

A RESEARCH PROGRAM IN ECOLOGY AND ECOMORPHOLOGY The 1999 Margaret Morse Nice Lecture

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I am pleased to have this opportunity to contribute to the series of papers that honor Margaret Morse Nice (1883–1974), whose pioneering research on the Song Sparrow (*Melospiza melodia*) was the first longitudinal study of a population of individually-marked birds in nature. As a young girl, Margaret was advised by her father to write at every opportunity. She took that advice to heart, writing four outstanding books (Nice 1937, 1939, 1943, 1979), numerous research reports, and many hundreds of reviews. It is that record of writing that reveals today how clearly she thought about her observations and their implications for population biology and behavioral ecology. Her reviews were critical, in the good sense of that word. She had a rigorous research perspective, testing ideas against evidence and not mincing words when they came up short. Given her limited opportunities for travel or to obtain support for her research, her accomplishments in both scholarship and leadership are even more remarkable. Her high standards are an inspiration to others, including me.

I did not know Margaret personally, so I cannot integrate my work with hers, as did Nicholas and Elsie Collias in the paper that accompanied the first Nice award (Collias and Collias 1998). Even so, there are some interesting parallels in our lives. I too went to Mt. Holyoke College (class of 1952 rather than 1906), was among the few women in my graduate program (at Louisiana State Univ. and the Univ. of Arkansas rather than Clark College), moved to the central states with my husband (Arkansas rather than Oklahoma), raised daughters (three, not four), and later was the first woman president of a major North American ornithological society (AOU 1984–1986, rather than WOS 1937). Social mores had changed sufficiently between Margaret's era and mine that I had the option of

moving into academia as my daughters grew up.

The assignment here is to review my own scientific progress. After giving some personal background, I will summarize each of five areas of interest. Because the first one (two types of hypothesis testing and two types of models) is not restricted to ornithology or even to biology, I will use it to construct a general framework for my discussion of the other four areas.

BACKGROUND

I grew up in suburban Philadelphia, where I had the good fortune as a child to tag along on the Expeditions for Everyone sponsored by the Academy of Natural Sciences. How well I remember Joe Cadbury standing in the rain in his poncho in Carpenter Woods naming all the migrant warblers he was hearing! I spent three teen-aged summers serving food to biologists in the dining hall at the Marine Biological Laboratory in Woods Hole, Massachusetts. Even before college I had listened to research seminars at Woods Hole and looked through Libby Hyman's microscope at the pulsing colors of squid embryos.

After Mt. Holyoke, I went to LSU to work with George Lowery on nocturnal migration. Armed with telescopes and stationed at various distances from the Mississippi River, Bob Newman and I and others watched the silhouettes of nocturnal migrants as they crossed the face of the full moon. We wanted to know whether small landbirds were being funneled during the fall by the great umbilicus of the Mississippi. They mostly were following the wind (James 1956, Lowery and Newman 1966). How migrants repeatedly find their specific breeding and wintering sites is still one of the biggest mysteries in ornithology.

In early 1954, I moved to Fayetteville, Arkansas, with my new husband, Douglas James, an ornithologist at the Univ. of Arkan-

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sas. Doug and I worked together on conservation issues such as protecting the Buffalo River in the Ozark Mountains. We kept up a card file of records of the birds of Arkansas and summarized recent bird records in the central southern region of the United States for *Audubon Field Notes*. Much later, he and Joe Neal were able to publish a fine state bird book (James and Neal 1986). When I became a doctoral student in 1965, my advisory committee wanted to counter the inevitable criticism that my husband was my major professor, so the committee was enlarged to include ornithologists from neighboring states: George Sutton from the Univ. of Oklahoma, Richard Johnston from the Univ. of Kansas, and Clarence Cottam from the Welder Wildlife Refuge in Texas. I was interested in two subjects: species specific habitat relationships in Arkansas birds, and how their patterns of geographic variation in morphology and plumage fit into broad scale continental patterns. The committee decided that the dissertation should be confined to the work on size variation.

Although the habitat work had been relegated to a side project, Hank Shugart and I were able to recommend a quantitative method for describing habitats to accompany bird census work (James and Shugart 1970), a method that was later officially recommended by the National Audubon Society and used during subsequent years in various types of ecological work. When used in conjunction with vegetation sampling in places specifically selected by individual birds, the method also allowed ordinations of species by their species specific habitat affinities (James 1971). I thought of the ordinations as a multivariate extension of a primarily Gleasonian approach to ecology (Gleason 1926, McIntosh 1975). At that time, the prevailing community approach viewed assemblages of birds as integrated units, but even then I viewed bird communities more as birds on study plots whose properties might be better understood from a causal viewpoint through study of the species individually. The ordination paper (James 1971) proposed a new construct, the niche gestalt, a hypothetical combination of just those elements of the structure of the vegetation that consistently were present where a species oc-

curs, elements presumably correlated with the specific resources that allow it to persist.

My dissertation was a descriptive analysis of patterns of size variation in 12 common species of birds in the eastern and central United States. Isophenetic lines of wing length, like isothermal lines on a weather map, showed that within each species the smallest birds were in the hot humid southeastern part and the largest in the colder drier northwestern part of the area. In addition, larger birds extended farther southward in the Appalachian Mountains, and smaller birds extended farther northward in the Mississippi Valley. The same clinal pattern occurred in all the species examined, even though they differed in behavior and diet. I concluded that the most probable cause was similar responses to climatic gradients and interpreted the results as supporting a modification of Bergmann's rule wherein the total heat of the air, not just dry bulb temperature, was a good predictor of intraspecific size variation at a fine geographic scale. My interpretation of the possible adaptive advantages of this phenomenon was thermal, like Bergmann's, but was not only in terms of decreasing external surface-to-volume ratio as birds get larger. It involved all avenues of heat loss—conduction, convection, and radiation from external surfaces and evaporation from the saturated surfaces of the lungs (James 1969, 1970). The biological mechanism that maintains such fine scale, predictable associations between climate and size variation is unknown, but I still say that the phenomenon is real and demands an explanation. I tried to learn more about biophysical ecology by collaborating with Hank Shugart in a study of the phenology of the nesting season in the American Robin (*Turdus migratorius*; James and Shugart 1974) and with Warren Porter in a study of how daily microclimatic conditions constrain the behavior of the African rainbow lizard (James and Porter 1979, Porter and James 1979).

With a Ph.D., two daughters in college, and a failing marriage, I moved with the youngest daughter, Avis, to Washington, D.C., in 1973 and worked for four years as a program officer at the National Science Foundation. It was a full time job, but I was given enough time off to allow a collaboration with researchers at the

Smithsonian Institution on geographic variation in Red-winged Blackbirds (*Agelaius phoeniceus*) in Florida (Howe et al. 1977) and with James Mosimann, a statistician at the National Institutes of Health. Jim had a deep understanding of morphometrics. He was able to use data from measurements of study skins of Red-winged Blackbirds taken in Florida to illustrate some fundamental points about size and shape relationships (Mosimann and James 1979, Darroch and Mosimann 1985). My oldest daughter, now Sigrid Bonner, made illustrations for me of the variation in bills of Red-winged Blackbirds during this period. The middle daughter, Helen, worked as a technician for Richard Zusi in the Bird Division of the National Museum of Natural History, later married curator Storrs Olson, and has now developed her own career in avian paleontology.

In 1977, when Avis was ready for college, she and I moved to Tallahassee, Florida, where I was hired as an associate professor and curator of birds and mammals in the Dept. of Biological Science at Florida State Univ. I dabbled in attempts to define the morphological space occupied by assemblages of birds (Karr and James 1975, James and Boecklen 1984), but I did not enter the fracas stirred up by my ecological colleagues who were challenging the idea of the primacy of interspecific competition as a driving force in determining the distribution of organisms. Instead, I continued to work on habitat relationships and ecomorphology. Eventually I added work in two other areas, the analysis of long term population trends in birds and the conservation of the endangered Red-cockaded Woodpecker (*Picoides borealis*).

Now I will summarize my work in the first three of the five areas of interest, discuss how each fits into the continuing cycle of a research program, and summarize briefly my work in the last two areas, which is ongoing.

- I. Two types of hypothesis testing and two types of models in a research program
- II. Habitat modeling and its implications for management
- III. Intraspecific variation in the size and shape of birds
- IV. Long term trends in bird populations
- V. Conservation of the Red-cockaded Woodpecker

AREAS OF INTEREST ADDRESSED IN MY WORK

I. Two Types of Hypothesis Testing and Two Types of Models in a Research Program

With help from several statisticians, especially Charles McCulloch, I have tried over the years to make contributions to problems of the logic of science and the tools of data analysis in ecology and ecomorphology (Mosimann and James 1979; James and Rathbun 1981; James and McCulloch 1985, 1990, 1995, in press; James et al. 1996, McCulloch et al. 1997).

I believe that biologists use the term "hypothesis testing" in two different ways, often without distinguishing between them. In addition, there are two major types of models, but these do not correspond directly to the two types of hypothesis testing. If more attention were paid to distinguishing these four constructs, a lot of confusion could be cleared up. Here are definitions of the four categories as we used them in James and McCulloch (1985).

Empirical versus process models:

- Empirical (descriptive, data-based) models describe relationships among variables but are not about processes.
- Process models describe relationships among variables that involve some form of causal relationships.

Statistical hypothesis testing versus theoretical hypothesis testing:

- Statistical hypothesis testing estimates the likelihood that relationships among variables in a sample also pertain to a larger population. When assumptions are met, it is appropriate to test predictions made from empirical and process models. Such tests do not test the models themselves.
- Theoretical hypothesis testing involves making comparisons among models. With process models it uses some form of experimental design that allows testing of ideas about causal relationships. In the ideal situation, sampling units are assigned randomly to treatments, and the design includes both control groups and replication. It is the logical design of the comparisons among sampling units that received different treatments that allows inference about causes.

