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INTRASPECIFIC VARIATION IN EGG SHAPE AMONG INDIVIDUAL EMPEROR GEESE

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Abstract.—Within-clutch variability in shape of 1743 eggs from 301 nests of Emperor Geese (*Chen canagicus*) laid over a 5-yr period was measured. Individual females laid similar shaped eggs in successive years, and eggs among clutches within females could not be distinguished. Cluster analysis correctly identified 69.9% of 136 known conspecific parasitic eggs. Repeatability estimates of elongation (0.73), sphericity (0.72), maximum width (0.69) and radius of the point (0.68) were high and similar to repeatability estimates of egg mass and volume of other species. Although width, volume and area measurements varied inversely with spring population size, shape variables did not. The consistency in shape variables despite changes in egg size suggests that shape variables may be used to separate and identify individuals within and among years despite changes in the population that may result in changes in egg size. Differences in egg shape among eggs within a nest are viable criteria for identifying parasitic eggs, especially when used in conjunction with other methods.

VARIACIÓN INTRAESPECÍFICA EN LA FORMA DE LOS HUEVOS DE *CHEN CANAGICUS*

Sinopsis.—Por 5 años se midieron 1743 huevos pertenecientes a 301 nidos de Ganzo Emperador (*Chan canagicus*) para tratar de determinar variación en la forma de éstos dentro de la camada. Hembras particulares pusieron huevos de similar tamaño en años sucesivos, y no se pudo distinguir entre huevos de las mismas hembras. Mediante análisis de agrupación, se pudo identificar correctamente el 69.9% de 136 puestos por hembras parasíticas. Estimados de repetición de elongación (0.73), esferidad (0.72), ancho máximo (0.69) y radio del punto (0.68) resultaron altos y similares a estimados de repetición de masa de huevos y volumen de otras especies. Aunque el ancho, volumen y medidas de área variaron inversamente con el tamaño de la población primaveral, no se encontró lo mismo para variables de tamaño. La consistencia en variables de tamaño (a pesar de los cambios en el tamaño de los huevos que puede haber) sugiere que las variables en tamaño pueden ser utilizadas para separar e identificar individuos, en un año particular o a través de los años. Las diferencias en tamaño entre huevos de un mismo nido, puede ser utilizadas como un buen criterio para identificar huevos de hembras parasíticas, especialmente cuando se utilice este criterio en unión a otros métodos.

Individuals of some species of wild birds lay eggs that vary in color, marking pattern, weight and shape (e.g., Boag and van Noordwijk 1987, Koskimies 1957, Lessells et al. 1989, Thomas et al. 1989). Repeatability of egg volume or mass among individuals is also high in some species (e.g., Leblanc 1989, Lessells et al. 1989, Ojanen et al. 1979, Prince et al. 1970, van Noordwijk et al. 1981, but see Duncan 1987). As a result of high variability and repeatability among females, it may be possible to identify eggs laid in nests by other females (intraspecific parasitic egg laying) (e.g., Freeman 1988, Thomas et al. 1989, Yom-Tov 1980). For species laying eggs without marking patterns and little differences in color (e.g., many waterfowl [Johnstone 1970]), identification of parasitic eggs is difficult. Differentiation of such eggs depends on the subjective observational skills of the observer, thus a method to quantify differences in egg shape is needed.

Here I quantify egg size and shape among Emperor Geese (*Chen canagicus*) and search for patterns of variation to test the following predictions. (1) If egg shapes are repeatable, then eggs laid by females in successive years are indistinguishable among years. (2) If females consistently lay similar shaped eggs, eggs of pairs of randomly selected females can be correctly identified as belonging to the females that laid the clutches. (3) If variation in egg shape is greater among than within females, then eggs known by other means to be parasitic can be separated from the host clutch by means of shape characteristics.

METHODS

Study species.—The Emperor Goose is a maritime goose that nests primarily in tundra habitats along the coastal fringe of the Yukon-Kuskokwim Delta, Alaska (Gabrielson and Lincoln 1959). Emperor Geese generally lay 4–6 eggs per clutch, with larger clutches attributed to eggs laid by additional females (Eisenhauer and Kirkpatrick 1977, Krechmar and Kondratiev 1982, Petersen 1992). Individual egg masses vary among clutches, and increased variability in individual egg mass with increased clutch size suggests undetected nest parasitism (Rohwer and Eisenhauer 1989).

