzard mass were adjusted for body mass (Table 2). Birds fed Diet 3 (energy-dilute by mass) had significantly greater ($P < 0.05$) body mass at the end of 5 weeks than those fed Diet 2 (energy-dilute by volume) or Diet 1 (energy dense), which were not statistically different. Birds fed diets 2 and 3 had greater intake, gizzard mass, and small-intestine length than birds fed Diet 1 (each $P < 0.05$). The combined ceca lengths did not vary among diets.

Irrespective of diet, fresh gizzard mass (mg) was linearly related to dry matter intake (g) as follows: gizzard mass = 491 + 57 × intake ($r^2 = 0.25$, $P = 0.003$). Small-intestine length was not related to dry-matter intake. However, small-intestine length (mm) and volumetric intake (cm^3) were related. The relationship is described by the following linear equation: small intestine length = 188 + 3 × volumetric intake ($r^2 = 0.15$, $P < 0.04$).

The cross sections of duodenal tissue of only 4 birds per diet were preserved well enough to prevent digestion of villus cells and to be used for measurements. The structure of the duodenum was similar among diet treatments. The inner layer of mucous membrane was formed by simple, unbranched villi, which were lined with absorptive columnar epithelial and goblet cells. No enteroendocrine cells were observed in Red-winged Blackbird duodenal villi. Crypts of Lieberkuhn opened at the base of the villi in the lamina propria. A thin muscularis mucosa projected fibers into the villi. The submucosa was rarely visible. The lamina muscularis, divided into an inner circular layer and outer longitudinal layer, was clearly discernible in each section. The serosa was thin, but clearly visible.

I found significant differences among diets in histological measures of the duodenum (Table 3). Birds on Diet 2 (energy-dilute by volume) had on average longer duodenal villi by 14%, deeper lamina muscularis by 21%, and larger outer diameter of the duodenum by 6% when compared with those fed Diet 1 (energy-dense). Birds fed Diet 2 had on average 8% longer duodenal villi than those fed Diet 3 ($P < 0.02$). Birds fed Diet 2 had fewer total cells and fewer absorptive cells per 100 μm than birds fed the other diets. The number of goblet cells per 100 μm did not differ significantly among diet treatments, but there was a trend ($P = 0.07$) of increased number of goblet cells in villi of birds fed the energy-dense diet (Table 3).

DISCUSSION

Both gross and microscopic structures of the gastrointestinal tract of Red-winged Blackbirds varied in response to diet quality. Such responses occurred when birds were switched from a maintenance diet that was dilute in available energy by mass, to either a diet that was dilute by volume or a diet that was energy dense. There was a linear relationship of fresh gizzard mass, adjusted for covariance with body mass, and dry-matter intake. Small-intestine length also was related linearly to volumetric intake but not dry matter intake. Duodenal outer diameter and villus length were greatest in birds fed the volumetrically dilute diet. These results suggest that small-intestine length, diameter (and therefore gut volume), and absorptive surface area increased in response to increased volume of food intake. These adaptations in the small intestine occurred within 5 weeks in adult male Red-winged Blackbirds.

TABLE 3. Measures ($\bar{x}$ ± SE) of duodenal microanatomy for 4 adult male Red-winged Blackbirds fed 1 of 3 diets for 5 weeks. See Table 1 for diet descriptions. Results of one-way repeated measures ANOVA are presented. Degrees of freedom for *F* are 3 for birds within each diet, 2 for diet, and 48 for error. Values followed by different letters within a row are significantly different as determined by multiple comparisons.

Dependent variable	Diet 1	Diet 2	Diet 3	*F*	*P*
Duodenal villus length (μm)	819.7 ± 31.0 A	938.4 ± 16.7 B	868.9 ± 16.3 AC	46.7	<0.01
Total cells (100 μm^{-1})	19.7 ± 0.4 A	17.4 ± 0.5 B	19.3 ± 0.5 A	7.3	<0.01
Absorptive cells (100 μm^{-1})	18.1 ± 0.4 A	16.3 ± 0.3 B	18.5 ± 0.4 A	8.4	<0.01
Goblet cells (100 μm^{-1})	1.6 ± 0.2	1.1 ± 0.2	0.9 ± 0.2	2.8	0.07
Lamina propria depth (μm)	308.2 ± 9.1	310.7 ± 10.1	319.5 ± 17.0	1.7	0.20
Lamina muscularis depth (μm)	68.8 ± 3.0 A	83.0 ± 5.0 B	74.5 ± 3.0 AB	4.9	0.01
Duodenal outer diameter (μm)	3,527.0 ± 110.0 A	3,743.0 ± 112.0 B	3,621.0 ± 101.0 C	12.6	<0.01
Duodenal inner diameter (μm)	1,444.0 ± 74.0	1,089.0 ± 87.0	1,105.0 ± 175.0	1.8	0.17

