Management Options for Preserving Genetic Diversity: Reintroduction of Guam Rails to the Wild

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Abstract: *Population management programs recognize the importance of managing genetic diversity in species that are candidates for eventual reintroduction to natural habitats. The planned 1989 release of captive-born Guam rails (*Rallus owstoni*), extinct in the wild since 1986, to the Northern Mariana island of Rota provides an opportunity to evaluate various management options for selecting breeders to produce young rails for release. Six options were compared to determine which one best replicated genetic diversity in the original captive founder population. Heterozygosity, allelic diversity, founder contribution, and founder genome equivalents were used as indicators of genetic diversity.*

Option 1: Randomly choose adults for breeding.
Option 2: Choose the most fecund captive breeders.
Option 3: Use allozyme data to choose parents that will produce the most genetically diverse chicks.
Option 4: Choose pairs to equalize founder contribution in the population.
Option 5: Choose pairs to maximize allelic diversity.

Resumen: *Los programas del manejo de las poblaciones reconocen la importancia de manejar la diversidad genética de las especies que son candidatos para la eventual reintroducción a los hábitats naturales. El caso de la reintroducción de Ralidos Guam (extintos en su hábitat original desde 1986) nacidos en cautiverio, planeada para 1989 en la isla de Rota (una isla Mariana Norteña), ofrece una oportunidad para evaluar varias opciones de manejo en la selección de las granjas que producirán los jóvenes rálidos que serán reintroducidos. Se compararon seis opciones para determinar cuál era la que replicaba mejor la diversidad genética de la población cautiva original (pie de cria). Como indicadores de diversidad genética se utilizaron la heterocigosis, la diversidad alélica, la contribución del pie de cría, y los equivalentes del genoma del pie de cría.*

Opción 1: Se escogieron adultos al azar, para que se reprodujeran.
Opción 2: Se escogieron los reproductores cautovis más fecundos.
Opción 3: Se usaron datos de alo-enzimas para escoger a los padres que producirían los pollos con más diversidad genética.
Opción 4: Se escogieron pares que igualaran la contribución de los fundadores en la población.
Opción 5: Se escogieron pares que maximizaran la diversidad alélica.

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Option 6: Choose pairs to maximize founder genome equivalents.

Genetic management options based on pedigree analysis (#4, 5, 6) produced the most genetically diverse release populations for Rota. Managing founder genome equivalents produced a balance between equalizing founder contribution and maximizing allelic diversity, and provided the most genetically diverse population. Randomly selecting breeding pairs, choosing the best captive breeding stock, or managing by allozyme data resulted in substantially reduced genetic diversity. Results illustrate that some of the most common approaches to population management or population reintroduction may produce significant loss of genetic diversity, whereas certain genetic management options may actually increase genetic diversity over current population levels.

Opción 6: Se escogieron pares para maximizar los equivalentes del genoma de los fundadores.

Las opciones de manejo genético basadas en el análisis de pedigrí (#4, 5, 6) produjeron la población con mayor diversidad genética para liberación en Rota. El manejo de equivalentes del genoma de los fundadores produjo un balance entre la igualdad de la contribución de los fundadores y la maximización de la diversidad alélica, y produjo la población con la mayor diversidad genética. La selección al azar de parejas para la reproducción, la selección del mejor reproductor en cautiverio, o el manejo por datos de aloenzimas, resultaron en una substancial reducción de diversidad genética. Los resultados ilustran que algunos de los criterios más comunes para el manejo o la reintroducción de las poblaciones pueden producir una pérdida significativa de diversidad genética, mientras que ciertas opciones de manejo pueden inclusive incrementar la diversidad genética arriba de los niveles actuales de población.

Introduction

Population stability is addressed by examining factors such as random genetic drift, effective population size, and rates of genotypic and phenotypic change (Wright 1951; Lewontin 1974; and others). These topics have now taken on particular importance with the realization that species' extinction rates are growing at an alarming rate (Soulé 1983). We are becoming increasingly proficient at quantifying genetic diversity in natural populations using field studies of marked individuals (e.g., Wolff et al. 1988), protein electrophoresis (e.g., Haig & Oring 1988), and more advanced molecular techniques such as mitochondrial DNA (e.g., Shields & Wilson 1987) or DNA fingerprinting (e.g., Wetton et al. 1987). The new challenge, however, is to determine how to preserve genetic diversity in populations or species that have suffered a severe decline (Lacy 1987; Lande & Barrowclough 1987).

Management of endangered species' gene pools requires knowledge of life history characters and demography, measurement of genetic diversity in the current population(s), an understanding of genetic relationships among individuals in the population, and quantifiable future population management goals. Individuals are then managed so that genetic diversity is retained (Foose & Ballou 1988), inbreeding is kept to a minimum (Wright 1921; Ralls et al. 1988), and adaptation to captivity is minimized (Seal 1977).

