ECOLOGICAL AND SOCIAL FACTORS AFFECTING HATCHABILITY OF EGGS

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ABSTRACT.—Hatchability, defined as the proportion of eggs surviving to the end of incubation that hatch, varies among populations of birds. Here, I examine the effects of a variety of variables on hatchability in a comparative analysis of 155 studies of 113 species. Of the ecological and geographical variables considered, latitude, diet, and nest type explain a significant amount of the variance in hatchability due to a significant increase in hatchability along a latitudinal gradient and a decrease in hatchability in carnivorous and hole-nesting species compared to herbivorous and open-nesting species. Of the variables related to sociality, all affect hatchability adversely as they increase along a sociality gradient (defined as the likelihood of increasing frequency of interactions with conspecifics), significantly so in the case of social organization and possibly incubation pattern. In addition, hatchability of eggs in nests of Acorn Woodpecker (*Melanerpes formicivorus*) groups containing more than one breeding male and/or female is significantly lower than that observed in groups with a single breeding individual of each sex. Although the causes of these trends in hatchability are unclear, these results provide comparative evidence to support the hypothesis that there is a direct, detectable reproductive cost to individuals pursuing strategies that are more social. *Received 9 March 1981, accepted 11 February 1982.*

An egg failing to hatch is a considerable energetic loss to the bird that laid it as well as to those that incubated it. As a result, selection can be expected to fine-tune the processes of fertilization and incubation and the physiology of the eggs themselves to maximize the probability of an embryo successfully forming, developing, and hatching. This process has not been perfected, and all species of birds for which a reasonable sample has been obtained suffer some hatching failure unrelated to predation or abandonment. Hatchability of eggs is known to have a genetic basis in domestic fowl (Moseley and Landauer 1949) and is known to be affected by numerous environmental and nutritional factors (Taylor 1949). However, little is known about what factors, if any, affect interspecific variability in hatchability or of social factors that might influence hatchability within a population.

The purpose of this paper is to begin to fill this gap. I examine, in a comparative fashion, the effects of a diverse array of variables on hatchability. Considerable variability is shown to exist, some of which can be correlated with both social and ecological factors. The correlations of the social variables with hatchability prompted a second analysis comparing hatchability among several subsets of a population of the cooperatively breeding Acorn Woodpecker (*Melanerpes formicivorus*). Significant variability in hatchability is also shown to be present within this species.

MATERIALS AND METHODS

Hatchability is defined here as the percentage of eggs surviving to the time of hatching that produce a chick. Thus, eggs lost to predation, abandonment, accidental breakage, or any other unknown factor are excluded. Two types of data were analyzed. First, I compiled hatchability data from the literature in as wide a variety of avian species as was practical. In all, data were extracted from 155 populations of 113 species, including representatives from 13 orders, 42 families, and 92 genera. (Sixteen species were the subject of 2 studies each, seven species were the subject of 3 studies, and a single species was the subject of each of 4, 5, and 6 studies [the American Robin (*Turdus migratorius*), the Herring Gull (*Larus argentatus*), and the Eastern Bluebird (*Sialia sialis*), respectively].) All but nine studies were done in the Northern Hemisphere. Nearly all were done at low altitudes (only seven were at an altitude above 1,000 m), and my search was biased toward North American rather than European studies. Otherwise, a

wide taxonomic, geographical, and ecological range of species was included. A list of the species used and references consulted is available from the author on request.

For each population, the following data were recorded. (1) Year the study was performed: before 1946, 1946–1965, or post-1965. This variable was used to test for a difference in hatchability in years before the use of DDT (pre-1946) compared to years when use was widespread (1946–1965) and years when use was declining or absent (post-1965). (2) Taxon: non-passerine or passerine. (3) Primary habitat type: aquatic or terrestrial. (4) Diet: primarily granivorous/herbivorous, insectivorous/primary carnivore, or secondary carnivore. (5) Nest location: ground, trees and shrubs, or cavity. (6) Latitude. (7) Approximate altitude. (8) Mean clutch size of the population. (9) Cube root of mean egg volume. Volume was estimated as length × breadth² × π/6; the cube root of this value is inversely proportional to the surface to volume ratio and thus directly proportional to an egg's thermal inertia (Kendeigh 1972). (10) Spacing pattern: all-purpose territory, mating and nesting territory used only for some food acquisition, or colonial. (11) Incubation: female only or both male and female. (12) Social organization: primarily monogamous, polygyny common, or cooperative breeder. (13) Number of eggs laid that was known to survive to the time of hatching. (14) Number of these eggs that hatched.