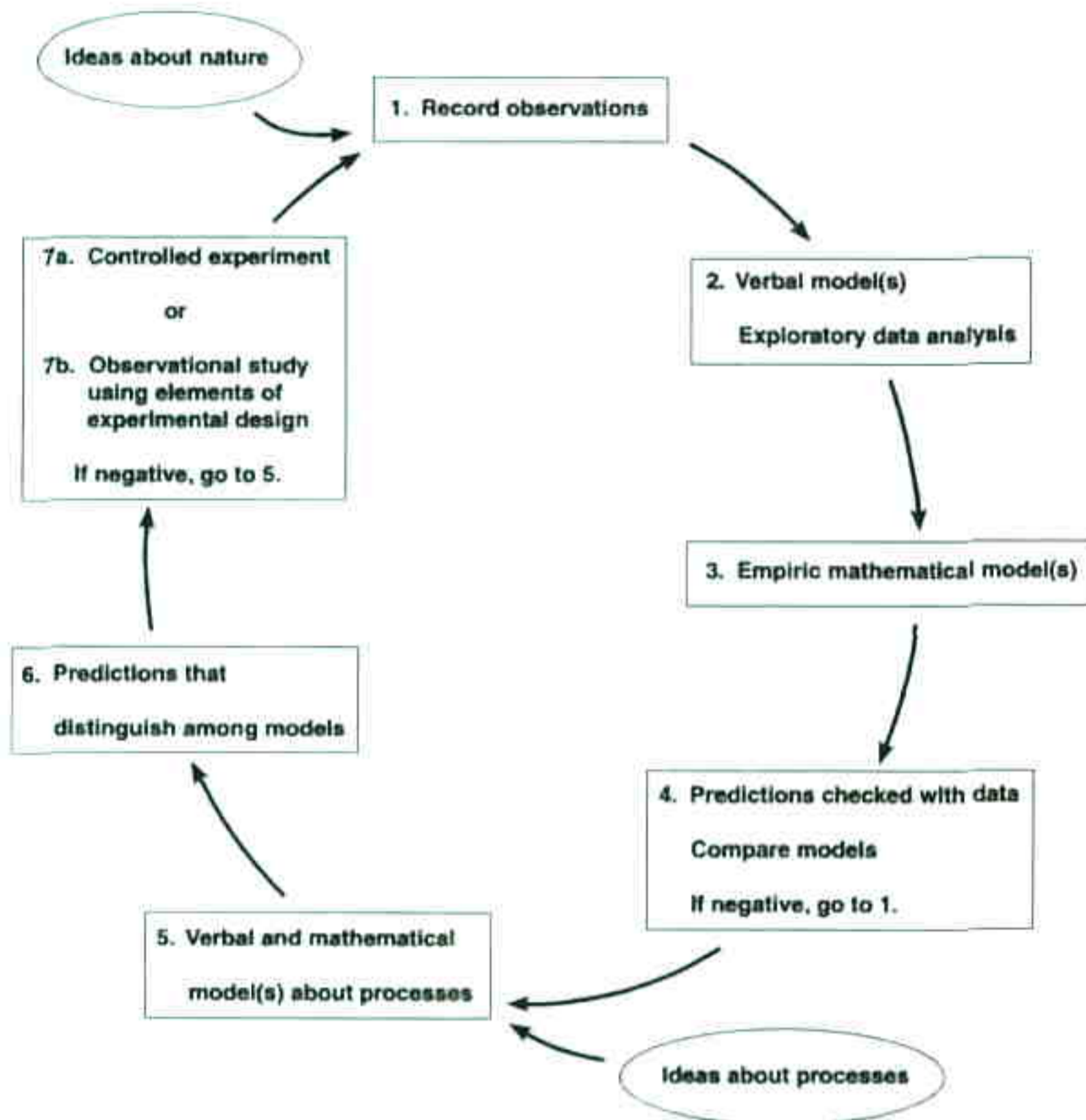


FIG. 1. The progression of a research program (modified from fig. 1 of James and McCulloch 1985). Statistical hypothesis testing of predictions may be warranted in steps 4 and 7. Theoretical hypothesis testing occurs with model comparisons, also in steps 4 and 7.

Headway also can be made with observational studies in which an intervention takes place and some elements of experimental design are retained, but sampling units are not assigned randomly to treatments (Rosenbaum 1995). With empirical models, theoretical hypothesis testing also involves selecting among alternatives (Burnham and Anderson 1998).

No agreed upon procedure exists for what is called the scientific method, but as John Stuart Mill pointed out long ago (Robson 1974:737), common sense is insufficient as a criterion for figuring out how the world works. The basic scheme in Fig. 1 provides a set of steps for progressive interactions between model building and data analysis. In James and McCulloch (1985) we emphasized that to prevent premature refinement of a research question, substantial scientific effort

should be devoted to the original development of plausible empirical and process models.

We think that the first step in a research program usually is to record observations based on ideas about nature. The second is to look for patterns in the data with exploratory data analysis and to develop verbal models for reasonable relationships among variables. Plotting data on maps and looking for patterns qualifies as exploratory data analysis. It can lead to tentatively considered statements about relationships among variables. The third step is expression of verbal models as candidate empirical models in mathematical terms.

An example of an empirical mathematical model is:

$$G_{H_2O} = a + b (Pb).$$

This model predicts that there is a linear relationship between the rate of water loss from

an egg (in mg/day \times torr) during incubation and the barometric pressure (torr) at the altitude where the egg was laid. The fourth step involves checking candidate empirical models with data. Carey et al. (1983) took step 4 when they collected eggs of Red-winged Blackbirds at seven different altitudes between Florida and Colorado and compared their rates of water loss in an incubator. They found higher rates of water loss in eggs from places with high barometric pressure (low altitude), a phenomenon that allows rates of daily water loss from eggs to be independent of altitude under natural conditions. No alternative empirical models fit the data so well. Note that an empirical model describes relationships among variables, but it is not about processes in the sense of perturbations and causes.

Ideas about processes can be used to initiate a research program or to progress from step 4 to step 5. Steps 5 and 6 develop verbal and mathematical models about processes and predictions from them that, if true, lend support to one model over another. With our example, Carey and coworkers might have asked whether individual female Red-winged Blackbirds could lay eggs having different rates of conductance if subjected to different barometric pressures. Had it been feasible, that experiment would have moved the research program to steps 6 and 7, in which a prediction of a process model would have been tested.

The usefulness of the process models is judged by comparisons that discriminate among competing models, as with empirical models, but in the case of process models, the power to discriminate among competing models depends upon experimental design (how sampling units were assigned to treatments, levels of control, and replication). Statisticians do not always agree on the best approaches for teasing apart causal relationships when experiments are not possible (Dawid 2000), but in many cases alternatives must be sought, and methods are available (Cook and Campbell 1979, Cochran 1983, Rosenbaum 1995). Weak inferences about ecological processes can be made from observational studies that record perturbations, depending on the extent to which elements of experimental design have been included in the analysis (James and McCulloch 1985, 1995; Diamond 1986; Eber-

hardt and Thomas 1991). An example of a simple case of an observational study is the history of the number of singing male Kirtland's Warblers (*Dendroica kirtlandi*) in Michigan before and after the 1990 Mack Lake fire (James and McCulloch 1995).

Where does statistical hypothesis testing enter the interactions between model building and data analysis in the cycle of Fig. 1? Perhaps in steps 4 and 7 if some restrictive assumptions are met about the sampling regime, the definition of the larger population of interest, and the distribution of the data, but ecological journals have been reporting a lot of inappropriate statistical hypothesis tests (Johnson 1999). Where does theoretical hypothesis testing come in? Again in steps 4 and 7 but only in terms of the power of comparisons among models or between treatment and control groups.

II. Habitat Modeling and Its Implications for Management

Empirical habitat modeling is worthwhile in itself, even though it gets only to step 4 in Fig. 1. In ecology it can advance the clarity and precision of descriptions of relationships between organisms and their environments. For example, validated predictions about where to expect a species to occur can be useful, even if the processes involved are poorly understood (Scott et al. 2002). If the processes regulating the distributions of organisms are operating at the level of populations of individual species, as advocated by Andrewartha and Birch (1984), McIntosh (1995, 1998), and others, the most insightful empirical and theoretical modeling will be at that level. One reason that theoretical community ecology has had so much trouble developing testable predictions about both ecological and evolutionary processes (James 1982, Simberloff 1982, Wiens 1989) probably is that its communities are not objective functioning units in nature. My approach to extending habitat modeling toward the analysis of processes would be to construct theoretical models for species-centered environmental analysis (James et al. 1997) and then to move into step 7 of Fig. 1. An example that accommodates interspecific interactions will be described below, in the section on conservation of the Red-cockaded Woodpecker.

An early choice is to decide whether to model the population of a single species or an assemblage. Assemblages of birds on study plots do differ in habitat specific ways in their density of individuals, species richness, and the relative abundances of the component species. Valid empirical comparisons require standardizing samples to equal-sized areas (by estimating the density of pairs in a fixed area) and then using rarefaction (Heck et al. 1975, Engstrom and James 1980) to find the expected number of species in samples of that size. Birds' relative abundances are best expressed in dominance diversity curves (James and Rathbun 1981).

Descriptive comparisons of species richness can be standardized either to equal numbers of individuals or to equal-sized areas. James and Wamer (1982) examined the structure of bird communities in 56 North American forests in relation to their vegetation structure. Coniferous forests and dense successional stands, having only one or two species of trees, had the fewest species of birds. The species richness was highest in mature deciduous forests, but not those that had the highest tree species richness, canopy height, or tree density. The number of pairs of breeding birds also was highest in mature deciduous forest, and in that case the highest densities occurred where tree species richness and canopy height were highest. Contour diagrams of standardized densities or species richness in a graphic principal components space for variation in the structure of the vegetation among samples show these relationships for areas standardized to 10 ha (Fig. 2). These results are not discernable from species/area curves, diversity indices, or correlation coefficients.

In James et al. (1984), we combined single and multiple species approaches by asking how densities of the Wood Thrush (*Hylocichla mustelina*) change first with habitat in seven regions of its geographic range and then with the densities of five ecologically similar species (four other Turdinines and the Ovenbird, *Seiurus aurocapillus*). Breeding Bird Survey data (Robbins et al. 1986) for 1966–1979 showed that peak densities of Wood Thrushes occurred in the Appalachian Mountains in mesic oak forests from Tennessee to Pennsylvania along the Blue Ridge and in hardwood forests of the Adirondack Mountains and south-

ern Maine. Neither the limits of the breeding range nor the density of Wood Thrushes within their range was highly related to the presence of similar species. Instead they were related to species specific nesting and foraging conditions, which in turn varied with vegetation structure. This neo-Grinnellian approach used multiple comparisons and might have detected interspecific niche shifts but was not cast in terms of communities.

Community ecologists like to start at step 5 in Fig. 1 by asking "What processes structure communities? Are biotic processes, such as predation or interspecific competition, more important than abiotic processes?" This approach risks premature model refinement. When it fails, calls for pluralism in approaches still miss the point that just beginning at the scale of the community may preclude important progress. If bird communities are epiphenomenal, in the sense that they are not functional units in nature, empirical models can describe their properties, but process models should be based on variables that have more objective reality.

Scott et al. (2002) contains state-of-the-art examples of empirical modeling efforts to predict species occurrences. Various authors are using geographic information systems to store geospatial data, including large data sets for landform, habitat, and climate variables; information from satellite imagery; and aerial photography (Austin et al. 1990, Scott et al. 1993, and many others). Verner et al. (1986) and James and McCulloch (2001) review how various approaches have developed. We think they could still be improved with more *a priori* thinking in model formulation, more attention to alternative models, more model validation, and some new software for spatial statistics (Cressie and Ver Hoef 1993). Even after that, to be most useful to managers, work will have to be focused on environmental processes that may be directly limiting and can be manipulated. That step would move the entire enterprise beyond step 4 in Fig. 1. Valid predictions based on empirical relationships can be important to managers, but they also come with dangers. Without some form of testing alternative processes (Caughley and Gunn 1995), they can be misleading.