While these guidelines are not new, their effective implementation is not always obvious. Clearly, no one measure of genetic diversity will provide all the necessary information, yet multiple measures of genetic diversity often provide conflicting messages to population managers. For example, management for maximum heterozygosity improves the probability of a species surviving selection immediately following a population bottleneck (Allendorf 1986; Quattro & Vrijenhoek

1989). However, such a management scheme can result in loss of rare alleles, and thereby reduce potential fitness of the population in later years (Fuerst & Maruyama 1986). Although the effect of selection in captivity is usually considered to be relaxed (or at least different) compared to natural populations (Frankham et al. 1986), concerns about the long-term effect of selection in the captive environment are warranted (Flesness & Cronquist-Jones 1987). Neither long-term effects of selection nor loss of genetic variability due to drift has been adequately modeled for conservation of captive or wild populations (Simberloff 1988).

Conservation biologists must continue their efforts to resolve these issues. In the meantime, decisions must be made. Generalized population management guidelines do not resolve specific population issues and a multitude of factors must be taken into consideration. In this paper, we examined effects of various population management options on retention of genetic diversity in a small population. These options were evaluated in order to develop a specific strategy for the 1989 reintroduction of Guam Rails (*Rallus owstoni*) to the wild.

Guam's Avifauna

The Pacific island of Guam (Fig. 1) has been subjected to typhoons, bombings, introduction of feral animals, and human development efforts, yet its avifauna were not severely affected until introduction of the brown tree snake (*Boiga irregularis*) in the 1940s (Savidge 1987). Of Guam's 11 native forest birds extant at the time of the snake's introduction, seven are now extinct and four survive in extremely reduced numbers (R. E. Beck, personal communication; U.S. Fish and Wildlife Service, 1984a,b).

Guam Rails

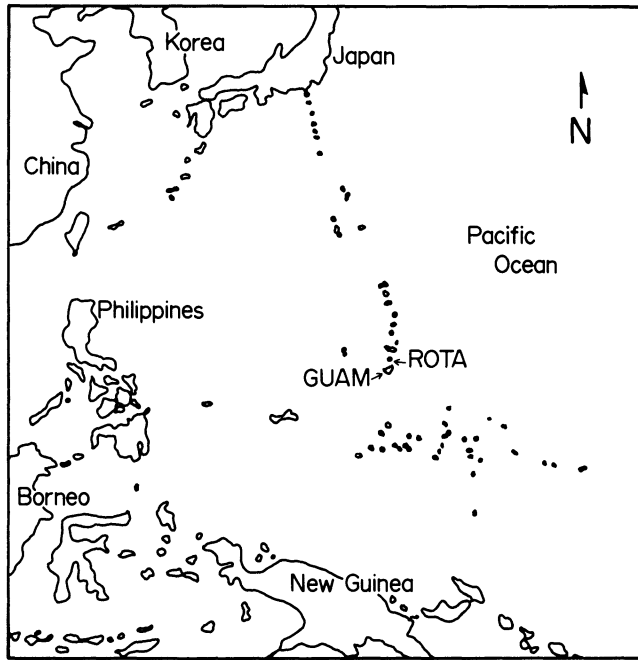The Guam Rail is an aggressive, ground-nesting, flightless rail endemic to Guam (Ripley 1977). They are om-

Figure 1. Locations of the Northern Mariana islands of Guam and Rota in the western Pacific Ocean and Philippine Sea.

nivorous feeders that were widely distributed in all but wetland habitats (Perez 1968; Jenkins 1979). These rails are monogamous, form long-term pair bonds, are highly territorial, and breed throughout the year (Jenkins 1979; Beck & Savidge 1985). Average clutch size ranges from one to five eggs and a single pair can raise up to five broods per year in captivity. Males and females reach sexual maturity at 5–6 months of age. During the 1960s, numbers of Guam Rails reached an estimated 80,000 individuals. By 1983, however, the rail had disappeared from southern and central Guam and fewer than 100 individuals remained in the northern portions of the island (Engbring & Pratt 1985). The last wild Guam Rail was seen in September 1986.

Rails were brought into captivity on Guam in 1983 and were subsequently brought to U.S. zoos in 1984. Initially, 21 birds were brought into captivity and are considered to be *founders* for the captive population. As of May 1989, 113 rails were being maintained in captivity (Table 1). A complete Guam Rail pedigree has been constructed of offspring resulting from captive founders (Derrickson 1989). The pedigree is shallow, since only three generations have reproduced, and two families are inbred (i.e., consist of sibling matings).

Guam Rail Reintroduction

Now that the captive population is well established, plans are under way to introduce Guam Rails to the nearby island of Rota (Fig. 1) (U.S. Fish and Wildlife

Service 1988). The brown tree snake has not declined on Guam, thus preventing any avian reintroductions to the island. Environmental conditions on Rota are quite similar to those on Guam, except that the snake is absent, as are other rail species. Plans currently exist to introduce 90 captive-bred rails per year. The first population size was determined to be 90 because it is the largest number of birds that could be realistically produced for reintroduction in a short period of time.