Known parasitic eggs included (1) all eggs added to a nest after incubation began, (2) eggs laid outside a nest and then found in the nest, (3) eggs with viable embryos that were not completely developed after most eggs hatched and the brood had abandoned the nest, and (4) eggs laid by one marked female in a nest that were subsequently incubated by another female (e.g., MacWhirter 1989, Yom-Tov 1980 and citations therein).

Egg measurements.—During the 5-yr period 1982–1986, I photographed 1743 Emperor Goose eggs associated with 301 nests. Of those eggs, 241 were from 15 marked females with clutches from two or more years. Each year, I selected 35 or more clutches at random for photographing and attempted to photograph the eggs of all individually marked (neck-banded) females. All clutches were laid at the Kokechik Bay, Alaska, study area (Petersen 1990, 1992). Estimates of spring population size are from annual surveys conducted by C. P. Dau and R. J. King, U.S. Fish and Wildlife Service (pers. comm.). Median nest initiation dates and conditions on spring staging areas are from Petersen (1992), and spring nesting conditions from Petersen (1990).

Eggs were photographed on a grid with reference points known to the nearest 0.05 mm. Photographs of each egg were printed on 12.7 × 17.8 cm paper to the approximate size of the egg. Each photo was digitized and points recorded in a manner similar to that described by Mänd et

TABLE 1. Variables used in comparison of shape characteristics.

Variable	Formula[1]	Source[2]
Sphericity	(100•maxwidth)/length	1
Ovoidness	(length − l_i)/l_i	1
Pearshape	100•(b_i − b_k)/b_i	1
Plumpness	(400•V)/(pi•length•maxwidth^2)	1
Conidity	100•(b_i − b_k)/maxwidth	1
Blunt convex	(2•b_i/maxwidth) − 1	1
Point convex	(2•b_k/maxwidth) − 1	1
Radius blunt (R_b)	ax^2/bx•(1 + c_1 + c_2)^2	2
Radius point (R_p)	ax^2/bx•(1 − c_1 + c_2)^2	2
Elongation	length/maxwidth	2
Asymmetry	(R_b − R_p)•length/maxwidth^2	2
Bicone	[(R_b + R_p)•length/maxwidth^2] − 1	2
Volume c_2	4/3•midwidth/2* sectarea	3
Volume c_2 integral	4/3•pi•ax^2•bx(1 + 0.4•c_2)	3
Volume ellipse max	(pi/6)length•maxwidth^2	3
Volume ellipse mid	(pi/6)length•midwidth^2	3
Konstant (k)	V/(length•maxwidth^2)	3
Volume (V)	k•length•maxwidth^2	3

[1] ax = semidiameter at the true equator; bx = half-length of the egg (Preston 1974); b_i = width at the half-distance from maximum width line to blunt end; b_k = width at the half-distance from the maximum width line to the pointed end; l_i = length from the maximum width line to blunt end; l_k = length from maximum width line to pointed end (Mänd et al. 1986); c_1 and c_2 are dimensionless constants that are particular to each individual egg (Preston 1953) and are "coefficients representing the departure of the oval from an ellipse" (Tatum 1975).

[2] 1 = Mänd et al. 1986; 2 = Preston 1968; 3 = Preston 1974.

al. (1986); however, I used an IBM-compatible digitizing tablet and Sigma-Scan (Acker and Mitchell 1988) software to generate x, y coordinates of each egg, and to store them in an ASCII file. Egg shape characteristics were calculated from the formulas in Preston (1968, 1974) and Mänd et al. (1986) (Table 1).

Statistical analysis.—I subjected shape characteristic values of each egg to principal component analysis to determine the variables best describing egg shape of the Emperor Goose. Cluster analysis tests of a subsample of 42 nests of marked females using the factors best describing variation in egg shape based on the principal component analysis produced similar results to tests using all variables. I therefore used the four components for all cluster analysis tests. I performed cluster analysis on shape variables of each egg in each clutch, among eggs in pairs of randomly selected clutches, and among eggs from two or more clutches of each marked female to identify mathematically eggs that were markedly different in shape. In paired comparisons and comparisons of clutches of marked females I excluded all previously known parasitic eggs. All variables were transformed to *z*-scores before analysis. Means and SE of all variables are from untransformed data. I used SPSS^x (SPSS 1988) software for all statistical tests. In the cluster analysis, I used squared Euclidean distances

TABLE 2. Summarization of measurement and shape variables of untransformed data for 1743 Emperor Goose eggs (see Table 1 for definitions).