Most data were derived from the original source when possible; exceptions were egg size (usually obtained from Murphy 1936, Witherby et al. 1938–1941, Brown and Amadon 1968, or Harrison 1978) and diet (usually derived from Bent 1919–1968, Witherby et al. 1938–1941, or Martin et al. 1951). Several commonly encountered problems were dealt with as follows. (1) When no clutch size was given for a population, this datum was omitted. (2) Presence of male incubation, when not known from the original source, was often inferred from Bent (1919–1968), Witherby et al. (1938–1941), Kendeigh (1952), Skutch (1957), or Verner and Willson (1969). If information on male incubation from these sources conflicted, this datum was omitted. (3) For cooperative breeders, the dichotomy for incubation was whether only a single female incubated or if more than one individual incubated. (4) The category of cooperative breeding as a type of social organization included all species that regularly breed in groups, regardless of the actual or presumed mating pattern within groups. (5) Because many studies lump all causes of egg mortality, care was taken to exclude studies from which it was not possible both to derive an unambiguous estimate of the number of eggs that survived to hatching and to have reasonable confidence about the subsequent fate of those eggs. Studies done on populations likely to have been affected by environmental contaminants were excluded, as were those

with a sample of less than 25 eggs. (6) Few studies provide information on the different causes of hatching failure (e.g. infertility versus embryo mortality or death during hatching); thus, all such losses were lumped together in determining hatchability.

Dividing the number of eggs hatching (variable 14, above) by the number surviving to the end of incubation (variable 13, above) yields the proportion of eggs hatching. The distribution of values for this variable from the 155 populations considered was tested with the Kolmogorov-Smirnov goodness of fit test (Siegel 1956) and found to be significantly non-normal ($D = 0.151$, $P < 0.01$). Arcsine transformation [$H = \arcsin \sqrt{p}$, where p = proportion of eggs hatching (Sokal and Rohlf 1969)] successfully normalized the hatchability distribution by this test. Neither the raw nor transformed data was found to be normally distributed, however, when tested by the more powerful Cramer-von Mises or Anderson-Darling statistics (Stephens 1974). Thus, nonparametric statistics were used except when no appropriate nonparametric test existed, in which case the arcsine transformed data were used. Two-tailed tests were used in order to reflect the absence of a priori assumptions as to the direction of differences to be expected.

Because numerous species are represented by two or more studies, I performed an analysis of variance of the transformed hatchability data (1) using sets of three or more studies of the same species as groups and (2) using sets of three or more studies of species within the same genus as groups, excluding genera for which all studies were of the same species. This procedure tests for the effect of considering each study an independent sample by assessing the relative variance in hatchability within studies of the same species compared to studies of species within the same genus (see Krebs and Davies 1981: 40). The mean square of hatchability within the 11 groups of studies of the same species was 26.1, whereas the mean square within the eight groups of species within the same genus was 25.3. Because no increase in variance is shown if species are considered rather than individual studies, there appears to be no reason to lump studies of the same species (Krebs and Davies 1981). As a precaution, however, all analyses discussed in the paper were also performed by using only the study with the greatest sample size for each species; the results of these analyses are discussed whenever they differ from those considering each study independently.

The second set of data considered was from the cooperatively breeding Acorn Woodpecker (*Melanerpes formicivorus*). Data were gathered in the field between 1975 and 1981 at Hastings Natural History Reservation, central coastal California. Acorn Woodpeckers live and breed in permanently territorial family groups of varying size (2–15 individuals) and composition (MacRoberts and MacRoberts 1976, Koenig and Pitelka 1979, Koenig et al. in press).

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TABLE 1. Effect of five miscellaneous variables on hatchability.[a]

Variables	$\bar{x}$ percentage hatchability	n	χ^2	P value
Year of study				
Before 1946	90.1	31		
1946–1965	90.8	44	1.29	0.53
Post-1965	90.8	80		
Taxon				
Nonpasserine	89.7	60	0.47	0.49
Passerine	91.2	95		
Habitat				
Terrestrial	90.6	107	0.06	0.81
Aquatic	90.7	48		
Diet				
Herbivores/granivores	92.6	53		
Primary carnivores	89.4	85	6.71	0.04
Secondary carnivores	89.9	17		
Herbivores/granivores	92.6	53	6.71	0.01
All carnivores	89.5	102		
Nest location				
Ground	91.5	71		
Trees and shrubs	90.6	52	4.39	0.11
Holes (closed)	88.7	32		
Open	91.0	123	3.80	0.05
Closed	88.7	32		

[a] Kruskal-Wallis 1-way ANOVA (Siegel 1956).