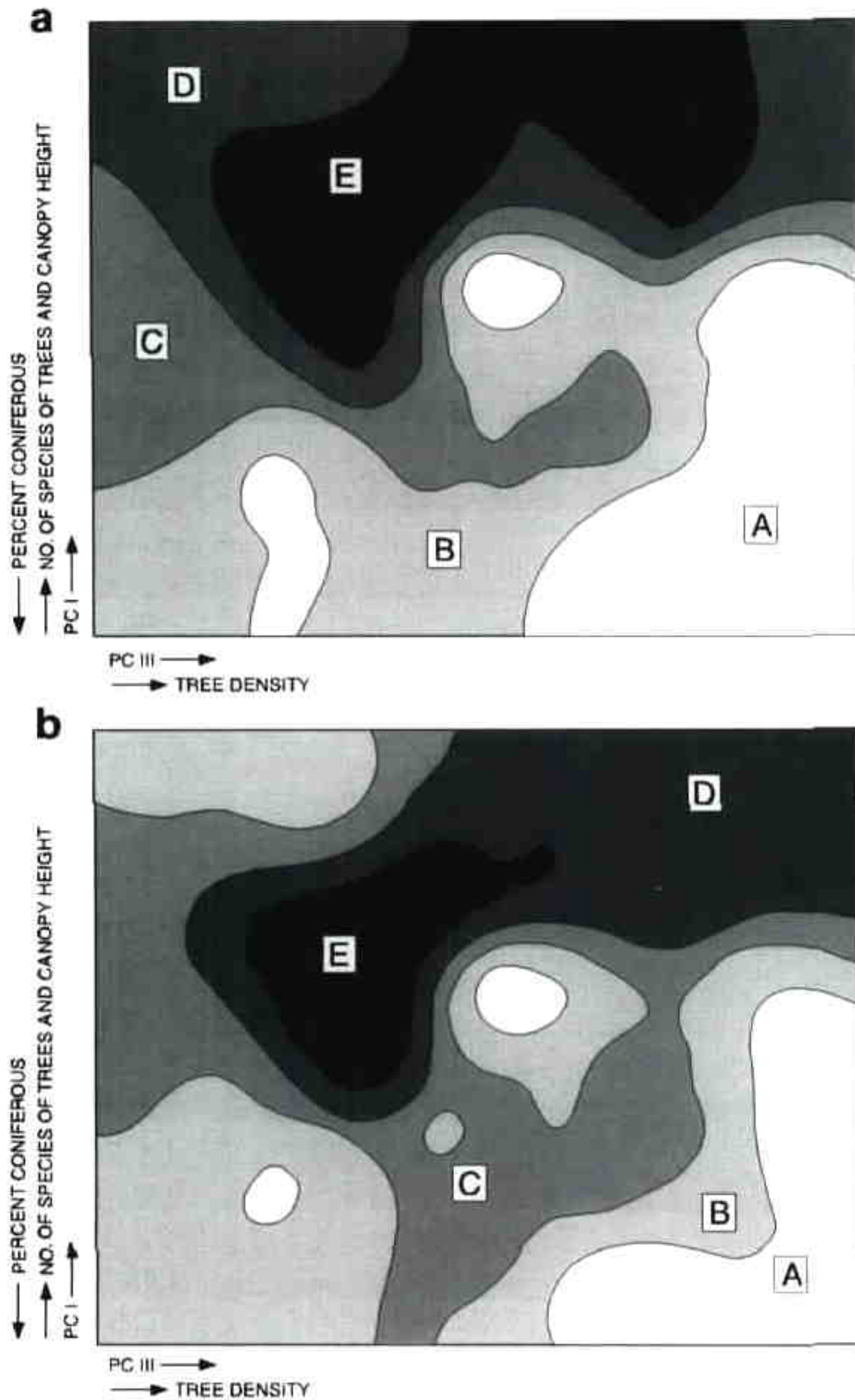


FIG. 2. Contour diagrams giving the density of birds and their species richness in forests of 10 ha (from fig. 6A of James and Wamer 1982). (A) The number of territorial pairs is A, 4–22; B, 22–40; C, 40–58; D, 58–76; E, 76–94. (B) The number of species is A, 4–8.4; B, 8.4–12.8; C, 12.8–17.2; D, 17.2–21.6; E, 21.6–26.0.

III. Intraspecific Variation in the Size and Shape of Birds

A. *Geographic variation in size and its environmental correlates.*—Bergmann's ecogeographic rule, as defined by Ernst Mayr (Mayr 1963) is a verbal empirical model:

“Races (of birds and mammals) from cooler climates tend to be larger. . . than races of the same species living in warmer climates.”

This one-sentence statement is frequently quoted, often in disparaging terms. Mayr re-

alized that he was omitting the controversial process model in Bergmann's monograph, but apparently he did not realize that what Bergmann actually proposed (Bergmann 1847) was a different empirical model. Bergmann said that if two animals in the same genus differed only with respect to size, the smaller would live in a warmer climate. Bergmann commented that he did not have evidence of patterns of size variation at the intraspecific level (see translation in the appendix of James 1970). Even so, many subsequent studies have been based on Mayr's generalization, and they often are attributed to Bergmann. Bergmann's theoretical model was that the surface-to-volume ratio of a bird or mammal is important to its thermoregulation. The animal maintains its constant temperature by balancing the production of heat within its volume with the loss of heat from its surface. A larger animal has a smaller surface relative to its volume and is therefore better able to withstand cold temperatures. Both Mayr's empirical model and Bergmann's process model are especially controversial among mammalogists and physiologists (Geist 1987, Paterson 1990 and citations therein). For example, because he does not see linear increases in large mammals in Canada and Alaska with latitude, Geist favors an interpretation of size variation in mammals in terms of the duration of a productivity pulse. Even so, the most recent summary of the literature on intraspecific size variation in mammals finds substantial support for traditional empirical models giving positive relationships with latitude and negative ones with dry bulb temperature (Ashton et al. 2000).

Zink and Remsen (1986) reviewed the large literature on the relationship between intraspecific size variation in birds and latitude and altitude, assuming, as have the mammalogists and many other ornithologists, that it would be colder farther north and higher up and that such relationships would be a test of Mayr's definition of Bergmann's rule. Zink and Remsen found that 29% of 92 species of birds contradicted these expectations, so they concluded that it is "somewhat surprising that Bergmann's rule and its physiological explanation continue to dominate our thinking." They also concluded that to propose that there was any one cause of intraspecific size variation would be overly simplistic.

What I had found in 1970 was that, at least for each of the 12 most common species of birds in the eastern and central United States for which data were available, size was not as highly related to latitude or dry bulb temperature as it was to climatic variables that were a function of both temperature and moisture. I proposed, as a neo-Bergmannian rule, that "intraspecific size variation in homeotherms is related to a combination of climatic variables that includes temperature and moisture. Small size is associated with hot humid conditions, larger size with cooler or drier conditions" (James 1970:387). Topographic features as subtle as the Appalachian Mountains, the Ozark Plateau, and Lake Michigan can be detected in isolines for size variation in birds, all of which fit into the larger picture. Empirical mathematical models using variables such as July mean noon wet bulb temperature, vapor pressure, and absolute humidity were all excellent predictors, and all are related to verbal models involving the total heat of the air.

Not all birds exhibit geographic size variation, and those that do exhibit it to varying degrees. Across broad regions the variation is clinal (gradual), detectable with large samples at the scale of even 1° latitude-longitude blocks (Fig. 3). To see whether there is concordance among species in their size variation, I made a list of the 263 species of passerine birds identified by Ridgway (Ridgway 1901, 1902, 1904, 1907) as having geographic variation (James 1991a). I then drew a random sample of 75 species from that list. Of these, 22 had at least two subspecies that occurred north of Mexico. One was the widespread American Robin. Having extensive data for geographic variation in the robin (Aldrich and James 1991), I checked to see whether the pattern of size variation in the other 21 species matched the pattern of size variation in the robin. As a size criterion I used wing length, which is highly related to other reasonable choices of size variables at the intraspecific level (Table 1). Only two of the 21 species were not in agreement, and the probability of obtaining such agreement by chance is 0.0001 (Table 2). In other words, there is striking concordance among passerine birds in their patterns of size variation. If a bird differs in size between two places in its geographic range that overlap with the range of the robin, it

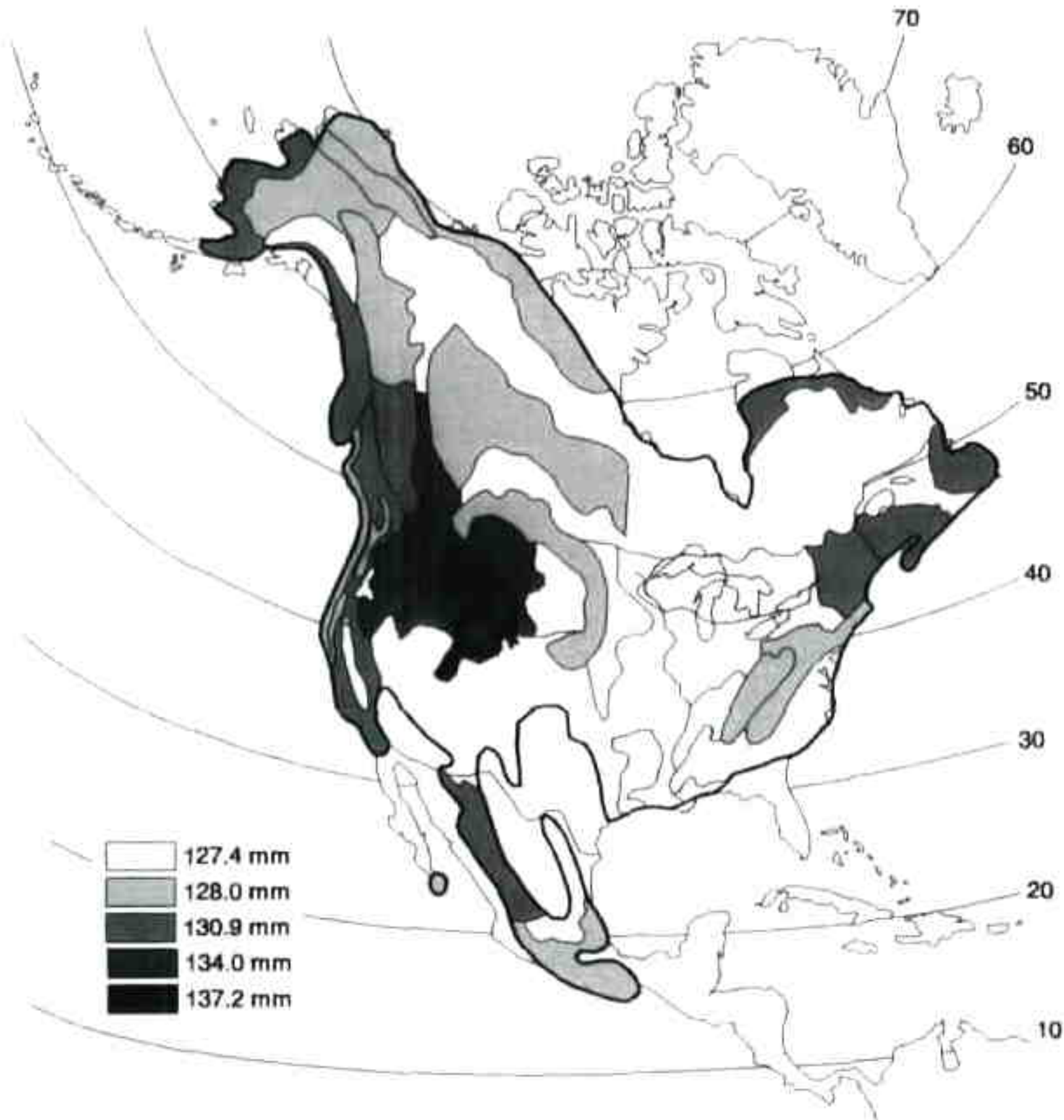


FIG. 3. Size variation in the American Robin (from fig. 2 of Aldrich and James 1991). Values are mean wing length.

TABLE 1. Pearson product-moment correlation matrix among various measures of general size for male American Robins ($n = 36$ ecoregions). The variables are as follows: median wing length (A), the sum of the medians of the seven size variables (B), the sum of the ranks of the medians of the seven size variables (C), the geometric mean of the seven size variables (D), the sum of the ranks of the geometric means of the seven size variables (E), principal component 1 of the variance-covariance matrix of the size variables (F), principal component 1 of the correlation matrix of the size variables (G), and log wing length (H). From Aldrich and James (1991).

	A	B	C	D	E	F	G
A							
B	0.96						
C	0.86	0.93					
D	0.86	0.95	0.97				
E	0.81	0.87	0.96	0.92			
F	0.82	0.89	0.78	0.88	0.76		
G	0.91	0.97	0.98	0.98	0.92	0.82	
H	1.00	0.96	0.86	0.87	0.80	0.82	0.91

probably will be larger where the robin is larger. This analysis did not use latitude; it asked simply whether passerine birds that exhibit geographic variation tend to have the same pattern. The idea of steps 1 and 2 in Fig. 1 is to let the data show the pattern before formulating the empirical mathematical model (step 3).