Variable	Mean	SE	CV	Minimum	Maximum
Length, mm	86.74	0.08	3.89	69.14	97.15
ax, mm	28.36	0.02	3.07	23.53	39.58
l_i, mm	39.71	0.04	4.41	31.26	49.11
l_k, mm	47.03	0.05	4.81	37.88	53.77
Maximum width, mm	56.97	0.04	3.05	47.18	79.52
Mid-width, mm	56.72	0.04	3.07	47.06	79.16
bx, mm	43.37	0.04	3.89	34.57	48.57
b_i, mm	49.26	0.04	3.03	41.15	70.20
b_k, mm	47.53	0.04	3.17	40.09	67.99
c_1	−0.10	0.00	29.90	−0.21	0.08
c_2	−0.06	0.00	46.88	−0.17	0.06
Section area, mm^2	38.03	0.05	5.60	28.49	52.85
Surface area, mm^2	119.47	0.16	5.60	89.52	166.04
Sphericity	65.75	0.06	4.06	57.85	94.18
Ovoidness	1.19	0.00	5.06	0.88	1.45
Pearshape	3.52	0.03	31.43	−3.32	7.78
Conidity	3.05	0.02	31.59	−2.76	6.74
Blunt convex	0.73	0.00	1.78	0.66	0.77
Point convex	0.67	0.00	2.84	0.60	0.75
Plumpness	64.54	0.02	1.26	61.63	68.17
Volume, cc	142.93	0.28	8.20	89.28	280.55
Konstant	0.51	0.00	1.18	0.48	0.54
Volume eclipse max, cm^3	147.67	0.29	8.29	90.22	279.61
Volume eclipse mid, cm^3	146.36	0.29	8.29	89.75	277.02
Volume c_2, cm^3	143.98	0.28	8.22	89.39	278.90
Volume c_2 integral, cm^3	142.60	0.28	8.21	89.20	280.10
Radius blunt	19.82	0.04	9.02	11.04	46.73
Radius point	13.14	0.04	12.76	7.85	32.32
Elongation	1.52	0.00	4.00	1.06	1.73
Asymmetry	0.18	0.00	29.61	−0.14	0.37
Bicone	−0.12	0.00	46.67	−0.31	0.12

as resemblance coefficients and average linkage between groups as the clustering method (Romesburg 1984). I used differences of ≥ 3.0 between adjacent coefficients to identify clusters within clutches.

Repeatability estimates are from untransformed data and calculated following Lessells and Boag (1987), and standard error of each mean was calculated following Becker (1984). Some size and shape characteristics differed among years and repeatability estimates were calculated on data after subtracting means for all nests sampled in that year (van Noordwijk et al. 1981). Size and shape characteristics for each year are calculated from means of each nest and presented as mean ± SE.

RESULTS

Egg characteristics.—The greatest variance in measurements of eggs occurred primarily in length, surface area and volume variables (Table 2). The first component, which included area and volume variables, de-

TABLE 3. Principal component analysis of shape characteristics from transformations to z-scores of 1743 Emperor Goose eggs.

	Factor 1	Factor 2	Factor 3	Factor 4
Asymmetry	0.1743	−0.7187	0.6672	−0.0520
Bicone	−0.1953	0.5729	0.7643	0.2157
Blunt convex	−0.0756	0.1465	0.9697*	0.1484
Conidity	0.2181	−0.8245*	0.4995	−0.1025
Elongation	0.1382	−0.3060	0.0062	0.9380*
Konstant	−0.2402	0.7845	0.5264	0.2189
Ovoidness	0.1507	−0.6659	0.7077	−0.0293
Pearshape	0.2215	−0.8335*	0.4812	−0.1078
Plumpness	−0.2402	0.7845	0.5264	0.2189
Point convex	−0.2691	0.9264*	0.1579	0.2045
Radius point	−0.0429	0.9560*	0.0824	−0.2636
Radius blunt	0.2324	0.1849	0.8043*	−0.5073
Section area	0.9636*	0.1735	0.0128	0.1993
Sphericity	−0.1203	0.3099	0.0038	−0.9427*
Surface area	0.9636*	0.1735	0.0128	0.1993
Volume	0.9629*	0.2685	0.0234	−0.0379
Volume ellipse max	0.9857*	0.1430	−0.0565	−0.0674
Volume ellipse mid	0.9758*	0.1859	−0.0932	−0.0654
Volume c_2	0.9681*	0.2444	−0.0242	−0.0474
Volume c_2 integral	0.9594*	0.2789	0.0194	−0.0362
Percent of variation	35.2	31.2	21.0	12.1
Cumulative percent	35.2	66.4	87.3	99.4

* Key variables within each factor.

scribed 35.1% of the variation in egg shapes. The second component, which included variables describing point characteristics, plumpness and conidity, described an additional 30.4%. The third component, which included blunt characteristics, explained an additional 21.3%. The fourth component, which included length to width characteristics, explained the remainder of the variation (Table 3).