Groups may contain 1–4 breeding males, 1 or 2 breeding females, and up to 9 offspring from 1 to 3 yr old. As group size and composition are highly variable, it is possible to test for the effects of differing types of group organization on hatchability within a single population.

Hatchability of nests with known final clutch size was determined by checking as soon as possible (within 8 days) after hatching. Only eggs still present in the nest when it was checked were assumed to have failed to hatch. This probably introduces a slight, but consistent, bias toward higher values than are actually the case, as some unhatched eggs may have been removed before the nest was checked. Runt eggs, which are common in groups of Acorn Woodpeckers with two communally nesting females (Koenig 1980), were excluded from the analysis.

RESULTS

Comparative hatchability of birds.—The mean hatchability for all 155 populations for which data were analyzed (calculated using the transformed data) was 90.6%. The results of tests measuring the effects of a series of variables, both ecological and geographical, on hatchability are presented in Tables 1 and 2. Of these

variables (which included variables 1 through 9, above), only latitude, diet, and nest type (open or closed) have a significant effect on hatchability. The correlations between hatchability and both clutch size and egg size, however, approach significance (both $0.05 < P < 0.10$), and there are, in addition, several significant correlations between some of the other variables besides hatchability (e.g. latitude and clutch size, Table 2). Thus, a stepwise multiple regression analysis was performed using the continuous variables (latitude, altitude, mean clutch size, and egg size) as independent variables in order to test their combined effects on hatchability (Table 3). This analysis confirms that of these variables only latitude has a significant effect. A graph of latitude versus hatchability is presented in Fig. 1.

Sociality is indexed here by the frequency of intraspecific interactions among breeding individuals in a population. Three variables related to sociality were tested for their influence on hatchability (Table 4).

Male incubation: species in which only the female incubates have higher hatchability than

TABLE 2. Correlation of hatchability, latitude, altitude, clutch size, and egg size.[a]

	Hatchability	Latitude	Altitude	Clutch size	Egg size$^{1/3}$
Hatchability	—	0.29***	−0.08	0.15	−0.14
Latitude	155	—	−0.35***	0.27**	0.01
Altitude	152	152	—	0.14	−0.28***
Clutch size	134	134	131	—	−0.53***
Egg size$^{1/3}$	155	155	152	134	—

[a] Spearman rank correlation coefficients above the diagonal, n below. Latitude is North or South. ** = $P < 0.01$, *** = $P < 0.001$; other $P > 0.05$.

those in which the male and female share incubation; this difference is significant for all data ($P = 0.05$) except when only a single sample for each species is considered (Kruskal-Wallis 1-way ANOVA, $\chi^2 = 1.47$, NS). Given that shared incubation will, on average, result in more interactions between members of a pair than will occur in species in which incubation is performed solely by the female, male incubation is considered more "social" for the purposes of this analysis.

Spacing pattern and territoriality: there is no significant effect of spacing pattern on hatchability (Table 4). There is a slight trend, however, toward increased hatchability as the territory becomes more all-inclusive, with colonial species having the lowest hatchability and those maintaining all-purpose territories the highest.

Social organization: the type of social organization has a strong, significant effect on hatchability ($P = 0.01$). Monogamous species have the highest hatchability, followed by polygynous species, and finally by cooperative breeders.

Of the 12 variables considered in the analyses, four by themselves explain a significant amount of variance in hatchability (latitude, diet, nest type, and social organization); in addition, incubation pattern has a significant effect when one considers each population studied independently but not otherwise. In an attempt to check the effects of these variables when considered together, I performed an analysis of covariance (Nie et al. 1975). Latitude was treated as a covariate, while nest type (open or closed), diet (herbivorous or carnivorous), incubation pattern (male incubates or not), and social organization (monogamous, polygynous, or cooperative breeder) were main factors. Latitude was assessed before the factors, which were all considered simultaneously; that is, each was tested while controlling for all other variables.