American Robins are highly migratory, but during the breeding season they sort themselves out into the pattern of size variation in Fig. 3 (Aldrich and James 1991, Sallabanks and James 1999). For the samples available to John Aldrich in his survey of study skins in museum collections, the smallest specimens of robins were from the southeastern coastal plain, where during the breeding season the absolute humidity of the air is highest within the robin's geographic range. The largest robins were from the Rocky Mountains and the northern North American deserts, where the

TABLE 2. The extent of concordance in patterns of size variation in North American passerine birds was tested by application of a sign test to 21 Spearman rank correlations between ranks of size (mean wing length of males) of subspecies with ranks of size for the American Robin in the same areas. Data for subspecies were taken from Ridgway (1901, 1902, 1904, 1907) and for the robin from Aldrich and James (1991). The species to be compared with the robin were randomly selected from the North American passerines that exhibit geographic variation. The probability of obtaining so many as 19 positive correlations out of 21 by chance is 0.00011. From James (1991a).

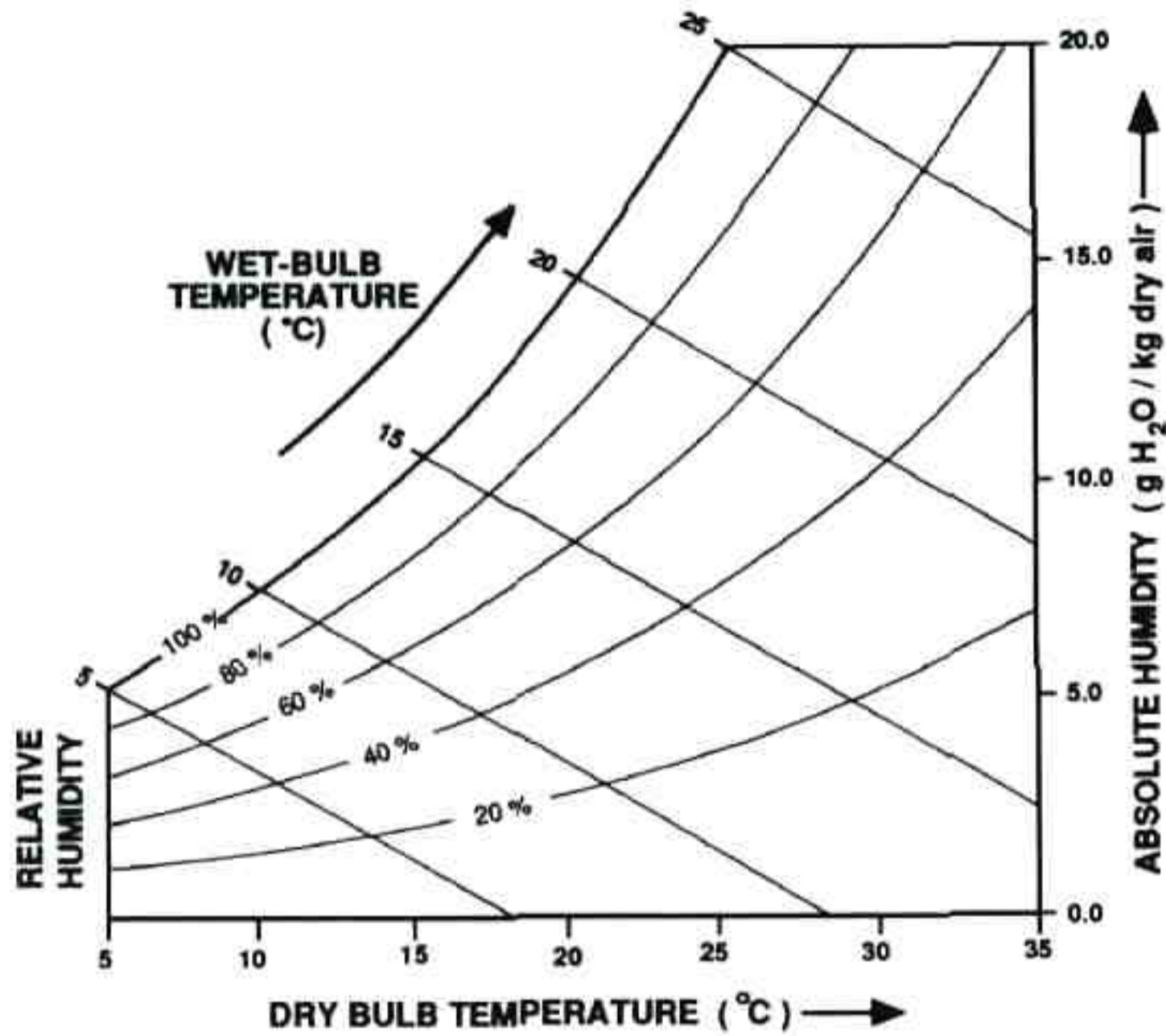
Species	Number of subspecies	Spearman rank correlation
1. <i>Eremophila alpestris</i>	10	0.57
2. <i>Hirundo pyrrhonota</i>	2	-1.0
3. <i>Cyanocitta stelleri</i>	5	0.7
4. <i>Corvus brachyrhynchos</i>	2	1.0
5. <i>Parus inornatus</i>	4	0.95
6. <i>Cistothorus palustris</i>	7	0.96
7. <i>Catharus ustulatus</i>	2	1.0
8. <i>Sialia mexicana</i>	2	1.0
9. <i>Toxostoma curvirostre</i>	2	1.0
10. <i>Vireo gilvus</i>	2	-1.0
11. <i>Dendroica petechia</i>	3	0.88
12. <i>Icteria virens</i>	2	1.0
13. <i>Quiscalus quiscula</i>	3	0.5
14. <i>Icterus cucullatus</i>	2	1.0
15. <i>Leucosticta arctoa</i>	4	1.0
16. <i>Carduelis tristis</i>	3	0.5
17. <i>Carpodacus purpureus</i>	2	1.0
18. <i>Spizella socialis</i>	2	1.0
19. <i>Spizella pusilla</i>	2	1.0
20. <i>Zonotrichia leucophrys</i>	2	1.0
21. <i>Pipilo erythrophthalmus</i>	6	0.33

absolute humidity during summer is lowest. Robins with the darkest plumage were from Newfoundland, where the percent saturation of the air is highest, as would have been predicted by Grinnell in 1910 but not by Gloger's ecogeographic rule. Addition of size variation in the robin, as different-sized circles, to a psychrometric chart of temperature-moisture relationships (Fig. 4A, B) makes clear that it is not dry bulb temperature that is most highly related to the size of the robin but rather wet bulb temperature or absolute humidity (Aldrich and James 1991, James 1991a). This graph allows a comparison of the predictive power of the three variables along its axes, representing three empirical models and extending the generality of the conclusions of James (1970). In combination with the test for passerine birds in general, we can say that, all across North America, intraspecific variation is related to climatic variables that are a function of measures of the total heat of the air during the breeding season. The total heat of the air can be estimated from its absolute hu-

midity, wet bulb temperature, or vapor pressure. This relationship leads to robust empirical models.

I think Bergmann should get more credit. Even before Darwin, he observed regularities in patterns of size variation among birds and mammals. His hypothesis about thermoregulation is controversial, but some physiologists agree that larger homeotherms tolerate cold better (Schmidt-Nielson 1984), and looking for exceptions by regressing size on latitude or altitude is not very informative. Instead, let the data reveal the pattern, examine the extent of concordance among species, and then develop empirical and process models that can be tested. Published maps of size variation in common, widespread species such as the robin (Fig. 3), Song Sparrow (Aldrich 1984), House Sparrow (*Passer domesticus*; Johnston and Selander 1971), and the six species for which there are maps in James (1970) all show the same pattern. Predictions of the association between size and climate continue if the analysis is extended to Mexico. Roxie Laybourne

a



b

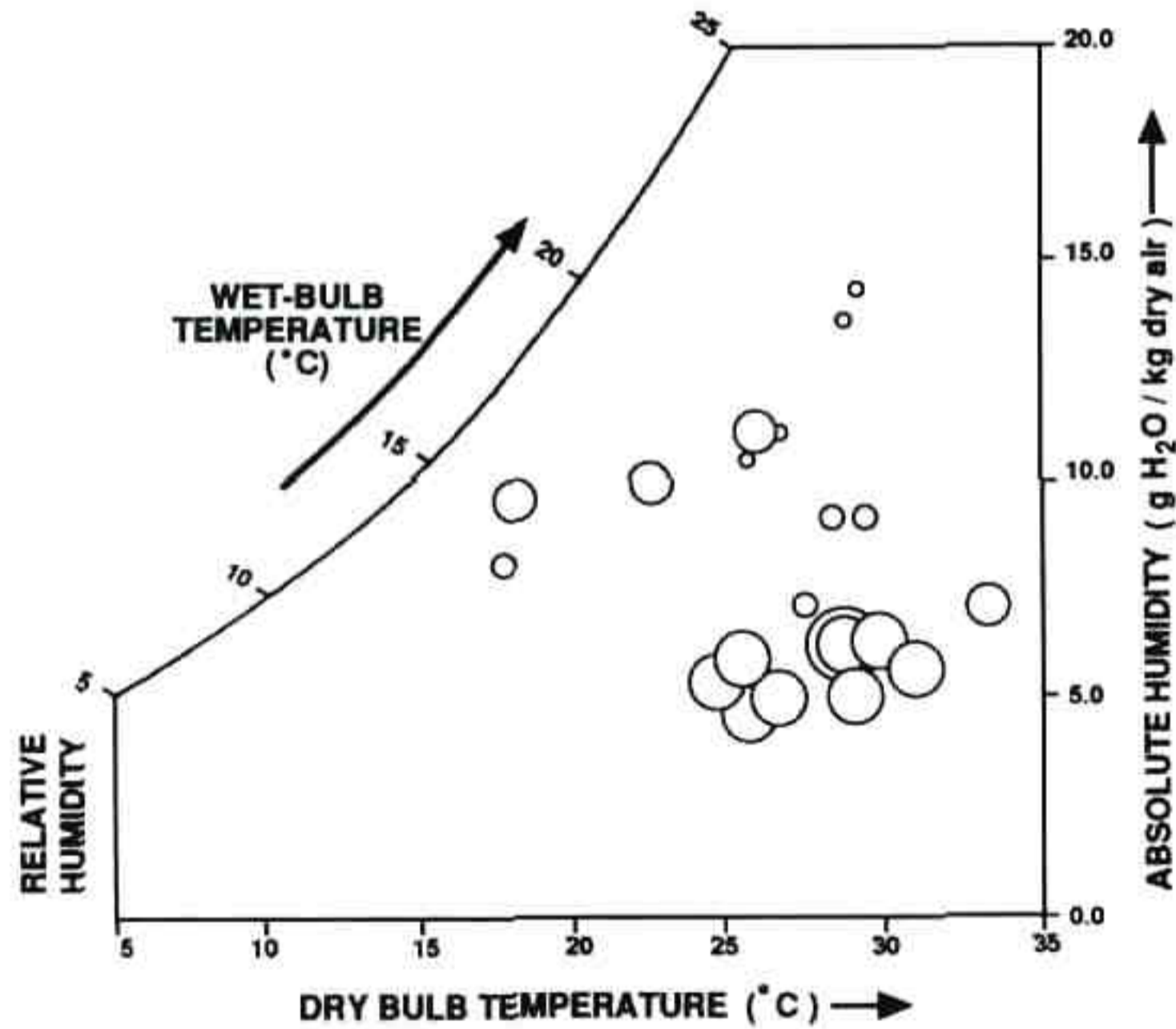


FIG. 4. Psychrometry and the size of the American Robin (modified from fig. 8 of Aldrich and James 1991). Sizes of circles are proportional to sizes (wing lengths) of robins.

and I put together a large set of measurements of study skins of adult Red-winged Blackbirds. They were smallest along the hot, humid Gulf of Mexico in Central America as well as in Florida and largest on the high dry

Mexican Plateau as well as in the Rocky Mountains and the northern Great Plains (Fig. 5; James et al. 1991).