Comparison of random pairs.—When egg shapes from two random pairs

TABLE 4. Proportion of eggs correctly identified as most similar to eggs within its own clutch or another clutch from comparisons of 50 random pairs.

	Eggs identified from shape[1] as	
Closest egg type[2]	Similar (%)	Different (%)
None[3]	5 (1.2)	26 (22.0)
Same clutch	336 (77.8)	54 (45.8)
Different clutch	91 (21.1)	38 (32.2)

[1] Shape was generally similar or different from eggs within own clutch.

[2] Egg shape most closely resembled an egg within the same clutch (similar) or an egg of the other clutch (different) within the paired comparison.

[3] Eggs within a cluster containing a single egg that more closely resembled an egg from its same clutch or a different clutch in the adjacent cluster.

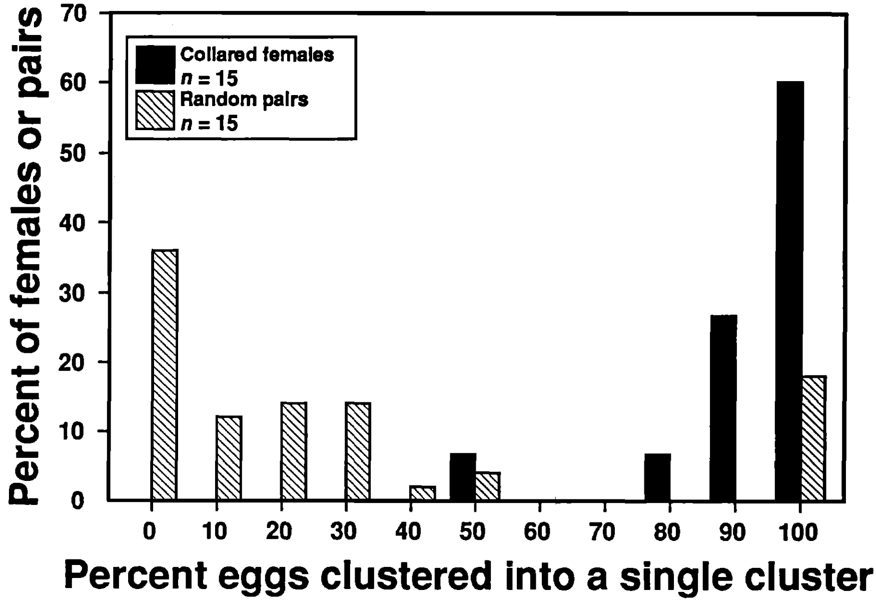

FIGURE 1. Percent of eggs clustered in the same group as all other eggs laid by that female (collared females) or clustered with eggs of the other clutch in paired comparisons (random pairs).

of clutches were compared, eggs from each nest were usually lumped in clusters primarily containing eggs from their own clutch and most closely resembled an egg from their clutch (77.8%) (Table 4). Although some eggs were generally similar in shape to eggs from the other clutch, they most closely resembled an egg from their own clutch (45.8%) (Table 4). A few eggs (31) were similar to eggs in neither clutch.

Variation within females.—Most eggs in clutches from a single female were similar among years. Only for one female could two clutches be identified as distinct shapes for two different years. The remainder of the eggs were similar among years, with a few eggs found to be different for some females (Fig. 1). Different clutches of a marked female were more clustered into a single group than were two clutches from randomly selected females (Fig. 1) (Kolmogorov-Smirnov $Z = 2.785$, $P < 0.001$).

Females tended to lay eggs with similar shapes each season. Elongation, sphericity, width and radius of the point accounted for 68–73% of the variance among individuals (Table 5). Mean egg width, area, and volume characteristics varied significantly among years (Table 5), and maximum width and volume were inversely correlated with spring population size (Fig. 2). Egg width, area and volume characteristics did not vary with spring temperatures on the staging areas ($P = 0.20$), snow melt from the nesting area ($P = 0.22$) or median nest initiation dates ($P = 0.11$) among years.