The results are shown in Table 5. Only latitude and social organization remain significant. The total amount of variance explained is highly significant ($P < 0.001$).

Group composition and hatchability in the Acorn Woodpecker.—The effects of the social variables considered above prompted an examination of hatchability within a population of the group-living Acorn Woodpecker. Groups were divided into those containing (1) a male-female pair only ($n = 18$ nests), (2) a pair along with one or more nonbreeding nest helpers ($n = 10$ nests), (3) groups with more than one communally nesting female ($n = 14$ nests), and (4) groups with more than one breeding male, but only one breeding female ($n = 34$ nests). The criteria for determining the category to which a group belong are based on the origins of banded individuals and are discussed in Koenig et al. (in press). Assignment is some-

TABLE 3. Stepwise multiple regression of hatchability on latitude, altitude, egg volume, and clutch size.[a]

Step	Variable	F to enter	Multiple r^2	Overall F	df
1	Latitude	15.2***	0.106	15.2***	1, 129
2	Egg volume$^{1/3}$	2.6	0.123	9.0***	2, 128
3	Altitude	0.3	0.125	6.1***	3, 127
4	$\bar{x}$ clutch size	0.1	0.126	4.5**	4, 126

[a] F values test the null hypothesis that the multiple correlation is zero either for the individual (F to enter) or combined set (overall F) of variables. ** = $P < 0.01$, *** = $P < 0.001$; other $P > 0.05$.
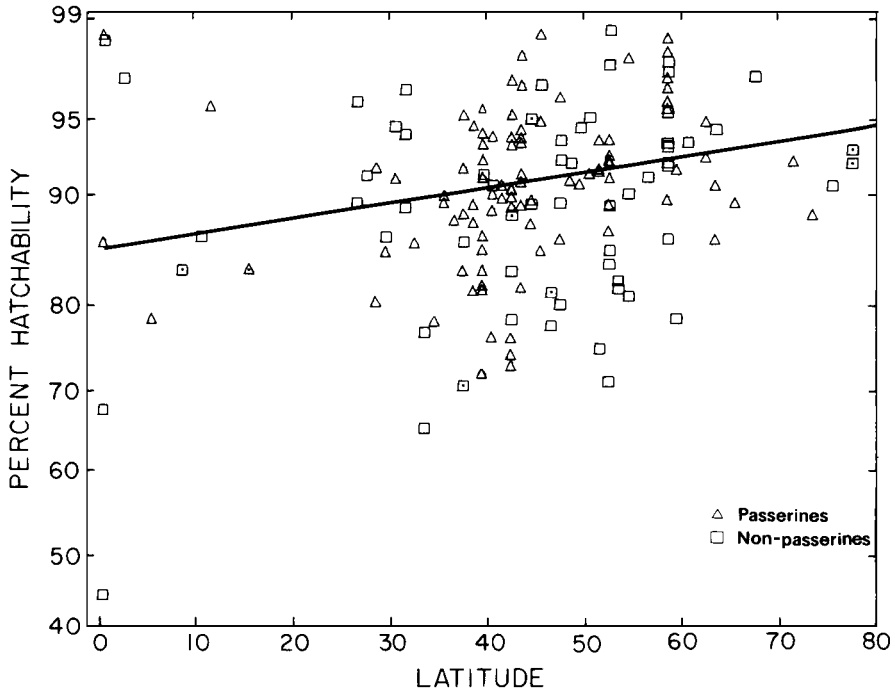
Fig. 1. Hatchability versus latitude for 155 populations of 113 species of birds. Symbols with dots are Southern Hemisphere populations. Regression line for all data (back transformed from the arcsine transformation) is plotted and in degrees is $y = \sin^2(0.1117x + 67.05)$, $r^2 = 0.06$, $F = 11.4$, df = 1,153, $P < 0.001$.

times inferential, however, and some groups ($n = 7$ nests) could not be unambiguously categorized.