To summarize, in North America some birds do not vary in size geographically, but

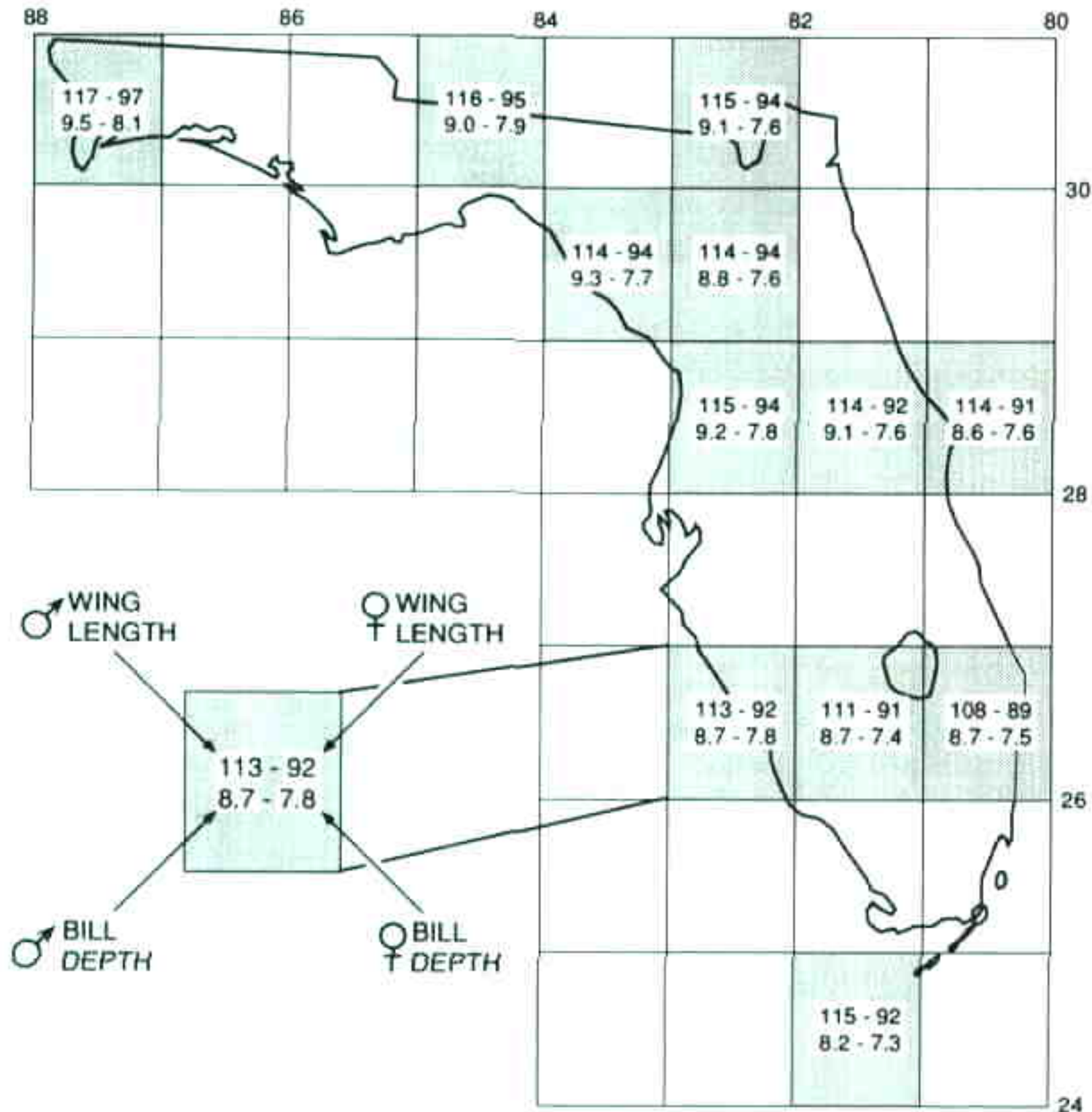


FIG. 5. Means of wing length for adult Red-winged Blackbirds in 1° latitude-longitude blocks in Florida (modified from fig. 1 of Mosimann and James 1979).

passerines during the breeding season, whether they are migratory or not, and many other species of birds that vary in size, tend to be smallest in southeastern Florida and southeastern Mexico. They are largest in the northern Great Plains, from the central Rocky Mountains along the continental divide into British Columbia, and on the Mexican Plateau. Within the United States, and probably elsewhere, this pattern is strikingly similar to climate variation in variables that estimate the total heat of the air during the breeding season. Empirical models expressing the relationship between size variation and July wet bulb temperature have more predictive power than do those for July dry bulb temperature. This pattern is more complex than could be detected in linear regressions of size on latitude or altitude. We do not know what processes maintain it.

B. Are there patterns of genetic variation that match the pattern of size variation?—We

can assume that the pattern of size variation in birds has at least a partly genetic basis, as do virtually all characters that have been measured in vertebrate animals (Wright 1978), but attempts to look for genetic variation that covaries with patterns of size variation have not been successful. Cox and James (1984) found no variation in the karyotypes of Red-winged Blackbirds taken in Florida, Colorado, and Minnesota. Ball et al. (1988) found virtually no structure in mtDNA haplotypes in red-wings taken all over North America. Similar cases are known for other species that have substantial geographic variation in size, such as the Downy Woodpecker (*Picoides pubescens*; Ball and Avise 1992) and the Song Sparrow (Zink and Dittman 1993). In cases where there is genetic structure, there is no apparent covariation among species or conformance to the pattern of size variation (Zink 1996). These results do not mean that the size variation does not have a genetic basis, only

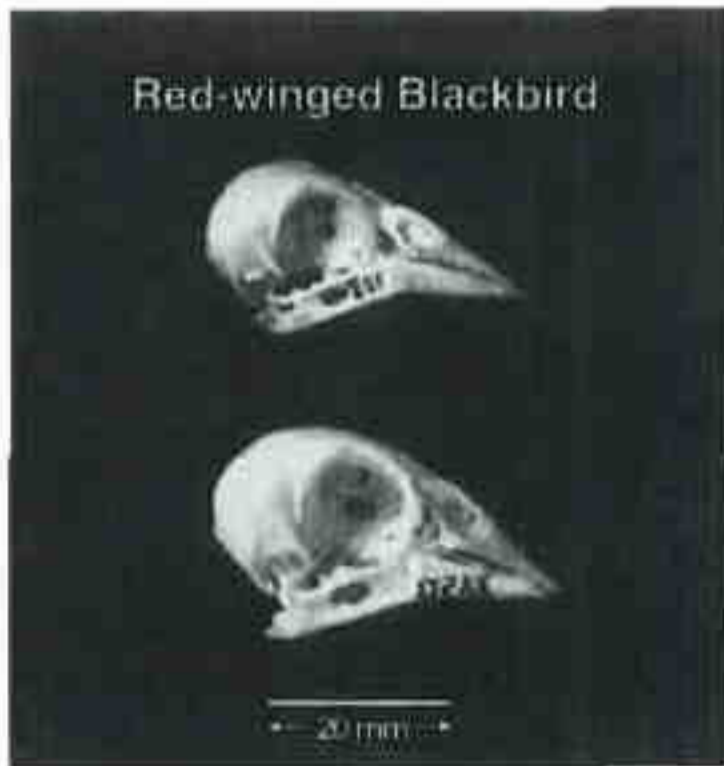


FIG. 6. A male Red-winged Blackbird skull from Florida (above) and one from Colorado (below).

that it is not detectable with present methods at the chromosomal or mtDNA level.

C. How does the shape of Red-winged Blackbirds vary with their size?—Allometry is the study of how shape varies with size, and a rich literature describes applications of multivariate analysis to such problems (Bookstein 1991; Zelditch et al. 1992; Rohlf and Marcus 1993a, b; Rohlf 1998). Allometry can refer to changes during the growth of individuals, differences among individuals at some stage in development in a population, or differences among populations. Mosimann and James (1979) contended that size and shape should be defined separately; then their covariation (or covariance) can be examined. The definition of size is context dependent. Reasonable size variables in different cases might be mass, individual measurements, averages of measurements, the geometric mean of measurements, or principal component 1 of measurements (Table 1). Shape can be expressed as outlines, proportions, ratios of measurements, angles of triangles connecting landmarks, or their multivariate combinations.

A photograph of a typical skull of a Red-winged Blackbird from central Colorado and one from Florida illustrates the extremes of the differences in size and shape of the skull within the United States (Fig. 6). It demonstrates one major allometric relationship, that larger birds tend to have proportionately deeper bills.

The allometric methods I have used are described in Mosimann and James (1979). If you make the reasonable assumption that the data

TABLE 3. Between-locality variance components for size variables, shape variables, and weight in 188 adult male Red-winged Blackbirds organized into 12 1° latitude-longitude blocks in Florida, estimated by one-way analysis of variance. Significant difference from zero at 0.01 is indicated by**. Multiply by 10^{-6} for actual variance estimates. From Table 2 of Mosimann and James (1979).

Variable	Variance
Size	
log (bill length)	13
log (bill depth)	213**
log (toe plus tarsus)	19**
log (wing length)	148**
log (tail length)	155**
log (weight)	923**
Shape	
log (bill length/bill depth)	212**
log (bill length/wing length)	197**
log (tail length/wing length)	10

are lognormally distributed, then differences between logarithms of the measurements express ratios, and linear statistical methods are available for allometric study. For example, among-locality variance components for selected log size and log shape variables for our sample of adult male Red-winged Blackbirds in 12 latitude-longitude blocks in Florida (Fig. 5) show significant geographic variation (Table 3). However, variation in log bill length and log toe-plus-tarsus length is negligible compared to that of log wing length, log tail length, and log bill depth. In shape, log (tail length/wing length) shows no significant geographic variation, even though both variables show considerable geographic variation in size. On the other hand, log (bill length/bill depth) and log (bill length/wing length) show substantial geographic variation. Note that it is due to variation in bill depth and wing length, not bill length. The same relationships are present in data for Florida females and for redwings throughout North America (FCJ unpubl. data). A study that looks at the characters independently can reveal differences among characters in their extent of geographic variation.

The methods of Mosimann and James (1979) for allometric studies also are amenable to general multivariate questions such as whether there is covariance structure in the size and shape of birds within and between localities. For example, Roxie Laybourne and

I measured museum study skins of adult male Red-winged Blackbirds taken during the breeding season from the United States and Mexico (James et al. 1991). For this large area we reported that the smallest redwings in terms of wing length tend to have the longest bills. The several shape variables transformed to logs (e.g., log wing length minus log bill length, log wing length minus log tarsus, and log bill length minus log bill depth) provided a vector of shape variables for each bird. Principal component 1 of the covariance matrix of the means of the three shape variables for seventeen 2° latitude-longitude blocks does not capture all the shape variation among localities, but it gives the primary axis of shape variation for the species. This component represents only shape (Darroch and Mosimann 1985), because size variation was not entered into the analysis. Then, using log wing length as size, we analyzed the covariance of size and shape within and between localities. The large ellipse in Fig. 7A and B shows the overall allometric pattern. Larger redwings have proportionately deeper bills and longer wings.

Small ellipses for variation within 17 geographic blocks show the same direction of covariation in some cases, but in the middle of the size range there is almost no indication of an association between size and shape either within or across blocks (Fig. 7B). These results do not support the assumption of Lande (1979) that phenotypic covariance matrices within populations remain stable as the means of the characters change across localities (James et al. 1991). If Lande's assumption were valid, it might be reasonable to assume that genetic covariance matrices within populations also were stable across localities.