A number of factors need to be considered in selecting the animals to be released (Griffith et al. 1989): behavioral, demographic, genetic, logistical constraints, and physical condition of each animal. Here we examine only genetic criteria for selecting release birds and specifically address the need to maximize genetic diversity. Genetic diversity may be important for maintaining individual fitness of individuals (Allendorf & Leary 1986) and for providing the introduced population with genetic variance required for adaptation (Hedrick et al. 1986). This may be especially critical since Guam rails will have gone through two major founding events (i.e., bottlenecks) in just five years. The first bottleneck occurred when birds were brought into captivity, and the second will occur with the reintroduction.

Six reintroduction strategies were examined. Each was used to choose captive breeding pairs that will produce 90 chicks to be introduced to Rota as adults. Each strategy was evaluated in terms of how well it maintained genetic diversity in the introduced population.

Methods

Reintroduction Options

OPTION 1: RANDOM SELECTION (RANDOM)

We began by examining an unbiased scenario that indicates lack of selection and sets a baseline for comparison among other options. To evaluate the effect of randomly selecting offspring for the reintroduction program, 100 sets of 90 offspring were randomly generated from the Guam Rail pedigree. Each set was derived by randomly selecting 30 clutches of three eggs per clutch to be produced by the current breeding population of 48 males and 53 females. To realistically model annual productivity, randomly selected pairs were limited to producing a maximum of four clutches. Results were calculated by averaging across all 100 random sets.

OPTION 2: SELECTION FOR REPRODUCTIVE FITNESS (FITNESS)

The most readily available animals for reintroduction from captive breeding programs are usually offspring from the most fecund pairs. Individual fecundity was chosen to examine effects of fitness selection on maintaining genetic diversity for the Rota population. To de-

termine the most "fit" individuals to produce 90 chicks in one year, we assumed Guam Rails were perennially monogamous (i.e., did not switch mates) and chose the birds that (1) had formed pair bonds in the past (some hand-reared adults have not formed pair bonds in captivity); (2) had produced two or more broods; and (3) had produced the most chicks. To further tighten the criteria, we assumed (based on their life history information) that a pair could produce four broods of three chicks in a year; hence, we would only need eight pairs to produce 90 offspring.

OPTION 3: MAXIMIZE ALLOZYME VARIABILITY (ALLOZYME)

Allozyme variability provides an empirical estimate of individual and population genetic variability. However, using allozyme data to manage captive populations remains controversial because it only samples a small portion of the bird's genome and frequently reveals only low levels of variability (e.g., compare Hedrick et al. 1986 with Wayne et al. 1986). Unfortunately, few studies have had both appropriate pedigrees and matching electrophoretic data to test opposing hypotheses. Since we do have both data sets, we evaluated the effects of using electrophoretic variability to choose individuals to maximize genetic diversity (i.e., allelic diversity and heterozygosity).

Blood samples (n = 112) were collected for protein electrophoresis from all living Guam Rails from 1987 to 1989. Horizontal starch-gel electrophoresis was performed at the Cornell Laboratory for Ecological and Evolutionary Genetis (CLEEG). Initial screening of 28 enzyme systems resulted in 21 enzymes that were sufficiently clear for inclusion in the study. Of 23 presumptive loci resolved, four were polymorphic (i.e., frequency of the most common allele did not exceed 0.99): glucosephosphate isomerase, lactate dehydrogenase, malate dehydrogenase, and phosphoglucomutase. Further details of electrophoresis are outlined in Haig et al. (in prep.). Genotypes of parents and offspring were matched for all polymorphic loci. Using individual genotypes from polymorphic electrophoretic loci, pairs were chosen that would produce offspring with equal allele frequencies of polymorphic loci and maximum heterozygosity within loci.

OPTION 4: EQUALIZE FOUNDER CONTRIBUTION (EFC)

One recommended method for genetically managing populations is to equalize distribution of each founder's genetic contribution to the living population's gene pool (equalize founder contribution, Foose 1983). Often, due to disproportionate reproduction, most of the population's gene pool has descended from only a small percentage of founders. Under the EFC strategy, managers attempt to retain genetic diversity in the population by establishing pairs that compensate for this dispropor-

tionate representation. Similarly, we created pairings that equalize the genetic contribution of the extant founders in the 90 offspring to be released.

OPTION 5: MAXIMIZE ALLELIC DIVERSITY (MAXA)

Equalizing founder contribution ignores loss of alleles due to genetic drift. When a pair of founders produces only one offspring, only 50 percent of their genetic diversity is passed to future generations: only two of their possible four alleles (see "gene drop methodology" and Fig. 2) survive. Therefore, an alternative to the EFC strategy is to maximize allelic diversity by establishing pairings that maximize survival of founder alleles in the population. This strategy maximizes retention of allele numbers in the population without regard to their distribution. We chose pairs that maximize number of alleles present in the 90 reintroduced offspring. This was accomplished considering that to be 99.6 percent certain that all four founder alleles present in parents will be passed to their offspring, each pair must produce ten chicks (Ballou 1984).

