IMPROVING ESTIMATES OF DOMINANCE BASED ON RATIOS[1]

Peter Arcese and Donald Ludwig

Institute of Animal Resource Ecology, University of British Columbia,
Vancouver, British Columbia V6T 1W5, Canada

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Fieldworkers often estimated the dominance of individuals by the dominance ratio (e.g., Fretwell 1969, Kikkawa 1980) or a variation of it (e.g., Searcy 1979). The dominance ratio is the number of supplants achieved per individual, divided by the total number of encounters in which the individual was observed. The ratio estimates the probability of achieving a supplant, and it can be a useful measure of dominance when knowledge of specific pair relations is not critical (Arcese and Smith 1985). However, ratios are inaccurate when the number of samples per individual is small. This problem is the subject of this note.

Estimation error can prevent statistically significant correlations from being observed even when biologically important correlations exist. The 95% confidence limits for a dominance ratio of 0.5 based on ten observations are plus or minus 0.31 (Sokal and Rohlf 1969). Although this is a very large estimation error, most researchers include animals with as few as five observations in their analyses (e.g., Fretwell 1969, Kikkawa 1980). The error of a ratio shrinks with increasing sample size; e.g., the 95% confidence limits of a dominance ratio of 0.5 based on a sample of 100 observations are plus or minus 0.12 (Sokal and Rohlf 1969). This suggests that larger minimum sample sizes are required for accurate analyses using dominance ratios. Of course, information is lost if ratios based on small samples are discarded. To avoid this loss, one might retain ratios estimated from small samples but weight these less heavily than those estimated from larger samples. Gilbert (1973) points out that the variance of a ratio, based on n independent observations, is proportional to $1/n$. He therefore recommended that ratios based on different sample sizes be weighted by their sample sizes (Gilbert 1973).

We explored these methods of accounting for error in dominance ratios by: (a) empirically determining the accuracy of our dominance ratios in order to test the independence assumption of Gilbert; (b) using dominance ratios based on successively larger numbers of observations in analyses subsequently using these ratios; and (c) weighting dominance ratios by their sample size.

We used data collected by one of us (PA) from a population of Song Sparrows (*Melospiza melodia*) on Mandarte Island, British Columbia, Canada. The dominance interactions observed were between individually marked yearlings, and most occurred at feeders. A detailed description of the study population and the methods employed are given elsewhere (Arcese and Smith 1985).

To determine the empirical relationship between the error of our dominance measure (wins/total encounters) and the number of observations it was based on, we used data from 24 sparrows that had been observed in over 100 encounters (range 112 to 200), and whose sequence of interactions in time was fully known. We calculated the

mean-squared error (MSE) as follows: for each observation (n; where $1 \leq n \leq 100$) and each individual (i; where $1 \leq i \leq 25$), we calculated the ratio $r_{n,i}$ from the first n observations of that individual. The MSE of successive observation numbers is given by

$$\text{MSE}(n) = \frac{1}{25} \sum_{i=1}^{25} (r_{n,i} - R_i)^2,$$

where R_i is the ratio as computed from the full set of observations for the i-th individual. A curve fitted to these points had the equation:

$$\text{MSE} = 0.24 \cdot n^{-0.93}; \qquad r\text{-squared} = 0.98.$$

The implied weight is remarkably close to the weight (n) suggested by Gilbert (1973).

We next determined whether the results of correlation analyses based on weighted dominance ratios were similar to those based on unweighted ratios. To do this, we compared the correlation coefficients (Person's r, Sokal and Rohlf 1969) from weighted analyses to those of analyses between the same variables when only dominance ratios based on successively larger minimum sample sizes per bird were used. We assumed that as minimum sample size was increased, correlation coefficients would become more accurate because they were based on ratios with smaller errors. Figure 1 shows that when the minimum acceptable
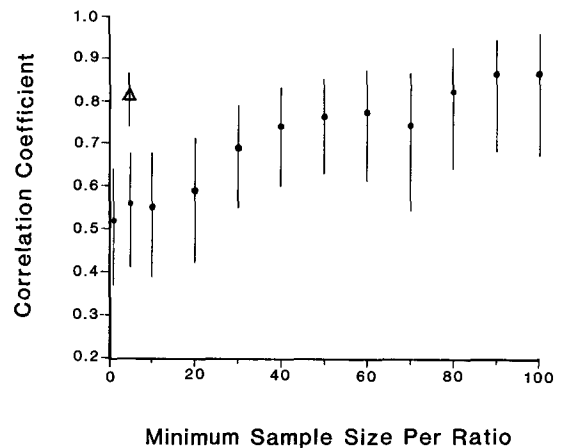
FIGURE 1. Estimates of the correlation coefficient between date of hatch and the dominance ratio (wins/total encounters). Points indicate the estimates from analyses based on birds with successively larger minimum numbers of observations per ratio (number of birds per coefficient decreases from 112 to 21). The triangle represents the estimate from a weighted analysis in which all birds with five or more observations per ratio were used (number of birds = 98). Bars show the 95% confidence interval of the estimates (Sokal and Rohlf 1969).