TABLE 5. Significant repeatability estimates of eggs of Emperor Geese.

Variable	Repeatability	SE	F ratio (df)	P
Elongation	0.731	0.173	8.62 (14, 27)	<0.0001
Sphericity	0.725	0.192	8.37 (14, 27)	<0.0001
Maximum width[1]	0.692	0.241	7.31 (14, 27)	<0.0001
Radius point	0.675	0.266	6.83 (14, 27)	<0.0001
Volume c_2[1]	0.620	0.365	5.58 (14, 27)	0.0001
Volume ellipse mid[1]	0.619	0.366	5.55 (14, 27)	0.0001
Volume c_2 integral[1]	0.617	0.367	5.55 (14, 27)	0.0001
Volume[1]	0.617	0.371	5.52 (14, 27)	0.0001
Length	0.592	0.421	5.06 (14, 27)	0.0002
Volume ellipse max[1]	0.588	0.429	5.00 (14, 27)	0.0002
Surface area[1]	0.567	0.474	4.68 (14, 27)	0.0003
Section area[1]	0.567	0.474	4.68 (14, 27)	0.0003
Point convex	0.500	0.632	3.09 (14, 27)	0.0058
Ovoidness	0.422	0.845	3.02 (14, 27)	0.0066
Pearshape	0.400	0.910	2.87 (14, 27)	0.0091
Conidity	0.394	0.929	2.82 (14, 27)	0.0100
Asymmetry	0.389	0.944	2.67 (14, 27)	0.0137
Plumpness	0.333	1.125	2.40 (14, 27)	0.0247
Radius blunt	0.263	1.374	2.50 (14, 27)	0.0199

[1] Significantly different among years. ANOVA, $P < 0.05$.

Identification of known parasitic eggs.—Most (69.9%) known parasitic eggs were of different shape characteristics than the other eggs in the nest (Table 6). Within a nest significant proportions of normal eggs and known parasitic eggs ($\chi^2 = 192.51$, df = 1, $P < 0.001$) separated into clusters with eggs from their identified group. "Normal" eggs were all eggs in the nest not positively identified as parasitic eggs using such criteria as delayed hatch date or observed parasitic event and may have been laid by a female other than the host. Up to 18.0% (Table 6) of "normal" eggs may have been laid parasitically.

DISCUSSION

Shape characteristics of Emperor Goose eggs can be quantified and there are significant differences in shape characteristics among females. Analysis of photographs of eggs suggests that nest parasitism occurs regularly, and that a large proportion of known parasitic eggs can be identified. Physiognomic and shape characteristics have been used to identify conspecific parasitic eggs (e.g., MacWhirter 1989, Thomas et al. 1989, Yom-Tov 1980). Thomas et al. (1989) presented a method of comparing eggs within the clutch based on discriminant function analysis of color, marking, and measurement characteristics. Others, such as Collias (1984), used one-way analysis of variance to compare variables among individuals. No one variable could be used consistently to separate groups of eggs. For Emperor Geese a combination of volume, surface area and shape variables were needed to identify eggs with differing shapes within a

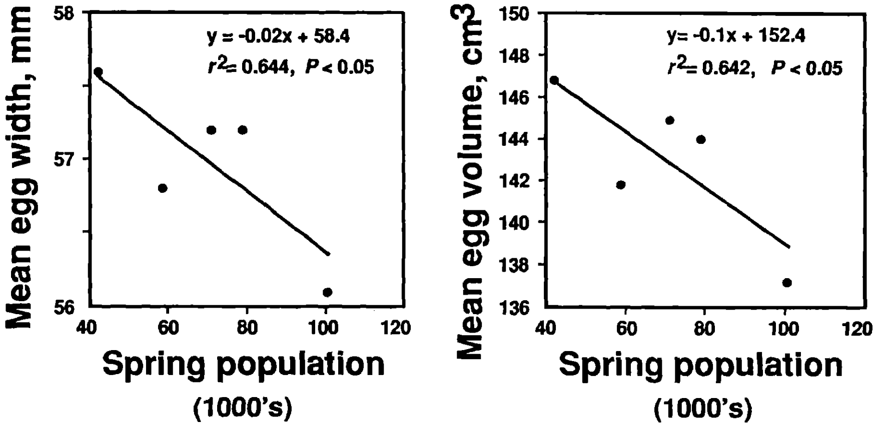

FIGURE 2. Mean egg width and volume change as related to spring population size.

clutch. Cluster analysis enabled me to use a number of different variables simultaneously on a sample of eggs laid by an unknown number of females to separate different groups of eggs. Some eggs that were classified as parasitic, however, were not sufficiently different from the remainder of the clutch to be identified using this method. Thus, differences in egg shape characteristics among eggs in a clutch should be used in conjunction with other methods, as summarized by Yom-Tov (1980) and MacWhirter (1989), to identify parasitic eggs.