OPTION 6: MAXIMIZE FOUNDER GENOME EQUIVALENTS (FGE)

Founder genome equivalents corrects for unequal founder contribution as well as loss of founder alleles due to genetic drift, rendering it a combination of the EFC and MAXA strategies. It is calculated from:

$$FGE = \frac{1}{\Sigma(p_i^2/r_i)}$$

where p_i is the proportion of the population's gene pool contributed by founder i and r_i is the expected proportion of founder i's alleles surviving in the population (Lacy 1989). FGE combines both founder contribution and allele survival by weighting a founder's contribution to the population by the proportion of its alleles that survive in the population. It is at a maximum when no alleles have been lost due to genetic drift and all founders are equally represented. It decreases if alleles are lost or founder contribution becomes disproportional. Pairings were chosen to produce chicks that would result in the maximum number of founder genome equivalents in the Rota population.

Gene Drop Analysis

For each of the aforementioned options, a gene drop pedigree analysis technique was used to measure genetic diversity in the 90 resultant offspring relative to allelic diversity of the founders. Gene drop analyses track movement of alleles through a known pedigree, such as we have for Guam Rails (Fig. 2, MacCluer et al. 1986; Mace 1986). The technique assumes that each run of the gene drop is independent from others, hence
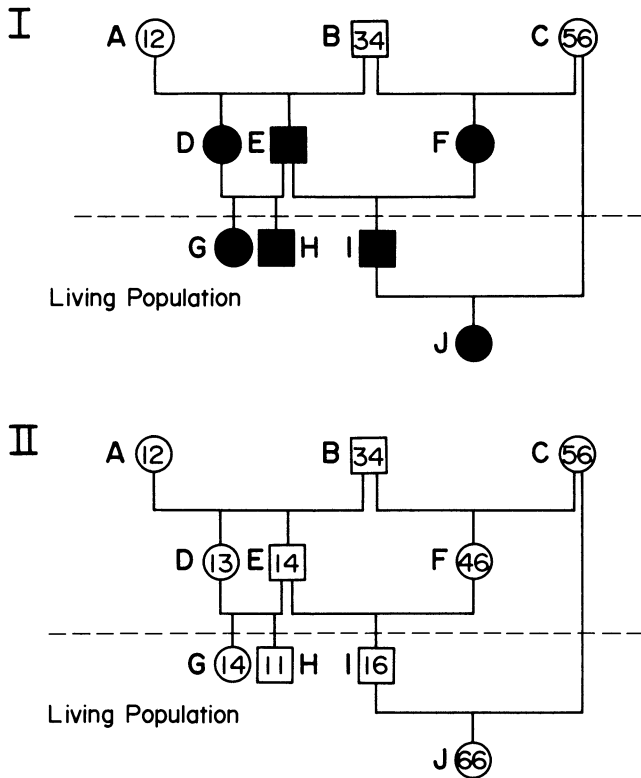
Figure 2. Use of gene drop pedigree analyses. I. In this sample pedigree, the three founders (A, B, C) have been given six unique alleles (# 1–6). II. The gene drop then randomly passes founder alleles through the pedigree from parents to offspring. After one simulation, birds H and J are homozygous, whereas others in the living population (birds G and I) are heterozygous (hence percent heterozygosity retained = 2/4 = 50 percent). In this living population, three unique alleles (# 1, 4, 6) have survived and all three founders are represented. Since some alleles have been lost (# 2, 3, 5) founder contribution is variable (e.g., p_i for founder A = 4/8 alleles = .50, p_i for founder B = 1/8 alleles = .125, and p_i for founder C = 3/8 = .375). To calculate r_is for this pedigree: consider that allele 1 from founder A made it to the living population, but allele 2 did not, hence r_i = 1/2 = .50. Likewise for founder B: allele 4 existed in the living population but allele 3 did not, hence r_i = 1/2 = .50. For founder C, allele 6 survived, but allele 5 did not, hence r_i = 1/2 = 50. This simulation would then be repeated 10,000 times to get statistical estimates of the parameters we examined.

linkage is ignored. Furthermore, the gene drop does not incorporate selection.

To begin, each founder is assigned two unique alleles. These alleles are then passed randomly through the pedigree from parent to offspring, following rules of Mendelian segregation. At the end of each simulation, every individual in the pedigree has a genotype. Frequency, correlation, and distribution of founder alleles in the individuals of interest (here the 90 offspring destined for introduction) are recorded and the simulation repeated. Unless otherwise noted, we repeated this Monte Carlo simulation 10,000 times for each option addressed. This simulated sampling one locus 10,000 times or an individual's entire genome (10,000 loci) once. The final result from multiple simulations is the proportion of simulations in which particular founder alleles are present or absent in the 90 offspring of interest. Thus, the gene drop generates a distribution of identity by descent probabilities for each individual and provides quantification of differences in genetic diversity among various reintroduction options.