Recall that, as with Florida Red-winged Blackbirds, we can ask how individual size and shape variables change at continental scales (Table 3). Overall, bill depth and wing length are more variable than bill length and tarsal length, but two shape variables (log bill length minus log bill depth, and log bill length minus log wing length) have even higher interlocality variance. These univariate estimates can allow insight into the allometry of intraspecific variation that may not be evident in purely multivariate applications.

D. Does environmental plasticity contribute to the geographic pattern of variation in size

and shape in birds?—To test predictions of the verbal process model that intraspecific variation in the size and shape of birds has an environmentally determined component, we conducted field and laboratory experiments during the 1980s. In 1980 and 1981, Katy NeSmith, James Cox, and I transplanted eggs of Red-winged Blackbirds between northern and southern Florida and between Colorado and Minnesota. The eggs were maintained in an incubator during transport, and their mothers were given dummy eggs so they could continue their period of incubation. Control groups were from eggs that also were put in an incubator but then returned to nests in their home locality. All nestlings were measured daily. Their shape variables, standardized to a fixed tarsal length (log x minus log tarsus of 20 mm), were used in a canonical discriminant function analysis that maximally separated the shapes of normal nestlings. Then the mean scores for control and transplanted groups were plotted along that axis (Fig. 8). A significant proportion of the differences in the shapes of nestlings at this stage was nongenetic, and the genetic and nongenetic components of phenotypic variation covaried. Note that these differences are in multivariate shape, not size or weight.

The extremes of size and shape variation in adult Red-winged Blackbirds are greater in Mexico than in the United States, so with substantial help from Mexican students, especially Romeo Dominguez Barradas, Jorge Vega Rivera, and Fannie Rebon, we spent the summers of 1983–1985 in Mexico continuing our transplant experiments. We made reciprocal transplants of eggs between nests near Tlacotalpan, Veracruz, where the adults are small and have thin bills, and nests near Coatetelco, Morelos, where adults are large and have proportionately deeper bills. The weights of the nestlings from transplanted eggs were not affected by the experiment. Apparently, their genetically determined appetites and their efficiency at processing food determined their weight gain, even though they were being reared in a locality where native birds developed differently. The most plastic character in both sexes was bill shape, and it changed toward that of the foster population (James and NeSmith 1988). We currently are conducting new analyses on these data with SAS PROC

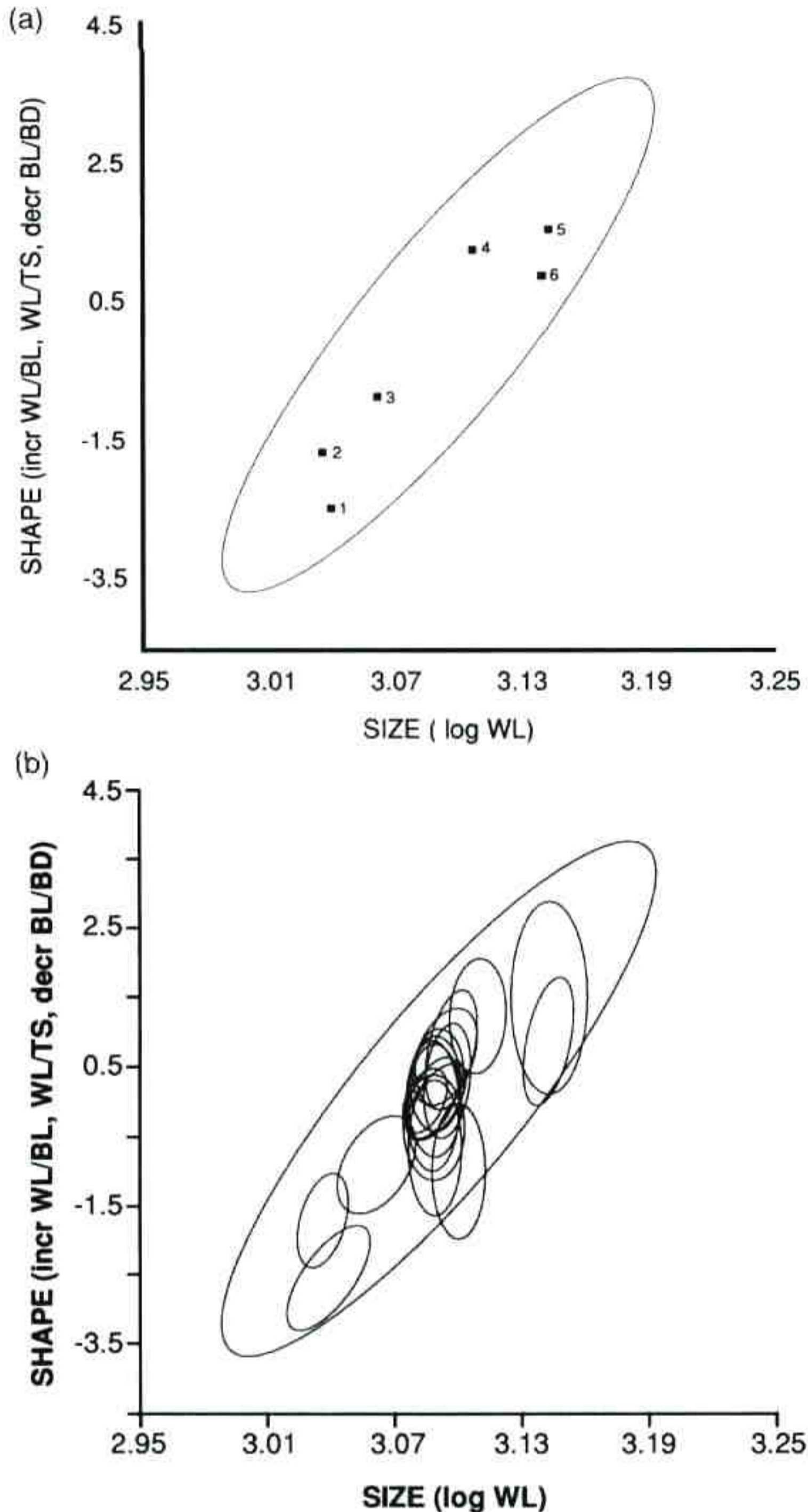


FIG. 7. Geographic variation in the size and shape of Red-winged Blackbirds based on data from 17 geographic blocks (from figs. 1 and 2 of James et al. 1991). Size is log wing length (multiplied by 100). Shape is principal component 1 of a covariance matrix among three log ratios. The ellipse is a 0.99 equal-frequency ellipse for mean values for each block. (A) Means for six of the blocks are identified with numbers: 1, Everglades, Florida; 2, Tlacotalpan, Veracruz, Mexico; 3, Tallahassee, Florida; 4, Greeley, Colorado; 5, El Carmen, Puebla, Mexico; 6, Coatetelco, Morelos, Mexico. (B) Small 0.5 equal-frequency ellipses for each of 17 geographic blocks show the extent of within-block covariation in size and shape within the overall pattern of covariation.

CANONICAL DISCRIMINANT FUNCTION ANALYSIS OF NESTLING SHAPE

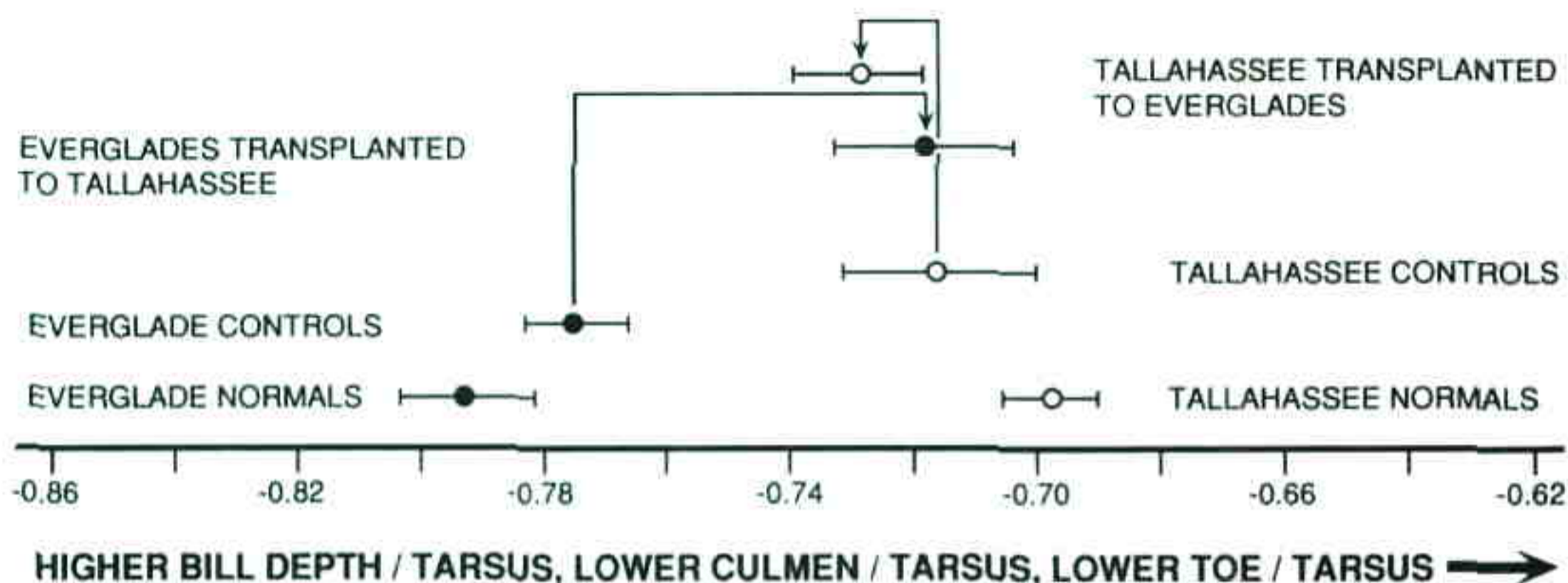


FIG. 8. Means and 95% confidence intervals for the shapes of nestling Red-winged Blackbirds in normal ($n = 13, 30$), control ($n = 19, 13$), and transplanted ($n = 16, 11$) groups reared in the Everglades and Tallahassee, Florida (from fig. 1A of James 1983). The shapes of transplanted nestlings shifted toward those of nestlings in the foster population. The canonical discriminant function axis was calculated to maximize the difference between normal (unmanipulated) birds.

MIXED, a program that can handle repeated measures analysis of variance when there are different numbers of measurements for different individuals. In combination with the results of the transplant experiments in the United States during 1980 and 1981, we concluded that there is significant environmental plasticity in some but not all aspects of the development of nestling Red-winged Blackbirds and that the plasticity is most evident in the size and shape of the bill. Smith (1993, 1998) reported similar results for transplant experiments with the Song Sparrow in California, but differences between her methods of data analysis and ours preclude direct comparisons.

In 1987, we performed a reciprocal transplant experiment with redwing eggs between Tallahassee, Florida, and Greeley, Colorado. Just before the birds were ready to fledge, we took them into captivity. At that stage, the growth of the tarsus was complete, but the wing length, bill length, and bill depth were only about half of their adult values. Again, the weights of the birds were not affected by the experiment. Some of the differences in measurements between control and transplanted groups were maintained in captivity for the next few weeks after fledging. Environmentally induced differences can therefore persist into the adult phenotype. The suggestion that

environmental plasticity itself may be an object of natural selection was discussed in James (1991a) and reviewed in Schlichting and Pigliucci (1998).