The hatchability of eggs in nests of groups belonging to each of the four categories is presented in Table 6. The highest hatchability was experienced by pairs, followed closely by pairs with helpers, then by groups with more than one breeding male (but only one female), and finally by those with more than one breeding female. A χ^2 goodness of fit test comparing hatchability among the four categories is not significant ($\chi^2 = 6.5$, df = 3, $P < 0.10$). Combining categories, however, I found that

TABLE 4. Effect of social variables on hatchability.[a]

Variables	$\bar{x}$ percentage hatchability	n	χ^2	P value
Incubation				
Female only	91.7	81	3.85	0.05
Male and female	89.5	71		
Spacing pattern				
All-purpose territory	91.3	90	3.99	0.14
Territory used for some food acquisition only	90.7	31		
Territory for nesting only (colonial)	88.6	33		
Social organization				
Monogamous	91.3	130	8.82	0.01
Regularly polygynous	90.2	12		
Cooperative breeder	82.7	12		

[a] Kruskal-Wallis 1-way ANOVA (Siegel 1956).

TABLE 5. Analysis of covariance of hatchability.[a]

	Mean adjusted value (%)	F value	df (.,144)	P value
Covariate				
Latitude	—	12.4	1	<0.001
Factors				
Nest type		1.5	1	0.23
Open	91.1			
Closed	89.4			
Diet		3.2	1	0.08
Herbivorous	92.1			
Carnivorous	90.0			
Incubation		2.8	1	0.10
Female only	91.6			
Male and female	89.8			
Social organization		4.9	2	<0.01
Monogamous	91.4			
Regularly polygynous	88.5			
Cooperative breeder	84.8			
Total explained ($r^2 = 0.18$)		5.4	6	<0.001

groups with only one breeding female have significantly higher hatchability than groups with two breeding females, and groups with one breeding member of both sexes have significantly higher hatchability than those with two breeding males and/or females (both $\chi^2 =$ 4.1, df = 1, $P < 0.05$). There is no significant difference between pairs with and without helpers ($\chi^2 = 0.0$, NS).

DISCUSSION

The above analyses show there to be significant heterogeneity in hatchability among, and in the case of the Acorn Woodpecker, within species of birds. Because hatchability may be an important aspect of reproductive success and therefore presumably of fitness, it is of interest to examine the variables found to be significant and attempt to understand why they have the effects that they do. In many cases, few data are available, and this exercise inevitably degenerates into speculation. To the extent that the trends discerned here may be real, however, such speculation is a necessary first step toward understanding the selective factors influencing hatchability and toward pointing out areas where our knowledge about those factors is weakest.

One pattern that emerges from the above analyses is that between hatchability and sociality. In all cases, hatchability decreases with

TABLE 6. Hatchability of Acorn Woodpecker eggs depending on group composition.[a]

Group composition	Eggs surviving to hatching	Eggs hatching	Percentage hatching	n nests
Pairs only	73	67	91.8	18
Pairs with helpers	43	39	90.7	10
Two breeding females	90	71	78.9	14
Two or more breeding males, one female only	141	120	85.1	34
All pairs	116	106	91.4	28
All groups with only one breeding female[b]	287	253	88.2	69
All groups with two or more breeders of either sex	231	191	82.7	48
All groups	377	324	85.9	83

[a] Runt eggs (Koenig 1980) are excluded. The first four categories are exclusive; others are combinations.
[b] Includes seven groups the exact composition of which was not known but that did not contain more than one breeding female.

increasing complexity of social structure. This holds both within the single population of Acorn Woodpeckers (Table 6) and for all three social variables used in the comparative analysis (Table 4), although not significantly so in the case of the spacing pattern. There are several largely speculative, possible explanations for this trend, four of which will be considered briefly.

(1) Increased competition for mates and/or intrasexual competition during egg laying leads to greater interference and a lower probability that eggs will be fertilized. This hypothesis could in part explain the lower hatchability of polygynous species and of cooperative breeders, for which the opportunities for interference during egg laying may be greater than in other species. It is also a likely explanation for the lower hatchability in Acorn Woodpecker groups with more than one breeder of either sex compared to those with only a single breeding male or female.

Evidence of the important effect of intrasexual competition on hatchability exists from the experiments of Allen (1934) on caged Ruffed Grouse (Bonasa umbellus). Allen observed marked changes in the fertility of eggs laid by birds in three social situations: 1 male and 2 females (fertility 92–96%), 5 males and 10 females (fertility 82%), and 9 males and 18 females (fertility 70%). Allen attributed this decrease to differences in reproductive synchrony (see below), but it is equally likely that the differences are attributable to increased mate competition and interference as the number of males competing for the females increases. Allen's descriptions of the fighting that occurred in the latter two experimental situations supports this interpretation.