Evaluation Criteria

Six criteria were chosen to evaluate genetic consequences of options for the introduced Rota population. (1) *Heterozygosity* is the proportion of heterozygosity retained in the Rota population relative to heterozygosity in captive founders. Since it is a relative measure, it is independent of the actual level of heterozygosity in the founders. (2) *Allelic diversity* is the number of unique founder alleles represented in the Rota population. Since there were only 21 founders, a maximum of 42 unique alleles can be present in the 90 offspring. The estimated number of unique alleles was based on an average of 10,000 simulations for all options but the RANDOM selection option, which was based on an average of 100 simulations averaged over the 100 randomly generated pedigrees. (3) *Founder equivalents* of a population is that number of equally contributing founders that would be expected to produce the same genetic diversity as the population to be examined (in this case, the 90 offspring chosen for each reintroduction option; Lacy 1989). It is calculated from:

$$FE = \frac{1}{\Sigma(p_i^2)}$$

where p_i is the proportion of the population's gene pool descended from founder *i* (Lacy 1989). FE is equal to the number of founders when they contribute equally to the gene pool and decreases as their contribution becomes more disproportionate. The p_is were calculated by determining the genetic contribution of each founder to each individual's genome assuming Mendelian laws of segregation using the additive relationship algorithm (Ballou 1983). Founders' genetic contributions to the total gene pool were then calculated by averaging across all offspring to be released. (4) *Founder genome equivalents* in our situation is that number of equally contributing founders that would be expected to produce the same genetic diversity as in the population resulting from each reintroduction option. (5) *Number*

of founders whose genes are represented in the Rota population was examined. (6) *Number of pairs* needed to produce the desired population was also considered as a practical aspect of option evaluation because not all males and females are sexually compatible and because shipping birds between facilities to form pairs can be hazardous. Therefore, options that require numerous shipments might need to be reconsidered.

Results

Heterozygosity

The percentage of heterozygosity retained in a population is a measure of the relative amount of heterozygosity that has been lost, regardless of the (true) original levels of heterozygosity in the founders. Overall, retained heterozygosity in the various options varied only slightly from the founding population. Heterozygosity in the current captive population has only declined by 0.2 percent. Choice of the RANDOM option results in the lowest heterozygosity, while FITNESS and EFC options yielded levels of heterozygosity similar to the current population. Choice of ALLOZYME, MAXA, or FGE options results in increased heterozygosity over current population levels.

Allelic Diversity

The number of unique alleles surviving in the current population represents a 25 percent loss of alleles from the initial captive founders. Among reintroduction options, the ALLOZYME option yielded the lowest number of unique alleles surviving (55 percent loss from the initial population), while genetic management options (EFC, MAXA, FGE) yielded the highest number of alleles surviving: 35.2 percent loss from the initial population for EFC, 30.5 percent for FGE, and 30.2 percent loss for MAXA. The Guam rail pedigree has two inbred families, hence it was impossible to increase the number of unique alleles surviving in the MAXA option to at least equal the current number of unique alleles.

Founder Contribution, Founder Equivalents, and Founders Represented

Figure 3 compares founder contribution in the current population with reintroduction options. Founder contribution is evaluated by examining the number of founders whose genes would be represented in the Rota population and the evenness of the distribution of each founder's contribution to the population. The current population has already lost the contribution of five founders (Founder #8, 10, 32, 33, and 36), and founder contribution is highly variable. The ALLOZYME and FITNESS options resulted in the greatest loss of founders (n = 9)

and had the highest variance in founder contribution (i.e., the lowest founder equivalents). Genetic management options (EFC, FGE, and MAXA) resulted in the least variable founder contribution and incorporated the greatest number of founders (n = 15). Founder #2 is underrepresented in the pedigree because it is closely linked to the highly inbred families. For Founder #2 to have both alleles represented for the MAXA option, we had to increase the number of offspring produced from birds with Founder #2s alleles. This prevented a more even founder contribution for the MAXA option. The EFC option represents the least variable founder contribution, hence the highest founder equivalent.

Founder Genome Equivalents

Attempts to maximize founder genome equivalents closely resembled results of founder equivalents. RANDOM, FITNESS, and ALLOZYME options yielded the lowest number of founder genome equivalents and resulted in lower founder genome equivalents than the current captive population. Genetic management options (EFC, MAXA, and FGE) represented a 22–27 percent increase in founder genome equivalents over the current population. Furthermore, the current population experienced a 50 percent loss in founder genome equivalents from the original 21 founders; genetic management options, however, resulted in only a 31–36 percent loss.

