CONSUMPTION OF COMMERCIALLY-GROWN GRAPES BY AMERICAN ROBINS: A FIELD EVALUATION OF LABORATORY ESTIMATES

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Experimental feeding of caged birds is a common technique for assessing the potential economic importance of crop predators (e.g., Avery 1979, Benigno et al. 1975, Brown 1976, Lynch et al. 1973, Tobin 1984, Weatherhead et al. 1982). This laboratory approach is particularly important with respect to commercially-grown fruits, such as wine grapes (*Vitis vinifera*), because juice and pulp are often difficult to quantify or even detect in the digestive tracts of field-collected birds (McAtee 1912, this study). Even when fruit remains can be detected, investigators often choose the more economical cage studies. However, one fundamental question (Neumann and Klopfer 1969) arising over the interpretation of cage studies is, "To what extent can results be expected to conform with field reality?" The obvious answer is, "To the extent that relevant field conditions are matched in the lab."

Food choices presented to caged birds are typically meager compared to the variety available to free-ranging birds, and this constitutes one of the most important sources of discordance between laboratory and field environments (hereafter referred to as diet-choice discordance). Studies of foraging behavior (e.g., Charnov 1976, Green 1980, Krebs et al. 1977, Pyke 1984) show that, within certain nutritional constraints, animals appear to rank foods according to energetic profitability, and that particular foods are regularly (i.e., other than occasional sampling) eaten only when alternative foods of higher profitability are not available. Accordingly, in the lab an animal's consumption of low-ranking foods should be sensitive to diet-choice discordance, while consumption of high-ranking foods should be relatively unaffected.

It follows that laboratory bias due to diet-choice discordance should be minimal when the food being tested is a superabundant, energy-rich item that the bird species being tested is adapted to exploit with high efficiency (i.e., profitability). These conditions are met in many cases of avian predation on commercially-grown fruits. Consequently, laboratory estimates of fruit consumption by frugivorous birds should conform well with field reality if differences between laboratory and field environments other than diet-choice discordance are unimportant. To test this expectation in the specific case of wine-grape predation by American Robins (*Turdus migratorius*), we directly estimated grape consumption by free-ranging birds and compared our field estimates to the results of an independent cage study conducted with birds from the same wild population (Tobin 1984). Although cage studies are often employed to help assess avian impact on agricultural crops, we are not aware of previous

reports that compare laboratory and field estimates of fruit consumption by birds.

METHODS

Our estimates of grape consumption by free-ranging robins involved 2 stages: (1) evaluation of grape digestion rates among captive birds to estimate digestibility correction factors (Coleman 1974), and (2) evaluation of the gizzard contents of birds shot while they were foraging in selected vineyards. To estimate average daily grape consumption of a robin, we applied digestibility correction factors to the mean quantity of grape remnants found in gizzards, and multiplied the resulting value by the estimated number of food-passage intervals per day. We also attempted to use these procedures to obtain field estimates of grape consumption by European Starlings (*Sturnus vulgaris*) and House Finches (*Carpodacus mexicanus*). However, our digestion-rate studies revealed that House Finches fed only on juice and pulp (after pecking through the skins of berries), the remnants of which we could neither identify nor quantify even from the digestive tracts of birds killed immediately after feeding. While this was not a problem with European Starlings, the small sample size ($N = 8$) for field-collected specimens limits the power of any comparisons with cage studies.

American Robins are major predators of grapes (e.g., Hothem et al. 1981), and we were able to collect adequate samples of this species. Robins typically consume grapes on the vine, often in thick foliage, where they pluck individual berries and swallow them whole (Kassa and Jackson 1979, cf. Paszkowski 1982, Tobin 1984). Grapes rarely fall from the vine prior to harvest and we observed robins eating grapes on the ground only when they were retrieving berries plucked from the vine and subsequently dropped. Due to poor visibility when robins are in the vines, and the restricted mobility of observers in trellis vineyards, grape consumption cannot be estimated via direct observations of foraging birds.

However, since grape skins and seeds are resistant to digestion, their remains in robin stomachs can be identified and quantified. Therefore, because robins (and starlings) swallow grapes whole, field estimates of grape consumption can be obtained via stomach content analysis. In contrast, because House Finches feed only on juice and pulp, even stomach content analysis will fail to provide useful quantification of grape consumption. House Finches provide an example of why laboratory feeding trials are often crucial for the study of economic ornithology.