(2) Increased intraspecific interactions result in greater neglect of eggs and, thus, higher embryo mortality. This hypothesis is plausible as an explanation for the lowered hatchability observed in colonial species and group-living (cooperative) species, for which intraspecific encounters with neighbors or groupmates are likely to exceed, both in numbers and time, those in less social populations. For example, fights among nesting Bank Swallows (Riparia riparia) for nest sites and nest materials increase in frequency in larger colonies (Hoogland and Sherman 1976); similar interference during the incubation or egg-laying periods might reduce hatchability. Although similar to the previous hypothesis, this suggestion predicts relatively higher embryo mortality than infertility.

(3) Lack of behavioral synchronization between the sexes results in reduced, delayed, or incompetent incubation by the male and thus higher embryo mortality. This hypothesis provides a possible explanation for the lower hatchability in species in which both sexes participate in incubation, a pattern that is questionable because it does not hold up when one considers only a single sample per species but that is nonetheless surprising inasmuch as such species tend to exhibit greater nest attentiveness than those in which only the female incubates (Skutch 1976). Detailed information on the incubation behavior of males, particularly early in the incubation period, is necessary in order to test this hypothesis.

(4) Greater population structuring leads to more inbreeding, a higher incidence of lethal recessives exposed during embryo development, and thus higher embryo mortality. This hypothesis is the primary alternative to the idea that lowered hatchability in social species is due to behavioral interference associated with intraspecific interactions. It suggests instead that lowered hatchability is a direct result of increasing population structuring and smaller effective population size in social species.

There is considerable evidence that inbreeding reduces both fertility and the proportion of fertile eggs that hatch in domestic fowl (Bernier 1947, Moseley and Landauer 1949, Romanoff 1972). Similar effects have been found in the Great Tit (Parus major) on the island of Vlieland in Holland (van Noordwijk and Scharloo 1981). Thus, variation in inbreeding can affect hatchability in natural populations as well.

At least two problems arise, however, when one extends this hypothesis to explain interspecific variation in hatchability. First, in the absence of wide temporal fluctuations in population structuring, chronic inbreeding should quickly weed out recessive lethals; thus, the conditions under which inbreeding could have a long-term, seemingly continuous effect on hatchability may not be generally present in natural populations. Second, it is not clearly established whether or not increased sociality results in greater population structuring and lower effective population size. This hypothesis, proposed by Wilson et al. (1975) and Bush

et al. (1977), has recently been challenged by a number of authors (Schwartz and Armitage 1980, Barrowclough 1980, Daly 1981). At present, there are too few data on population structuring in birds to permit generalizations, although, at least in the case of cooperative breeders, the early hypothesis that their apparently closed social organization results in significant inbreeding (Brown 1974) has not been supported by more recent findings (Brown 1978, Koenig and Pitelka 1979, Johnson and Brown 1980). Clearly more data from long-term studies of marked individuals are needed.

Regardless of the exact causes for the inverse relationship between hatchability and sociality, these results provide support for Alexander's (1974) assertion that sociality entails automatic costs (e.g. greater competition for resources and interference) while providing no necessary (or automatic) benefits. Sociality in birds, as indexed by their social organization, incubation pattern, and, to a lesser extent, their spacing pattern during breeding, is associated with decreased hatchability and thus entails a direct reproductive disadvantage. This is the first direct evidence for such an effect to be found in natural populations.

A second striking pattern found in the above analyses is the highly significant latitudinal gradient, with hatchability increasing slightly over 1% for every 10° increase in latitude. This trend is not an artifact of the low hatchability found in a few of the tropical studies, as a correlation excluding studies done at latitudes below 16° is still highly significant. Interestingly, this trend reinforces the well-known latitudinal gradient in clutch size; thus, populations farther from the equator not only lay more eggs, but a higher proportion of those eggs hatch. Possibly, these trends are related: the higher hatchability in high latitudes may result from selection for greater fecundity, which not only increases clutch size but improves the physiological and/or behavioral mechanisms that affect fertilization and/or embryo development. No doubt other plausible hypotheses could be proposed.