Number of Pairs

The number of pairs needed to produce the various reintroduction options varied from 8 to 23 and did not represent prohibitive logistical constraints in setting up pairs. Furthermore, the number of pairs used was not correlated with genetic diversity: both RANDOM and MAXA options required 23 pairs, yet they differed greatly among all measures of genetic diversity examined.

Discussion

Consequences of Reintroduction Options

From our randomly generated pair choices (RANDOM), we determined that the resulting Rota population would have low heterozygosity relative to other options, a severe loss in the number of unique alleles from the original captive population, and variable founder contribution. Although this option is unrealistic, it was used as a baseline for comparison among other options. It might also be one method of constructing populations with high genetic diversity: if enough random populations were generated, eventually an optimal population might be created. However, 100 random pedigrees were clearly an insufficient number to generate a pedigree
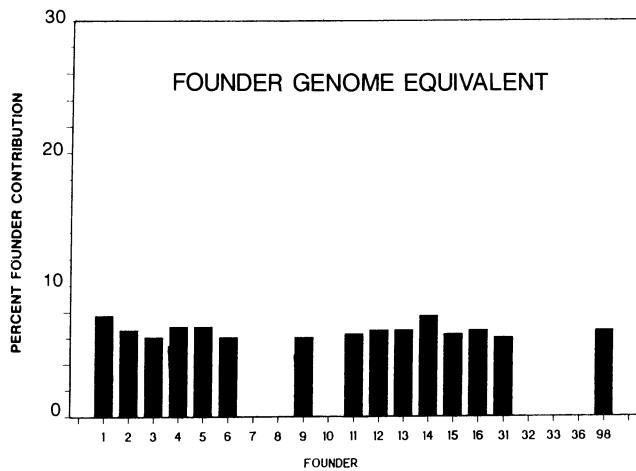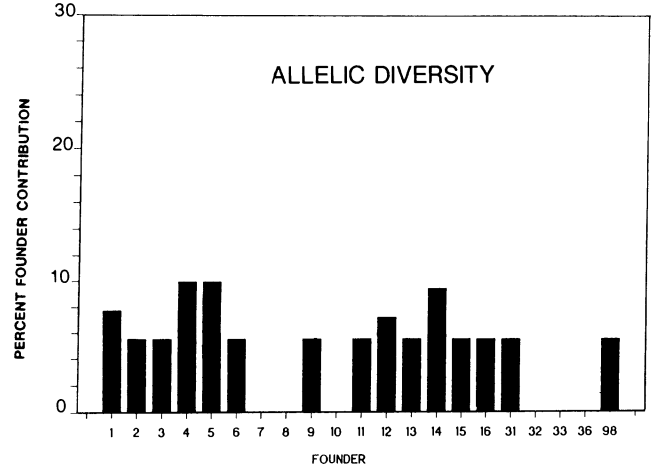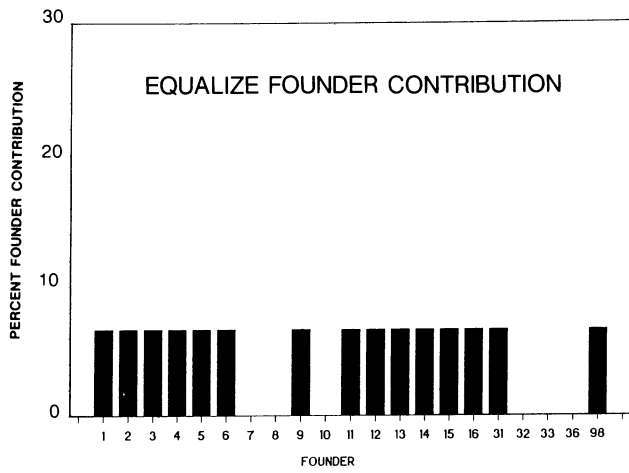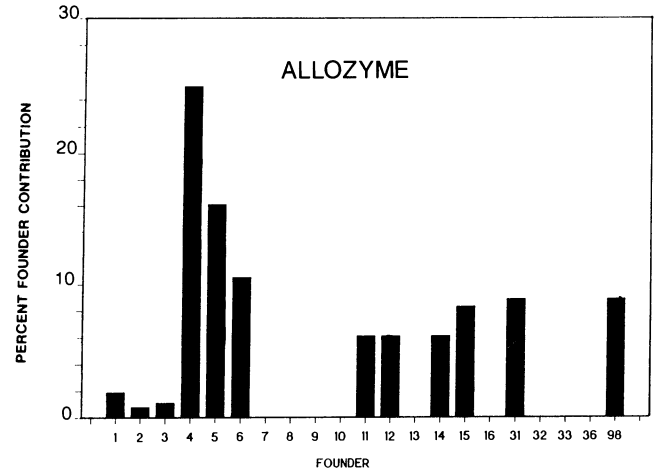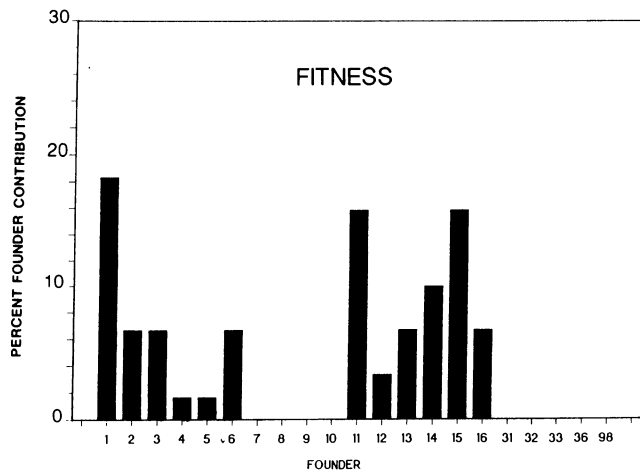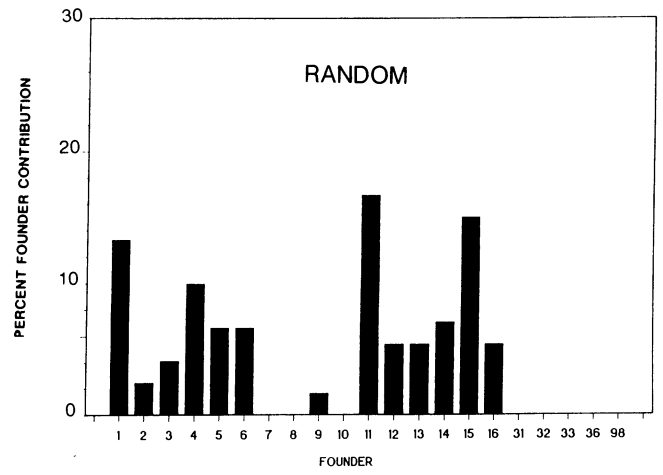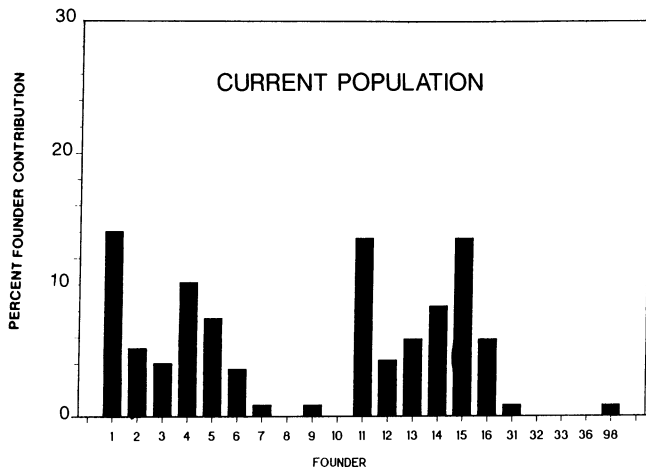
Figure 3. Founder contribution of the current captive Guam rail population compared with different reintroduction options. Founder number indicates unique numbers given to founding captive Guam rails.