Grape digestion-rate trials.—About 2 months before digestion trials began, 18 robins (11 ♂♂, 7 ♀♀) were captured in mist nets at a vineyard owned by Cortopassi Farms, located 10 km NE of Stockton, California. The birds were transported to U.S. Fish & Wildlife Service lab facilities located 5 km NE of Dixon, California, where they were banded, weighed, and maintained in a communal 5.0 × 2.5 × 2.0-m outdoor aviary. Pretest feeding evaluations were conducted with all birds to determine the amount of time required for them to calm down and consume at least 1

grape. Based on these evaluations, we chose a 20-min feeding period for the digestion trials.

Five days before the digestion trials began, each robin was placed in a separate 43 × 47 × 62-cm outdoor cage and provided with unlimited access to poultry pellets, grapes, and water. Immediately prior to the trials, all birds were denied food for 17 h (1600–0900 h). Then, during the 20 min feeding period, they had free access to grapes.

The grapes were Cabernet Sauvignon variety which were picked within 3 weeks of the feeding trials and refrigerated. Large bunches with average sugar levels >20° Brix (as measured with a portable refractometer) were separated into smaller bunches consisting of 15 berries each. One small bunch was then weighed to the nearest 1 mg and hung in each bird's cage just above the perch. After the feeding period, unconsumed grapes were again weighed to the nearest 1 mg. The difference in weight before and after the feeding period was the amount consumed by each bird.

The birds were randomly assigned to 1 of 4 groups which were allowed to digest their meals for 0, 30, 60, and 120 min before being killed by cervical displacement. Identifiable grape remnants found in the gizzards were blotted, air-dried for 15 min, and weighed to the nearest 1 mg. The mean weight of grape remnants for each digestion interval group, expressed as a percent of grape matter ingested, was plotted against time to produce a decay curve; a digestibility correction factor was calculated following the methods of Coleman (1974).

Field collections. —From 12 August to 27 September 1982, we opportunistically shot 45 robins in 2 vineyards: (1) Cortopassi vineyard (see above) and (2) Parr vineyard located 8 km W of Calistoga, California. Our field collections temporarily substituted for ongoing bird-control programs previously initiated by the growers. Immediately after shooting each bird, we weighed it to the nearest 0.5 g, and injected 10% formalin into the stomach to arrest post-mortem digestion. Carcasses were placed on ice in a cooler and frozen later the same day for subsequent examination. We collected birds primarily between sunrise and solar noon (=1300 h). Since the diurnal pattern of feeding activity in temperate passerine birds is approximately symmetrical with respect to solar noon (Gartshore et al. 1982, Lees 1948, Morton 1967), the weighted (by time of day) mean quantity of grape remnants recovered from robin gizzards was assumed to have approximated the weighted mean value for a full diurnal cycle (i.e., the daily average value).

Since most birds had an empty esophagus and proventriculus (=gullet), we restricted analysis to the gizzard contents, as advocated by Custer and Pitelka (1975). In the laboratory, the contents of each gizzard were segregated into 3 categories: (1) grape matter, (2) other plant matter, and (3) animal matter. All gizzard contents were blotted, air-dried for 15 min, and then weighed to the nearest 1 mg.

Adults and juveniles each made up about 50% of all specimens collected. Since robins are not sexually dimorphic in body weight (Eiserer

1976, also see below), and since post-reproductive nutritional require-
ments should be similar for both sexes, we pooled the sexes for our
analyses. Likewise, the mean weights of hatching-year (HY) and after-
hatching-year (AHY) birds differed by less than 5% (males: HY = 80.6
g, AHY = 84.1 g, $t = 1.88$, $P > 0.05$, df = 21; females: HY = 81.0 g,
AHY = 83.0 g, $t = 0.83$, $P > 0.05$, df = 19), and since the efficiency of
exploiting superabundant commercial fruits should not depend on pre-
vious experience (cf. Gochfeld and Burger 1984), we also pooled the age
classes. We summarized relative diet composition by the aggregate per-
cent method (Swanson et al. 1974).