Two other variables found to have a significant effect on hatchability were nest type and diet. The reasons for this are again largely speculative. In the case of nest type, one possibility is that the lower hatchability found in hole-nesting species is an indirect result of a correlation between hatchability, predation,

and inexperienced breeders. If inexperienced birds are more likely both to have their nests depredated and to have lower hatchability (see below), then species whose nests are preyed upon less frequently (such as hole nesters) would indirectly appear to have lower hatchability, simply because fewer nests of inexperienced birds would get destroyed. This possibility could be tested by carefully analyzing the relationship between hatchability and predation rates.

Diet was examined primarily in order to assess the possibility that environmental contaminants reduce hatchability in species higher in the food chain. Although this hypothesis was supported by the relatively high hatchability in herbivorous and granivorous species, there was no difference between species considered to be primary carnivores and those that are secondary carnivores, where the greatest effect of contaminants would be expected to occur. The increased hatchability in species depending on plant rather than animal food is perhaps an indirect result of lower nest attentiveness in insectivores due to the longer time they may require for foraging (Skutch 1976). Alternatively, the effect of diet could be an artifact of synchronous compared to asynchronous hatching, given the assumptions that carnivorous species are more likely to hatch their eggs asynchronously and that hatchability is likely to be lower if birds must begin foraging for food before the hatching of all eggs in a clutch. Additional hypotheses can certainly be envisioned.

Several authors have suggested a detrimental effect of pesticide residues on hatchability (Rothstein 1973, Furness and Hutton 1980), presumably by eggshell thinning (see Schreiber 1980 and references therein). Although environmental contamination may depress hatchability in individual populations, the data collected here show neither a general decrease in hatchability since the introduction of DDT in about 1946, nor a depression in hatchability in species highest in the food chain (see above). Thus, there does not appear to be a detectable effect of contaminants on interspecific variation in hatchability in birds.

In addition to the factors considered above, at least six other variables have been proposed to influence hatchability in wild populations of birds.

(1) Season. Hatchability has been found to

decrease in second broods and/or late in the season in Eastern Bluebirds (Musselman 1935, Norris 1958, Peakall 1970, White and Woolfenden 1973) and to increase late in the season in Dickcissels (*Spiza americana*; Harmeson 1974).

(2) Age of parents. Hatchability is higher in nests of older, presumably more experienced individuals in Snow Geese (*Chen caerulescens*; Finney and Cooke 1978) and in the European Blackbird (*Turdus merula*; Snow 1958).

(3) Clutch size. Hatchability varied with clutch size, being highest in intermediate-sized clutches, in a population of Western Gulls (*Larus occidentalis*; Hunt and Hunt 1973). No obvious effect of clutch size on hatchability was recorded for the European Blackbird (Snow 1958).

(4) Population density. Allen (1934) suggested that birds living at low densities (for instance, at the periphery of their range) should have lower hatchability due to greater difficulty of "synchronizing reproduction" between the sexes (see below). To my knowledge, the only author subsequently invoking this hypothesis is Shields (1935) to explain the apparently low hatchability he observed in Savannah Sparrows (*Passerculus sandwichensis*). Shields' sample size (eight eggs), however, is too small to allow one to draw conclusions. Furthermore, the data presented here suggest that the opposite could be true, namely, that hatchability might increase in sparse populations because of lessened intraspecific interference.

(5) Reproductive synchrony. Synchrony between the sexes is important in gamete production and for appropriate behavioral responses. The former is not likely to be of significance to hatchability, however, because the relatively low cost of sperm production makes it likely that males will be fecund at all times of potential female receptivity. Appropriate behavioral responses are equally important (Moore 1980), however, and could be of particular importance in species in which incubation is shared (see above).

(6) Life-history strategy. At least two papers have proposed that low hatchability is an adaptation to reduce brood size in the face of selection for lowered fecundity (Long 1963, Ligon and Ligon 1978). This hypothesis seems unlikely, primarily because of the energetic waste incurred by females adopting such a strategy

compared to the alternative of simply laying fewer eggs. Of course, the magnitude of the energetic loss, and thus the strength of selection against laying infertile eggs, would depend on egg size and foraging conditions during the egg-laying period and could vary considerably among species (J. D. Ligon pers. comm.).

CONCLUSION

Hatchability is a complex phenomenon influenced by a variety of ecological, geographical, and social variables. Although some of the variability in hatchability can be plausibly interpreted at this time, there are, in general, few data to help one to understand the patterns and trends that emerge from the analyses performed here. Clearly, this phenomenon is worthy of increased attention and additional analysis.

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