Two mechanisms can promote an increase in tissue size: increase in cell size (hypertrophy) or growth by cell accumulation (hyperplasy). Both mechanisms may be responsible for the anatomical changes observed in Red-winged Blackbirds. The changes in small-intestine length of Red-winged Blackbirds were relatively small compared with those of other birds that have been studied. For example, the small intestines of Red-winged Blackbirds fed the volumetrically dilute diet were on average 6% longer after 35 days than those of birds fed the energy-dense diet. This response was correlated with a 34% difference in dry-matter intake, which I use to standardize the comparisons. In comparison, a 20% increase in mean small-intestine length (from 27.5 cm to 33 cm) was elicited in captive European Starlings (*Sturnus vulgaris*) after 14 days in response to a fivefold increase in dry matter intake (from 8 g/day to 40 g/day; Al-Joborae 1979). Additionally, a 43% increase in mean small-intestine length was elicited in Japanese Quail (*Coturnix japonica*) in 21 days in response to a 34% increase in dry-matter intake (Savory and Gentle 1976a, b). Because so little change in intestine length was identified in Red-winged Blackbirds after a relatively long exposure to a dilute diet, hypertrophy in response to increased intake might be the simplest explanation for increased small-intestine length.

Hypertrophy clearly accounts for increased villus length in Red-winged Blackbirds fed the volumetrically dilute Diet 2, compared with birds fed either diets 1 or 3. Individuals fed Diet 2 had fewer absorptive epithelial cells per 100 μm in mid-villus than those fed diets 1 (13.2% fewer) or 3 (9.8% fewer). These differences in cell numbers closely account for the increased villus size of birds fed Diet 2, which suggests that villus size increased because fewer and larger cells were present. However, the greater lengths of duodenal villi still could reflect increased enterocyte production in the crypts or decreased cell loss at the villus tip. Neither could be measured because of densely overlapping layers of cells at the tips and crypts, which could not be separated for counting.

Hyperplasy, or actual tissue growth, possibly occurred in the gizzard, villus, and lamina muscularis in response to diet dilution. Simple hypertrophy would not produce change in the mass of the gizzard, unless the greater gizzard masses of birds on the dilute diets reflected a change in water content of the gizzard cells. Rather, the greater gizzard mass of birds fed energy-dilute diets probably resulted from development of muscles surrounding the gizzard. Such muscle hyperplasy can occur from increased contractions associated with increased intake (Moss 1989). Because I measured only fresh mass, not dry mass, the exact mechanism for increased gizzard mass was not determined.

The observed trend of increased number of goblet cells in mid-villus of the birds fed the energy-dense diet suggests that differential cell production, and therefore hyperplasy, occurred in the villus. Goblet cells, which produce mucous, are typically rare in the duodenum of mammals but the frequency in birds is unknown. They possibly play a role in protecting the mucosal epithelium from potentially noxious substances. Why the density of goblet cells increased in the villi of birds that ate an energy-dense diet is not clear. However, if the trend of increased number of goblet cells reflects a general pattern of cellular adaptation to diet, then not only the number and size of villus

cells, but also the type of cells produced in the crypts, are regulated.

The observed thickening of the lamina muscularis in response to diet dilution could be due to hyperplasy in the circular or longitudinal layers of muscle surrounding the intestine, which would facilitate increased contractions needed to move a large volume of digesta. Comparable data are not available for other wild birds. However, increased thickness of the lamina muscularis and elongation of villi in response to diet dilution are known in poultry (Rubio et al. 1989) and mammals (Goss 1978), and are attributed to increased cell production.

Birds could achieve fine adjustment of tissue mass in the digestive tract solely by regulating villus-cell production. To understand the involvement of so many tissues may require an energy-based explanation. Assuming that (1) several small enterocytes cost more to produce than a few large enterocytes, and (2) absorption, standardized by surface area, is identical in small and large cells (Harris et al. 1988), then a bird eating a low-quality diet should increase absorptive surface area by regulating the size of its enterocytes rather than produce more cells. At the same time, a bird faced with abundant energy in its diet could readily minimize energy allocated to the gut, yet maintain sufficient uptake of nutrients, by reducing absorptive surface area through regulation of cell numbers. Thus, energy balance in the digestive tract could be managed rapidly with minimal investment by varying only the digestive and absorptive surface area that is in direct contact with digesta, and not the surrounding tissue layers. The evidence I present, however, suggests that the guts of Red-winged Blackbirds respond to manipulations in diet by altering several facets of digestion. For example, the volumetric capacity of the gut changes via small-intestine length and diameter. Particle size of the digesta is affected by gizzard mass. The rate of passage is influenced by depth of the lamina muscularis, and the absorptive capacity is affected by villus length and structure. These responses interact to yield a potentially wide range of metabolizable energy efficiencies of birds on a variety of foods.

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LITERATURE CITED

AL-DABBAGH, K. Y., J. H. JIAD, & I. N. WAHEED. 1987. The influence of diet on the intestine length of the White-cheeked Bulbul. Ornis Scandinavica 18: 150–152.

AL-JOBORAE, F. F. 1979. The influence of diet on the gut morphology of the starling (*Sturnis vulgaris* L. 1758). Ph.D. dissertation, Oxford, Oxford Univ.

ANKNEY, C. D., & D. M. SCOTT. 1988. Size of digestive organs in breeding Brown-headed Cowbirds, *Molothrus ater*, relative to diet. Can. J. Zool. 66: 1254–1257.