Laboratory assessment of grape consumption.—In 1981, Tobin (1984)
measured the daily consumption of grapes by caged robins, starlings, and
House Finches to assess their relative grape-damaging potentials. During
his study, wild robins were captured from the same wine-grape regions
of California that we sampled and were held in captivity at the same
facilities we used. For 90–120 days, Tobin's robins were provided free
access to water and poultry pellets. Two groups of 6 robins each were
then tested in separate outdoor communal cages during a 5-week period
(August–September) coinciding with the ripening/harvest season for
north-central California wine grapes. Each group was offered water,
poultry pellets, and grapes (1 group received Zinfandel grapes, the other
Ruby Cabernet). Consumption of grapes and poultry pellets during spec-
ified 24-h periods was measured twice weekly. For additional details of
this study see Tobin (1984).

RESULTS

Digestibility correction factor.—The decay curve obtained from our grape
digestion-rate trials is illustrated in Figure 1. One robin in the zero-
digestion group died during the digestion-rate trials, thereby reducing
the group's sample size to only 3 birds. However, the amounts of quan-
tifiable grape remnants recovered from robins in this group showed rel-
atively little variation (range = 10–20% of consumption). The mean
value of 15.9% compares closely to the mean value of 15.2% obtained
from a group of simultaneously tested starlings (Skorupa and Hothem,
unpubl. data). The results were consistent, despite small sample sizes,
and we believe larger sample sizes would not appreciably improve the
decay curve.

We do not know why one of our captive robins died, however, its
weight (54.9 g) fell substantially below the 95% confidence interval around
the mean weight for the remainder of our captive birds (77.5 ± 9.4 g).
No other individual's weight fell outside the 95% confidence interval and
therefore the bird that died is best treated as an anomalous individual.
The mean weight of wild robins (82.3 g) was 6.2% higher than the mean
reported above for post-trial captive robins. However, we found that
starlings lost an average of 6.5% of their body weight during the pre-
trial fasting (these data were not collected for robins). Consequently,
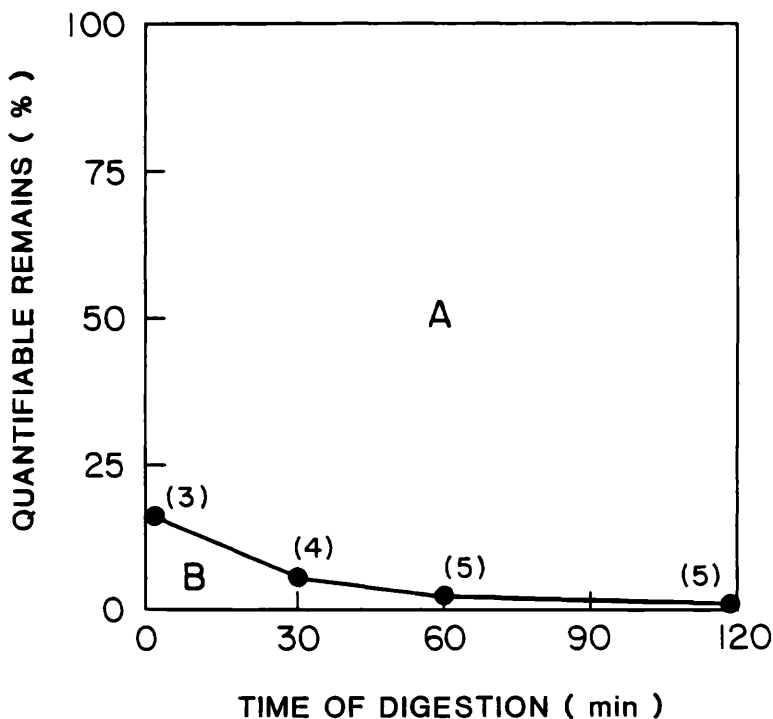with the exception of one individual, we believe that our captive robins

FIGURE 1. Decay curve for grape matter in American Robin gizzards. The digestibility correction factor equals area (A + B)/area B (=21.1). Numbers above each point equal the sample size.

were in good body condition immediately prior to the digestibility trials, that they were not unreasonably stressed by our protocol, and that they provided a reliable estimate of grape passage rates.