The high repeatability of egg measurements of Emperor Geese is consistent with similar data for Canada Geese (*Branta canadensis*) where high repeatabilities of volume, length and width were also recorded (Leblanc 1989). Repeatability estimates of egg mass were also high for other species of waterfowl such as Snow Geese (*Anser caerulescens*), Mallard

TABLE 6. Proportion of eggs identified as being similar or different shaped from other eggs within the nest.

	Eggs identified from shape[2] as	
Egg type[1]	Similar (%)	Different (%)
Normal egg	1279 (82.0)	280 (18.0)
Parasitic egg	41 (30.1)	95 (69.9)
Unknown	22 (56.4)	17 (43.6)

[1] Normal eggs = eggs that were in similar incubation stages as the majority of eggs within the nest. Parasitic eggs = eggs either laid outside the nest then pulled into the nest, or eggs laid in the nest by other females after incubation began. Unknown eggs = all eggs whose incubation stage in relationship to the other eggs in the nest was not determined.

[2] Egg shape was most similar to normal eggs or different from normal eggs within the clutch.

(*Anas platyrhynchos*) (Batt and Prince 1978, Prince et al. 1970), and Northern Pintail (*Anas acuta*) (Duncan 1987). This is consistent with studies of passerines (Ojanen et al. 1979, van Noordwijk et al. 1981, Wiggins 1990), shorebirds (Thomas et al. 1989), and grouse (Moss and Watson 1982). These studies demonstrated high repeatabilities of egg measurements such as mass, length, width, volume and shape index. As with the White-winged Scoter (*Melanitta fusca*) (Koskimies 1957) and the Least Flycatcher (*Empidonax minimus*) (Briskie and Sealy 1990), size characteristics of Emperor Geese varied among years, but shape characteristics did not. Egg sizes of waterfowl have been reported to vary with changes in food quality (Duncan 1987, Krapu 1979, Pehrsson 1991).

Egg volumes, width and areas of Emperor Geese varied among years. This variability was not correlated with temperatures in spring on the staging areas, or temperatures or timing of snow melt on the nesting areas, or date of nest initiation among years, but maximum width, volume, volume c_2, and volume c_2 integral were negatively correlated with spring population size. This correlation may be the effect of density dependent factors resulting in intraspecific competition for preferred foods (Pehrsson 1991), changes in population structure resulting in smaller eggs being laid by some portion of the population, or other extrinsic factors. The high repeatability in shape variables within individuals despite changes in mean egg size of the population suggests that shape variables may be used to separate and identify individuals within and among years despite differences that may result in changes in egg size.

As most eggs laid by females in successive years are indistinguishable among years, eggs of most females can be distinguished among females, and a high proportion of known parasitic eggs can be separated from the clutch based on shape characteristics, then differences in egg shapes within a nest are a viable tool for identifying parasitic eggs especially when used in conjunction with other methods.

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COMMITTEE FOR THE NATIONAL INSTITUTES FOR THE ENVIRONMENT SEEKS INFORMATION ON ENVIRONMENTAL RESEARCH NEEDS

The Committee for the National Institutes for the Environment (CNIE) is trying to determine priority needs in environmental research and training that are not supported by present funding sources. CNIE is also seeking examples of "success stories" where environmental research and training has led to solutions or amelioration of environmental problems and saved money and examples of "horror stories" where lack of environmental research and training has hindered progress towards solving environmental problems and has resulted in wasted money. This material will be useful in the design of the National Institutes for the Environment (NIE), which is presently under study by the National Academy of Sciences. Please send comments about priority needs (including comments about why these are not being addressed by existing funding agencies) and well-documented examples, including citations or reprints to Committee for the NIE, 730 11th St. NW, Washington, DC 20001-4521; phone 202-628-4303; fax 202-628-4311; BITNET AIBS@GWUVM.