nearly as efficient at maintaining genetic diversity as those derived by considering genetic criteria. Founder genome equivalents from the FGE pedigree, for example, were six standard deviations above the mean derived from random pedigrees. Overall, this option is not appropriate due to the resulting loss of genetic diversity.

The ALLOZYME option resulted in the lowest genetic diversity among all criteria tested with the exception of heterozygosity. Low diversity may be partially due to one family in the pedigree containing the vast majority of allozyme allelic variability. To capture this variability, these family members would be bred more often than others in the pedigree. Without pedigree information indicating degrees of relatedness, it might be tempting to breed these "variable" individuals. With pedigree data we would know not to create sibling pairings.

Wayne et al. (1986) recommend that management programs use electrophoretic analyses to identify individuals for breeding. Results presented here indicate that data from electrophoretic analyses are inappropriate for selecting breeding pairs to retain genetic diversity. Protein electrophoresis yields so few polymorphic loci in birds that it is a poor indicator of individual levels of heterozygosity. Furthermore, selection of individuals based on rare allozyme alleles may result in increased homozygosity in alleles at other loci that could, for instance, adversely affect fecundity or fertility (Hedrick et al. 1986). Since rare alleles are especially susceptible to loss during a bottleneck (Guam Rails will undergo two severe bottlenecks in five years) and because they have minimal effect on overall heterozygosity (Allendorf 1986), managing for rare electrophoretic alleles is inappropriate. The best use of allozyme data in population management is in determining overall levels of population heterozygosity rather than as a tool to choose particular individuals for genetic management. In all cases, it should be matched with complementary information such as pedigree, morphological or more specific molecular (e.g., DNA fingerprinting) data.