E. What causes the environmental plasticity in nestling Red-winged Blackbirds?—The close match between size variation in birds and the continental pattern of variation in summer wet bulb temperature or absolute humidity may be due to adaptations involving thermoregulation, the *Warmoeconomie* of Bergmann (1847), but in terms of the total heat of the air rather than just dry bulb temperature. Other possibilities are simply environmental correlates of this pattern. For example, the phenology of the nesting season of the robin has much the same pattern (James and Shugart 1974), and perhaps the pulse of food availability, as advocated by Fleischer and Johnston (1982) and Murphy (1985).

The way to check the prediction of the process model that the microclimate of the nest has direct environmental effects on plasticity in the development of nestlings is to conduct an experiment in which related birds are reared on the same food in different physical environments. NeSmith (1985) conducted this experiment. She randomly assigned four-day-old sibling Red-winged Blackbirds from Lake Jackson, Leon Co., Florida, to one of three

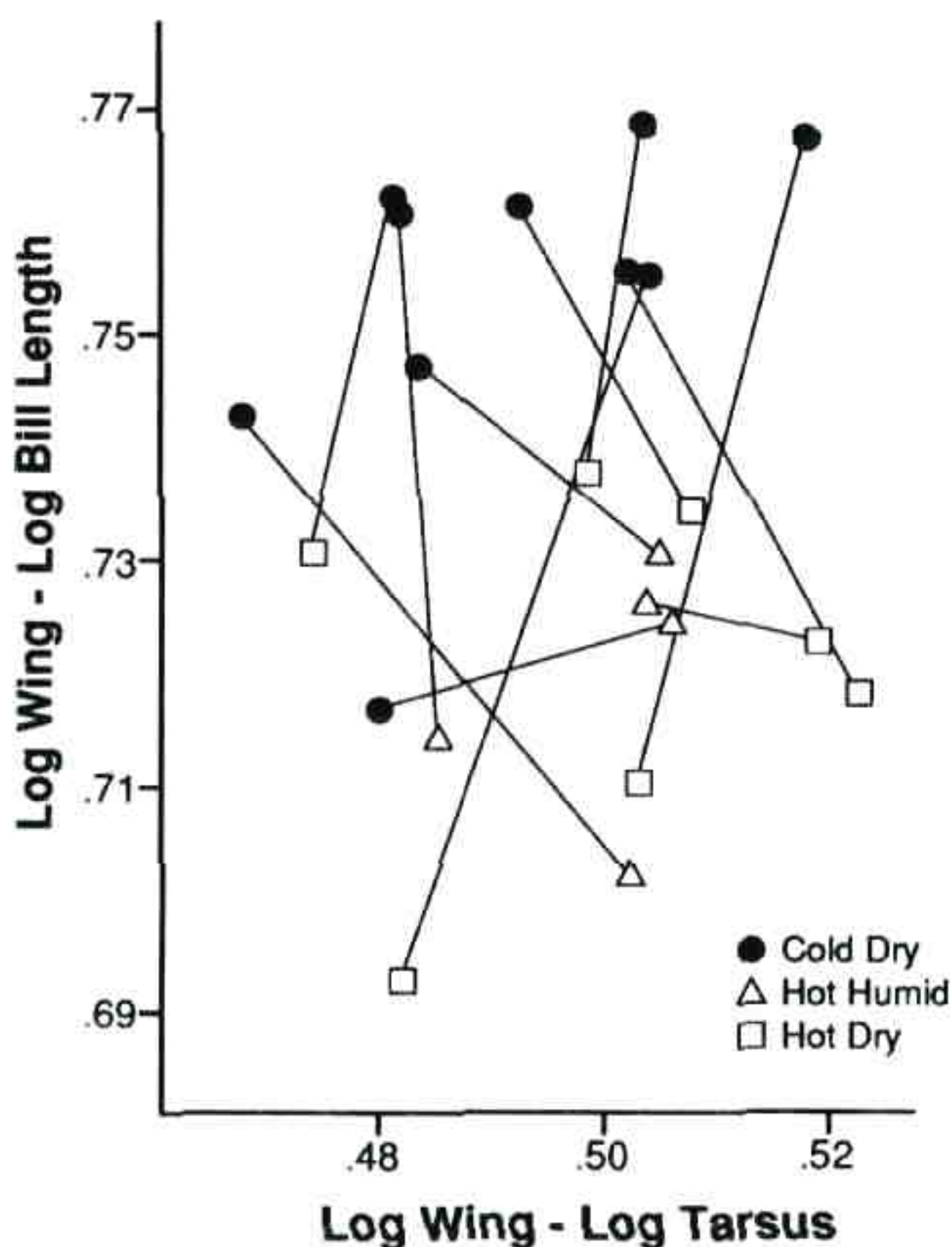


FIG. 9. Nine of 11 pairs of 20-d-old sibling Red-winged Blackbirds reared in a cold dry chamber had proportionately shorter bills (log wing length minus log bill length; modified from NeSmith 1985 and fig. 3 of James 1991a).

environmental chambers: (a) cold and relatively dry, (b) hot and humid, (c) hot and dry. She fed them crickets and chicken starter mash on demand. At 20 d of age, most of the birds in the cold chamber had proportionately shorter bills than did their siblings in the other chambers (Fig. 9), so the prediction was borne out. Other measurements and weights were not consistently affected.

IV. Long Term Trends in Bird Populations

The Biological Resources Division of the U.S. Geological Survey generously allows access to its more than three decades of annual Breeding Bird Survey data for the United States and Canada. Although analysis of such data is fraught with difficulties, it is tempting to try because the data are likely to contain important information about the large scale dynamics of trends and may even lead to in-

ferences about causal factors affecting bird distribution. My own efforts have been in collaboration with Charles McCulloch, David Wiedenfeld, Lori Wolfe, and Lyla Messick. We have proposed formal methods (nonparametric nonlinear route regression) for the examination of trends, and we emphasize making comparisons among regions (James et al. 1990, 1992, 1996; McCulloch et al. 1997). We have been able to show that, in the eastern United States between 1966 and 1987, some species of warblers were declining in the highlands while they were stable or increasing in the lowlands (James et al. 1992, 1996; McCulloch et al. 1997). We think that correlates of elevation may be factors in regulation of populations of warblers and other land birds. We do not agree with Robbins et al. (1986) that the Breeding Bird Survey data show overall population declines in eastern forest birds

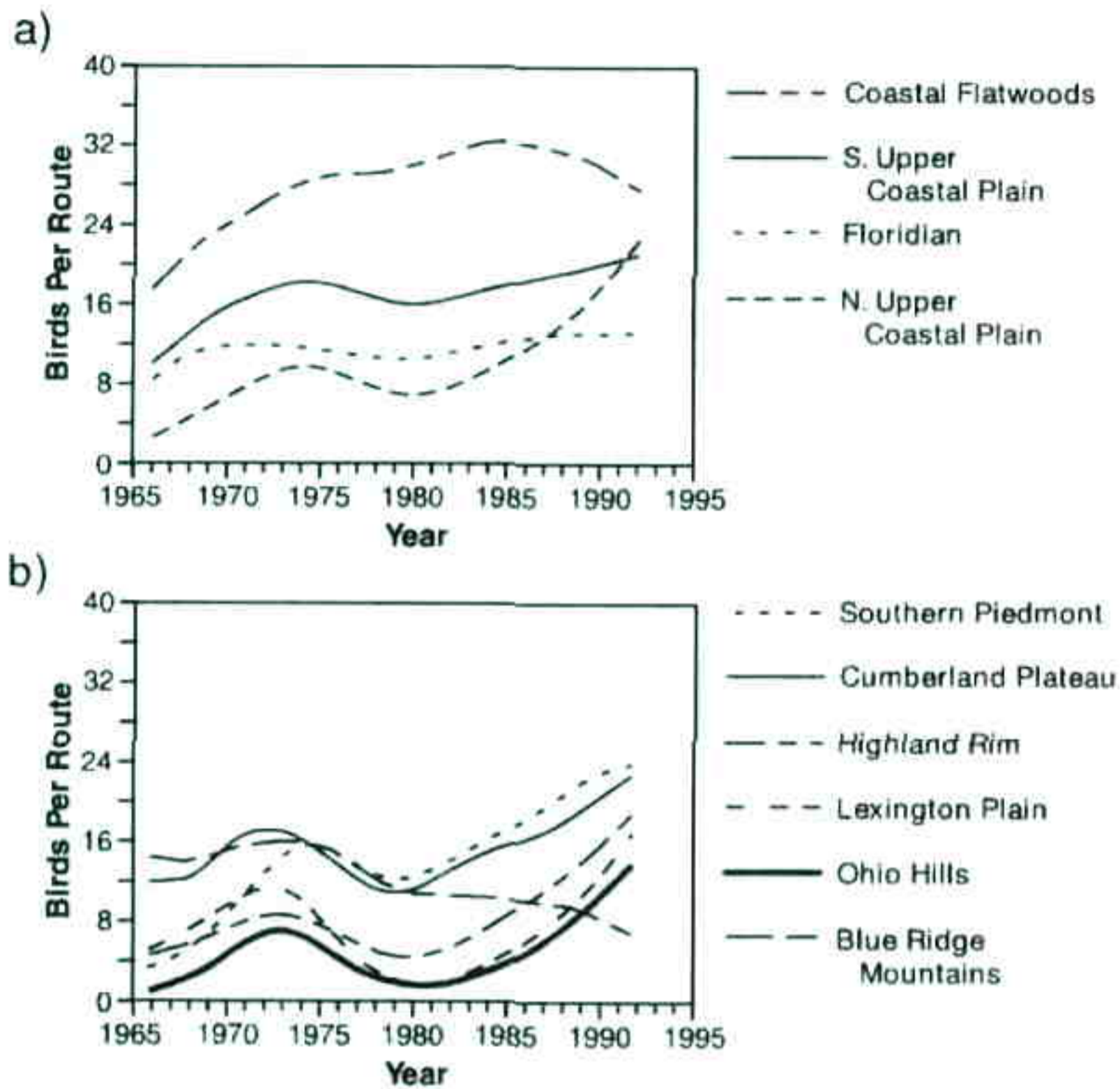


FIG. 10. Population trends in the Carolina Wren based on Breeding Bird Survey data (fig. 2 of James and McCulloch 1995).

that migrate to the Neotropics. Subsequent analyses indicate that, although some species of warblers certainly are declining, just as many species are increasing (James et al. 1996, McCulloch et al. 1997). We think a good way to move such work toward causal models is to make comparisons among regions that have been subjected to differing environmental conditions. For example, you can see the impact of the severe ice storms of the winters of 1976–1977 and 1977–1978 on populations of the Carolina Wren (*Thryothorus ludovicianus*) and the extent of its subsequent recovery by the examination of nonlinear trends for different ecoregions (Fig. 10; James and McCulloch 1995; see also Robbins et al. 1986). The graphs show a time series model with presumably differing levels of intervention (prolonged cold weather) in different regions. We hope to design some further observational studies in the near future. Of course, these studies are just supplementary to those that study the bird populations more directly.