The curve illustrated in Figure 1 exhibits a smooth monotonic decline, reaching zero at approximately 120 min. Based on Figure 1 (cf. Coleman 1974), a correction factor of 21.1 should be employed to convert the weight of grape remnants found in field-collected gizzards to the weight of grapes actually consumed during the 2 h prior to collection. Assuming there are 13 h available for foraging during the season we collected specimens (National Weather Service Data, Sacramento office), robins would have about 6.5 (13 h/2 h) food-passage intervals per day.

Gizzard contents of field-collected birds.—Grape matter made up 82% of food remnants in the gizzards of birds collected at Parr vineyard and 88% of food remnants in the gizzards of birds collected at Cortopassi vineyard (Table 1). The mean per capita absolute weight of grape remnants from Parr vineyard was slightly higher than from Cortopassi vineyard (Table 2), but the difference was not statistically significant ($t' =$

TABLE 1.   Relative composition of foods recovered from the gizzards of American Robins
      shot in California vineyards during August and September 1982.

Vineyard	Percent grape	Percent animal	Percent other plant
Parr	82[a]	12	6
Cortopossi	88	11	1

[a] All values are aggregate percents (Swanson et al. 1974) rounded to the nearest percent.

0.55, $P > 0.50$; Sokal and Rohlf 1969:374). Although the Parr and
Cortopassi vineyards are located about 170 km apart in slightly different
climatic regions (Crase et al. 1976), and consist of plantings of different
grape varieties (Table 2), the similarity of our results at the 2 sites
suggests that these factors were not major sources of variation influencing
grape consumption. Therefore, we pooled our samples to obtain a
weighted (by time of day) mean value for the quantity of grape remnants
recovered from gizzards of field-collected birds (Table 3).

Comparison of laboratory and field estimates.—Our field estimates of
mean daily grape consumption correspond closely to Tobin's (1984) lab-
oratory estimates, with the various per capita values only ranging from
57–69 g (Table 4). The field estimate based on pooled samples and a
weighted mean (62 g per bird) differs by only 3% from the laboratory
estimate based on pooled samples (60 g per bird). Since the laboratory
estimates were based on 24-h feeding periods in a controlled environment
and the field estimates were extrapolated from 2-h samples (i.e., the
contents of each gizzard represent 2 h of feeding) in an uncontrolled
environment, the 2 methods generated unequal estimates of variance
(Table 4; $F = 4.26$, $P < 0.002$, df $= 44,119$; Sokal and Rohlf 1969:185–
186). However, even if we employ the lower laboratory estimate of vari-
ance, the difference between field and laboratory estimates of grape con-
sumption (based on pooled samples) is not statistically significant ($t = 0.35$, $P > 0.50$, df $= 163$).

DISCUSSION

The close match between our field estimates and Tobin's (1984) lab-
oratory estimates is consistent with our expectation based on the as-
sumptions that: (1) diet-choice discordance is a major source of laboratory
bias, and (2) simple principles of foraging behavior could be used to
predict when such bias would be minimal. Although simple optimal diet
models (Pyke 1984) may have restricted applicability (Altmann 1984,
Belovsky 1978, Rapport 1980), our results suggest they provide reason-
able criteria for guiding the judicious use of cage studies in economic
ornithology. Our results also suggest these models provide a good con-
ceptual basis for evaluating the probable realism of results from past
laboratory studies.

For example, since European Starlings are not primarily frugivorous
(e.g., Eriksson and Nummi 1982, Feare 1984:5, Martin et al. 1951:149,

TABLE 2.   Absolute quantity of grape remnants (g) recovered from the gizzards of American Robins shot in California vineyards during August and September 1982.

Vineyard	N	x̄	SD
Parr[a]	25	0.504	0.298
Cortopossi[b]	20	0.439	0.460

[a] Birds collected at Parr vineyard fed on Chardonnay and Pinot Noir grapes.
[b] Birds collected at Cortopossi vineyard fed on Zinfandel grapes.