Selection of individuals based on previous reproductive success (FITNESS) might make intuitive sense because offspring from the best breeders would be represented in the release population. Genetically, however, the Rota population would suffer a great loss of unique alleles and founder representation. The most successful breeders represent only a few of the founder lineages and excluding less successful breeders eliminates the genetic diversity of many founders. Overall, genetic diversity is decreased. There is also concern over the effect that selection for adaptation to a captive environment might have on an individual's ability to survive in the wild (Frankham et al. 1986; Flesness & Cronquist-Jones 1987; Mace, in press). Natural selection in a captive environment is probably significantly less than it would be in a more natural environment. However, "unconscious" selection for tameness, ease of handling,

and low aggression is common in captive populations. Selecting those individuals proven best suited to captivity for reintroduction may result in releasing those birds that are less well suited for a more natural environment. The impact of selection in captivity on reintroduction is poorly understood and clearly needs further research.

While genetic management options produced the most genetically variable populations, as expected, selecting the best option among the three choices remains problematic. Maximizing allelic diversity (MAXA) is initially appealing because it maximizes the number of alleles in the Rota population. This allelic diversity may provide Rota birds with the flexibility to adapt to a new environment. Maximizing allelic diversity can only be achieved, however, by reducing some founders' genes in preference to others, causing unequal founder contribution. This results in a greater loss of founder representation than either the EFC or FGE options. This loss in genetic diversity again reflects the problem of managing rare alleles without regard to their distribution. In this case, both alleles of a founder may be present, but only occur once among the Rota birds, whereas other individuals may have many copies of founder alleles present.

Numerous authors addressing population management strategies have promoted the need to equalize the contribution of original founders in subsequent populations or reintroductions (Chesser et al. 1980; Foose 1983; Foose et al. 1986; Lacy 1989; and others). By equalizing founder contribution, variance in genetic diversity decreases, thus maximizing genetic diversity. In many populations, equalization of founder contribution may not be possible due to specific characteristics of the pedigrees. However, we were able to equalize founder contribution in Guam Rails, largely because the pedigree is not too deep. In several cases we were forced to select related individuals as mates to increase the founder contribution of specific founders. In the process 2.1 alleles were lost: breeding individuals who carried these genes would have resulted in the genetic overrepresentation of one or more founders. Thus, EFC or MAXA strategies either maximize the number of alleles present or equalize founder contribution, but not both.

Maximizing founder genome equivalents attempts to mitigate this problem by taking both founder contribution and number of alleles into consideration. FGE combines EFC and MAXA so that although founder contribution is more variable than that obtained under the EFC strategy and the number of alleles is less than with the MAXA strategy, it does result in the maximum number of founder genome equivalents. FGE not only maximizes genetic diversity according to our criteria, but describes the genetic base of the Rota population as a genetically equivalent number of equally represented founders if no alleles have been lost by drift (Lacy 1989). While our FGE option results in less than the 20 founder genome

equivalents suggested by Lacy to ensure adequate genetic variability in the long-term, it is almost a 50 percent increase in founder genome equivalents over the current captive population.

Finally, genetic recommendations proposed in this paper are made with the understanding that reintroductions are a learning process and frequently do not succeed with the first release of animals. We determined that the FGE option was the most appropriate strategy for reintroduction of Guam Rails, but will not try to maximize founder genome equivalents with the first release of birds on Rota. Rather, a few birds will be released at a time until their survival is assured and reintroduction techniques are perfected. We will then try to maximize founder genome equivalents with subsequent releases so that our goal will be achieved over the period of one Guam Rail generation length. As in any reintroduction, details of the releases will depend on a variety of biological, political, and logistical factors.

Summary

These analyses used concepts from theoretical population biology to evaluate genetic differences in population management strategies and assist in designing a Guam Rail reintroduction into the wild. They illustrate the following points: first, in small populations, genetic diversity can be lost in a short period of time. The effect of Guam Rails undergoing two major bottlenecks in just five years, as with other species experiencing bottlenecks (Temple & Cade 1988), will not occur without genetic consequence. Therefore, even with the best management, the new population on Rota will suffer a 30 percent loss of alleles from the captive founding population. Furthermore, we have shown the importance of single individuals to small populations. If even one living Guam Rail does not breed, we risk losing the contribution of one founder.

Speed of reintroduction and decreasing the time birds spend in captivity may be important for successful establishment of wild Guam Rails. Since Guam Rails are aggressive, zoos may be tempted to impose unconscious artificial selection on their captive situation by breeding less aggressive birds. This selection reduces overall genetic diversity and introduces potentially deleterious traits in the new wild birds that might seriously affect fitness traits necessary for survival in the wild.

Comparisons made among six reintroduction options should prove valuable both for selecting animals for reintroduction programs and for developing genetic management strategies in captive and wild populations. Selection criteria that rely solely on past reproductive performance, allozyme variation from electrophoretic studies, or random selection are likely to result in significant reduction of genetic variation. Detailed analyses
of pedigrees are required to identify specific individuals that need to be bred to maintain extant genetic diversity.

Acknowledgments

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