number of observations per ratio was increased from one to 100, the correlation coefficient between the dominance ratio and date of hatch increased from 0.52 to 0.86 (number of birds $n = 112$ to 21). When all birds with five or more observations were included in a weighted analysis (weight = number of observations), the corresponding correlation coefficient was 0.81 ($n = 98$). This figure was similar to that obtained when only ratios based on 100 observations per bird were used (t-test, $t = 0.09$, ns), but its confidence interval was much smaller (Fig. 1). In contrast, when significant correlations were not found between dominance ratios and other independent variables in weighted analyses (e.g., morphological characters; see Arcese and Smith 1985), neither were they found when only ratios based on a large number of observations per bird were used.

Our results suggest three conclusions about the dominance ratio: (a) the standard procedure of not weighting ratios according to their sample size and of including ratios with as few as five samples is unacceptable because of the large variance of such ratios; (b) our empirically determined weight agreed closely with the weight suggested by theory (Gilbert 1973); and (c) correlation coefficients estimated from analyses based on weighted ratios were similar to those obtained when only ratios based on a large number of observations per bird were used. However, using weighted ratios produced more accurate estimates (i.e., smaller confidence intervals) because information was retained by not excluding birds from the analyses.

Although estimates are improved by weighting, weighting is no alternative to rigorous data collection; if all ratios are based on small samples, estimation error may still obscure important relationships. We suggest that when the structure of hierarchies is not at issue, dominance ratios can estimate dominance, and that weighting can reduce the error of these ratios.

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PREDATION ON BLACK RAILS DURING HIGH TIDES IN SALT MARSHES[1]

JULES EVENS AND GARY W. PAGE
Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970 USA

Grinnell and Miller (1944) close their account on the Black Rail (*Laterallus jamaicensis*) with the statement that the "most important hazards to existence on salt marshes appear to be extra high tides." High tides are known to destroy Black Rail nests in California salt marshes (Ingersoll 1909, Huey 1916, Dawson 1923) and during winter to cause some adults to temporarily leave marshes (Stallcup and Greenberg 1974, Manolis 1978, Winter and Manolis 1978). Our observations of predators capturing Black Rails during high tides at two California salt marshes reveal another hazard to which Grinnell and Miller (1944) may have been referring.

During the winters of 1981 to 1982 and 1982 to 1983, we coordinated 11 high tide censuses of Black Rails at Corte Madera Ecological Reserve (CMER), a 35 ha *Salicornia virginica*-dominated salt marsh on the northwest shore of San Francisco Bay, Marin County, California. Volunteer observers, stationed around the margin of the

marsh, counted the numbers of each rail species leaving the marsh, the times of departure, the modes of exodus (swimming, walking, or flying), and the types of cover into which they disappeared. Mostly this cover was sweet fennel (*Foeniculum vulgare*) which grew in thick stands adjacent to the salt marsh. In 290 observer hr spread over 11 days, we saw 31 Black Rails, 86 Clapper Rails (*Rallus longirostris*), 26 Virginia Rails (*R. limicola*), and 12 Soras (*Porzana carolina*) leaving the marsh.

No one saw rails captured in the upland cover, but Northern Harriers (*Circus cyaneus*) caught two Black Rails that remained in the marsh after inundation, when partly submerged gum plants (*Grindelia* sp.) and widely scattered tops of the tallest *Salicornia* plants were the only emergent marsh vegetation. On 29 November 1982, 30 min before high tide (1.9 m above mean low water), Evens saw a female harrier land on a *Grindelia* bush. During a 10 min observation period, it rose in the air then landed several times before finally hovering over and dropping into the bush, rising afterwards with an apparent Black Rail. About 12 Ring-billed Gulls (*Larus delawarensis*) converged on the harrier as it flew off, causing it to drop the rail in the water. One gull picked up the slow-swimming rail in its bill, then dropped it. After three attempts the harrier retrieved the rail from the water, flew off to an emergent bush, and ate the rail. On 30 December, 25 min before a similar high tide, Evens and two other observers saw a