Russell 1971, Thompson and Willson 1979), their use of fruit may be highly dependent on the availability of alternative foods. Arthropods appear to be the most energetically profitable (i.e., preferred) class of foods for European Starlings (Feare 1984:5, Taitt 1973, Thompson and Grant 1968), but Tobin (1984) did not include this class as an alternative food in his laboratory studies of grape consumption by starlings (a severe, but not uncommon, example of diet-choice discordance). Thus, we would expect the realism of his results to be poor. In fact, the small sample of free-ranging starlings we collected in vineyards ($N = 8$) suggests that per capita daily consumption of grapes (26.1 g/bird-day) is substantially less than Tobin's (1984) lab estimate (61.3 g/bird-day). We suggest that, as a general rule, laboratory assessments of fruit consumption by primarily insectivorous birds will not correspond well with field reality because the relative availability of arthropods in the field is difficult to simulate in the laboratory.

About half of the 20 species of birds known to feed on grapes in California vineyards (Hothem, unpubl. data) are primarily frugivorous during the late summer and fall (i.e., their diets comprise >60% fruit). Thus, our results suggest that cage studies could play a significant role in determining the relative economic importance of avian predators on this crop. As Wiens and Dyer (1975) emphasized, direct impacts such as food consumption are of greatest immediate importance in assessing the potential for avian damage to agricultural crops. However, consumption is not strictly equivalent to damage (cf. Avery 1979). Tobin (pers. comm.) found that robins actually ate only 84% of the grapes they

TABLE 3.   Grape remnants (g) recovered from the gizzards of American Robins shot in California vineyards during August and September 1982, pooled by time of collection.

Collection time[a]	N	x̄[b]	SD
0800–0959	21	0.614	0.412
1000–1159	19	0.341	0.284
1200–1359	5	0.402	0.378

[a] Gizzard contents of birds collected between 0800–0959 represent foods eaten between 0600–0959, and so on.
[b] Equally weighting each time interval, the weighted mean gizzard contents included 0.452 g of grape remnants.

TABLE 4. Comparison of laboratory and field estimates of grape consumption by American Robins in California vineyards.

Field estimates[a]			Laboratory estimates[b]		
Sample (vineyard)	x̄ (g/bird-day)	SD	Sample (grape variety)	x̄ (g/bird-day)	SD
Parr	69.2	40.9	Ruby Cabernet	57.1	22.8
Cortopassi	60.2	63.1	Zinfandel	63.9	26.4
Pooled sample	62.0[c]	50.8	Pooled sample	60.5	24.6[d]

[a] Field estimates are calculated by the formula: (x̄ grape remnants/gizzard) × (digestibility correction factor) × (no. food-passage intervals/day) = mean daily consumption/bird.

[b] Laboratory estimates are from Tobin (1984, see text).

[c] Weighted estimate (by time of collection).

[d] Calculated from the original data (Tobin, pers. comm.).

plucked, implying that an average per capita consumption of 60 g/day would lead to a per capita destruction of about 70 g/day. Similar harvesting inefficiency has been noted in the field for starlings (Anon. 1973).

Furthermore, the potential economic importance of different species, on a per capita basis, is not necessarily indicative of their relative importance on a populational basis since some species naturally occur at much higher densities than others. Therefore, a species such as the European Starling, which may only supplement its diet with fruit, can be economically important at high densities. Conversely, although American Robins are highly frugivorous, they rarely achieve the density (ca. 350 birds/ha) required to cause a 10% crop loss in an average California wine-grape vineyard. As convenient and efficient as laboratory studies are, and even under circumstances which make them a judicious choice, practical interpretation of their results depends on, and is limited by, the extent to which a species' natural history has been elucidated in the field.

SUMMARY

Studies of food consumption by caged birds are often employed to assess potential economic impacts of crop predators. We propose that cage studies are most likely to yield results that match field reality when the crop being tested is a highly ranked food type of the bird species under study. This condition is likely to hold for many cases of avian predation on commercially-grown fruits. Therefore, to test our proposal we estimated the daily consumption of wine-grapes by free-ranging American Robins and compared our estimate to the results of an independent cage study. The estimates produced by the 2 methods differed by only 3%, thereby supporting our expectations. In contrast, we propose that cage studies of fruit consumption by primarily insectivorous birds, such as European Starlings, will not correspond well with field reality. Data from a small sample of free-ranging starlings suggested there were

large differences (ca. 100%) between cage results and field reality. We conclude that the general rules of optimal diet theory (Pyke 1984) provide reasonable criteria for guiding the judicious use of cage studies in economic ornithology.

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