V. Conservation of the Red-cockaded Woodpecker

Also during the 1990s, I have been studying the longleaf pine ecosystem and its endangered Red-cockaded Woodpeckers. The species still occurs in isolated populations from Virginia to Texas, but the populations that are not declining are being supported by the provision of artificial cavities (U.S. Fish and Wildlife Service 2000). The health of the longleaf pine ecosystem today depends largely on forest management. Without frequent prescribed burning, the forest will be overgrown by woody shrubs and then hardwood trees. Past timber management has allowed the pine trees to become too dense for the full diversity of the forest's biota to thrive. We found that the population of woodpeckers on the Wakulla Ranger District of the Apalachicola National Forest near Tallahassee, Florida, is declining, and that the population on the Apalachicola Ranger District, which is the largest remaining

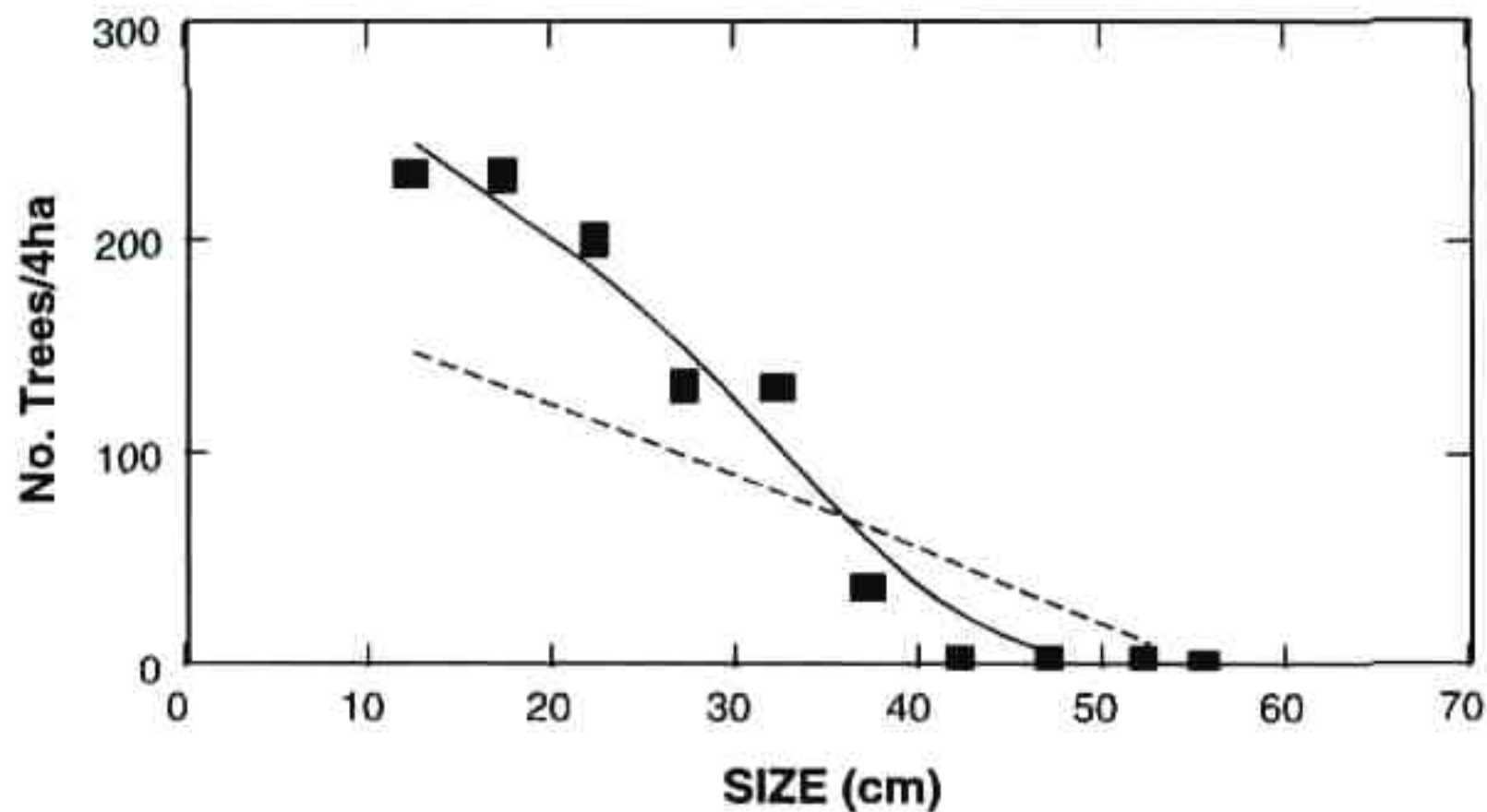


FIG. 11. Current distribution of pine trees by size class in key stands of Red-cockaded Woodpecker habitat in the Wakulla Ranger District of the Apalachicola National Forest, where the population of woodpeckers is declining (solid line), and the distribution in the Apalachicola Ranger District, where the population of woodpeckers is large and stable (dashed line; fig. 7B of James et al. 2001).

population anywhere, is stable (James 1991b, 1995).

By monitoring banded birds and their habitat in randomly selected samples of sites in both districts, we have been able to demonstrate important habitat correlates with the group size and productivity of individual social units (James et al. 1997, 2001). The most striking empirical relationship is that woodpecker groups are more productive in territories that have been subjected to more frequent prescribed fires. Such territories have a higher percentage of herbaceous vegetation in the ground cover.

In collaboration with the U.S. Forest Service, we designed a large scale five-year experiment in prescribed burning. Sixty management compartments, averaging more than 600 ha each, were randomly assigned to one of three prescribed burning regimes. After four years we see important differences in the percent of herbaceous ground cover in areas receiving the different treatments. We also are using the relationship between forest structure and the health of social groups of Red-cockaded Woodpeckers to advocate trials of some new types of timber harvest (Fig. 11). For example, over a period of several decades it should be possible to manage timber on the Wakulla Ranger District to mimic the tree structure on the Apalachicola Ranger District.

One of our objectives is to devise a simulation model for processes limiting popula-

tions of Red-cockaded Woodpeckers. Sub-models will be for major categories within an envirogram (Fig. 12). The simulation model will include assignments of rates to processes that affect the size of the future population of birds. The results of both experiments and observational studies in step 7 of Fig. 1 can contribute to this assignment. We plan to use the model to compare estimates of alternative management scenarios.

SYNTHESIS OF IDEAS ABOUT ECOMORPHOLOGY AND THE NICHE GESTALT

What have I learned from half a century of studying birds? First, that although all the steps in Fig. 1 are important in the continuing progression of the research process, I think the real originality in science is at steps 2 and 5, the formulation of insightful empirical and process models. The actual work of testing predictions of models and comparing alternative models is important, but secondary. I agree with Casella and Schwartz (2000) that, in practice, scientific theories (verbal empirical models and verbal models about processes) are only rarely verified or falsified by direct observation or crucial experiment. Rather they are "accepted or rejected on the basis of how well they explain selected sets of data, how elegant, simple and useful they are, how well they do against competing theories."

The two examples described in this paper

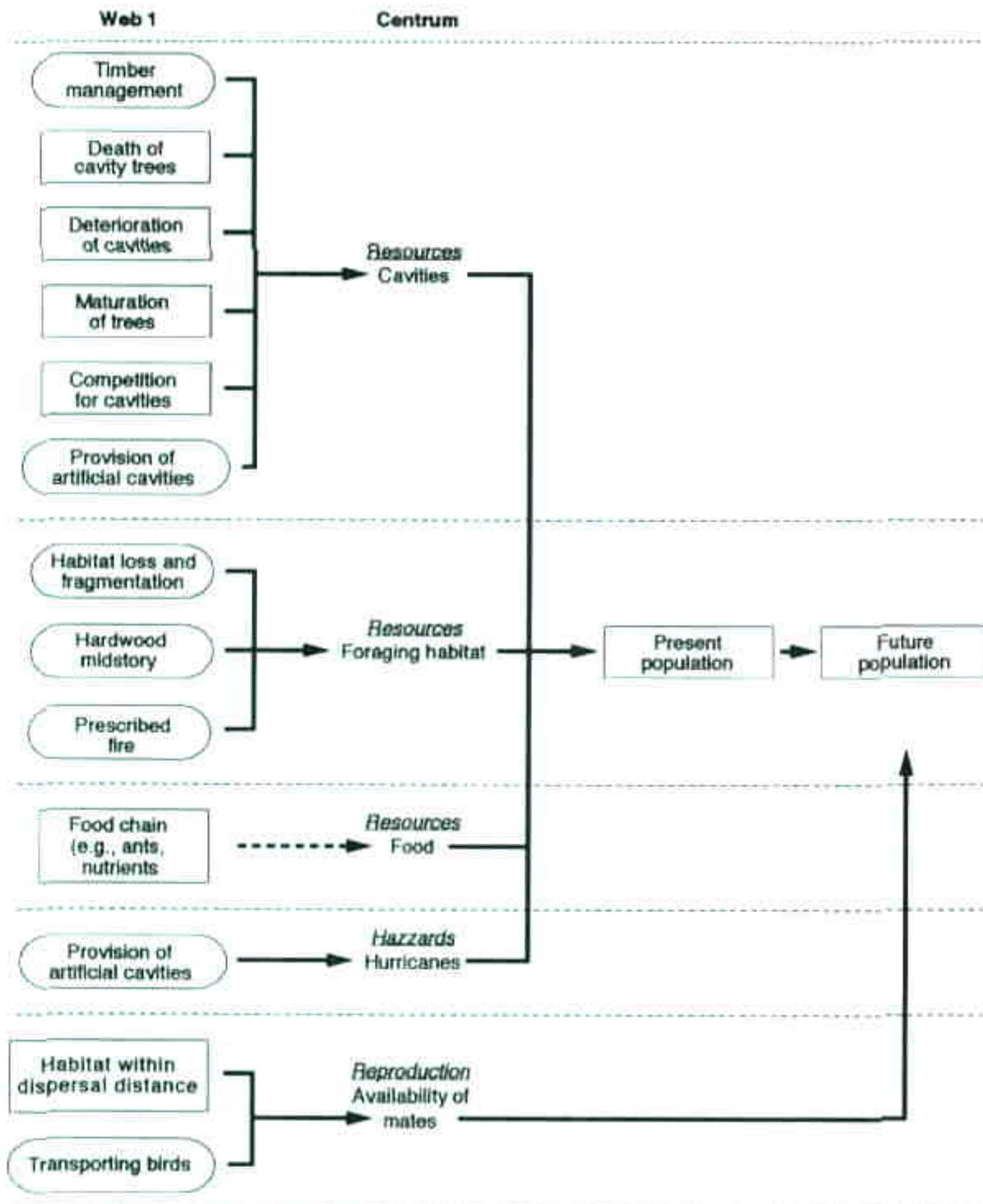


FIG. 12. Envirogram for the Red-cockaded Woodpecker, giving factors (processes) that if changed will affect the number of birds (modified from fig. 1 of James et al. 1997). Factors in ovals can be affected by management.

are studies of intraspecific variation in external morphology and exploration of the ecological concept of the niche gestalt. What I see is a striking concordance in patterns of intraspecific size variation among birds (James 1991a), one that is highly related to certain climatic gradients. None of the various proposed causes for the pattern except for thermal adaptations accounts for the fine scale of the phenomenon, which can be detected even in 1° latitude-longitude blocks across areas such as Florida with its minimal geographic gradients in climate (Mosimann and James 1979).

Intraspecific variation in birds has a statistically significant nongenetic component. The first results of transplant experiments (James

1983) were based on a multivariate analysis of shape variables. The subsequent transplant experiments in Mexico (James and NeSmith 1988) showed that weights and most measurements are remarkably invariant among nestlings from transplanted and control eggs. The exception is the size and shape of the bill, which is consistently plastic and tends toward the phenotype of the foster population. In a controlled laboratory experiment, the bill lengths of sibling Red-winged Blackbirds reared on the same diet grew more slowly in birds reared in a colder drier chamber (Ne-Smith 1985, James 1991a).

The niche gestalt is a theoretical construct (James 1971), the Grinnellian idea that there is a subset of the structure of the vegetation

that is correlated with species specific resources that allow a species of bird to thrive. It cannot be measured directly, but it can be deduced from examination of the many places where a species lives and deciphering of which elements of the structure of the vegetation are consistently present. Recently, we applied this construct to plans for the restoration of habitat for the endangered Red-cockaded Woodpecker. We recommended trials of prescribed burning and forestry practices that promote a long term trajectory toward the habitat that exists today where the only recovered population occurs (James et al. 2001). Even if we do not understand all the processes involved, we think such trials may lead to management that promotes self-sustaining populations.

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