BALDWIN, S. P., H. C. OBERHOLSER, & L. G. WORLEY. 1931. Measurements of birds. Cleveland Mus. Nat. Hist. Sci. Publ. 17.

BEAL, F. E. L. 1900. Food of the Bobolink, blackbirds, and grackles. U.S. Dep. Agric. Biol. Surv. Bull. 13: 1–77.

BRENNER, F. J. 1966. Energy and nutrient requirements of the Red-winged Blackbird. Wilson Bull. 78: 111–120.

BRUGGER, K. E. 1989. Digestive responses to changes in diet, season, photoperiod, and temperature in the Red-winged Blackbird (*Agelaius phoeniceus*). Ph.D. dissertation, Gainesville, Univ. Florida.

DAVIS, J. 1961. Some seasonal changes in morphology of the Rufous-sided Towhee. Condor 63: 313–321.

DAY, R. W., & G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59: 433–463.

FREEHLING, M. D., & J. MOORE. 1987. A comparison of two techniques for measuring intestinal length. J. Wildl. Manage. 51: 108–111.

GOLDSTEIN, D. L. 1989. Absorption by the cecum of wild birds: Is there interspecific variation? J. Exp. Zool. Suppl. 3: 103–110.

GOSS, R. J. 1978. The physiology of growth. New York, Academic Press.

HANSSEN, I. 1979. Micromorphological studies on the small intestine and caeca in wild and captive Willow Grouse (*Lagopus lagopus lacopus*). Acta Vet. Scandinavica 20: 351–364.

HARRIS, M. S., J. G. KENNEDY, K. A. SIEGESMUND, & D. E. YORDE. 1988. Relationship between disten-

tion and absorption in rat intestine. I. Effect of luminal volume on the morphology of the absorbing surface. Gastroenterology 94: 1164–1171.

IMONDI, A. R., & F. H. BIRD. 1966. The turnover of intestinal epithelium in the chick. Poult. Sci. 45: 142–147.

JOHNSON, L. R. 1987. Regulation of gastrointestinal growth. Pp. 301–333 *in* Physiology of the gastrointestinal tract, 2nd ed. (L. R. Johnson, Ed.). New York, Raven Press.

KENWARD, R. E., & R. M. SIBLY. 1977. A Wood Pigeon (*Columba palumbus*) feeding preference explained by a digestive bottleneck. J. Appl. Ecol. 14: 815–826.

LEOPOLD, A. S. 1953. Intestinal morphology of gallinaceous birds in relation to food habits. J. Wildl. Manage. 17: 197–203.

LEVEY, D. J., & W. H. KARASOV. 1989. Digestive responses of temperate birds switched to fruit or insect diets. Auk 106: 675–686.

MCLELLAND, J. 1979. Digestive system. Pp. 69–181 *in* Form and function in birds (A. S. King and J. McLelland, Eds.). London, Academic Press.

MILLER, M. R. 1975. Gut morphology of Mallards in relation to diet quality. J. Wildl. Manage. 39: 168–173.

MOSS, R. 1972. Effects of captivity on gut lengths in red grouse. J. Wildl. Manage. 36: 99–104.

———. 1989. Gut size and the digestion of fibrous diets by Tetraonid birds. J. Exp. Zool. Suppl. 3: 61–65.

PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Red-winged Blackbirds. Univ. Calif. Publ. Zool. 90: 1–137.

REMINGTON, T. E. 1989. Why do grouse have ceca? A test of the fiber digestion theory. J. Exp. Zool. Suppl. 3: 87–94.

ROBEL, R. J., M. E. BARNES, K. E. KEMP, & J. L. ZIMMERMAN. 1990. Influences of time postmortem, feeding activity, and diet on digestive organ morphology of two Emberizids. Auk 107: 669–677.

RUBIO, L. A., A. BRENES, & M. CASTANO. 1989. Histological alterations to the pancreas and the intestinal tract produced by raw Faba bean (*Vicia faba* L. minor) diets in growing chicks. Br. Poult. Sci. 30: 101–114.

SAVORY, C. J., & M. J. GENTLE. 1976a. Changes in food intake and gut size in Japanese Quail in response to manipulation of dietary fibre content. Br. Poult. Sci. 17: 571–580.

———, & ———. 1976b. Effects of dietary dilution with fibre on the food intake and gut dimensions of Japanese Quail. Br. Poult. Sci. 17: 561–570.

SIBLY, R. M. 1981. Strategies of digestion and defecation. Pp. 109–138 *in* Physiological ecology: an evolutionary approach to resource use (C. R. Townsend and P. Calow, Eds.). Sunderland, Sinauer Assoc.

TARPEY, R. W. 1965. Evaluating dietary volume measurements. Poult. Sci. 44: 495–500.

VAN SOEST, P. J. 1982. Nutritional ecology of the ruminant. Ithaca, Cornell Univ. Press.

WEBSTER, A. J. F. 1981. The energetic efficiency of metabolism. Proc. Nutr. Soc. 40: 121–128.

WILKINSON, L. 1987. Systat: the system for statistics. Evanston, Systat, Inc.