In the first part of the study parental visits to the nest during the incubation period, from the laying of the last egg to the hatching of the young, are presented in the form of continuous actograms of 4 examples. The results were analyzed with especial reference to the duration of brooding phases and periods off the nest (and partly also in relation to the temperatures prevailing at the corresponding times).

The second part of the study demonstrates from two examples (extended brooding experiments) that the brooding rhythm continues normally for quite a time after completion of the actual brooding period.

In the Great Tit broods investigated, interruptions of brooding for several hours occurred only in the early morning during the first days of incubation. On the other hand, shortly before the abandonment of the nest, they occurred at midday and in the afternoon — the pattern in reverse.

The investigations are to be continued on an extended scale.

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Some aspects of individual variation in birds

by Eberhard Curio

In the following some generalities concerning individual variation in birds will be critically examined ending with a brief discussion of whether such variation is adaptive.

1. Scaling effects

As a rule individual variation becomes interesting only if one compares samples of individuals that differ in terms of sex, age, place, etc. Such a comparison is easily confounded, however, if scaling effects are given their due attention. There is some definite relationship between the range of variation and the absolute magnitude of the associated mean M (or whatever value is used to denote the central tendency of a measure). Commonly, s (standard deviation) and M covary. Thus, there is no variation in the number of secondaries in the oscines where they are species-specifically either nine *or* ten; variation increasing in the white stork

(Ciconia ciconia) to 23 to 24, and to 38 to 40 in *Diomedea* (STRESEMANN & STRESEMANN 1966). A similar correlation can be found in the number of body segments in myriapods (MAYNARD SMITH 1960) and the number of teeth of Odontoceti (KEIL 1966). In Darwin's finches, *Geospiza fuliginosa* on Indefatigable Island responds much more strongly than *G. difficilis* on Tower Island to certain novel and enemy stimuli. It is noteworthy that *G. difficilis* exhibits a smaller individual variation of response strength than *G. fuliginosa* (pooled data, P = 0.008). Thus, again variation increases with performance. From a consideration of predator pressure on the two islands one would have expected the reverse to be true; whereas predators are virtually absent from Tower Island their pressure is maximal on Indefatigable where it should exert stabilizing selection. Perhaps epigenetic factors are more important in determining the degree of variation than the selection forces that have molded the response in question: The more energy growth of an organ or performance of a behaviour demands, the less rigidly is either controlled by the genome, although stabilizing selection need not be less than in other cases where comparable precision is demanded (CURIO 1969). MAYNARD SMITH (1960) has developed three models that can account for species-specific numbers of meristic units (feathers, teeth) of an animal. Numbers have been found to be invariant up to about 30. Beyond that threshold number epigenetic errors begin to creep in that lead to individual variation of those numbers. There exists no model that can account for precision of behavioural performance of a species, largely because it is not clear what the „units" are that cause behaviour to vary individually.

Strangely, for some metric traits of mammals the reverse is true, i. e., individual variation decreases as M increases (YABLOKOV 1974).

Generally the relationship between the magnitude of the mean and the variance is only too readily obscured or overlooked by computing the coefficient of variation $V = \frac{s \cdot 100}{M}$ thereby removing scaling effects. It should be stressed, however, that they present an important challenge to the developmental physiologist who is interested in what determines the range of *absolute* variation. For comparative purposes, of course, some measure of relative variability like V is indispensable.

2. Morphological and behavioural variation

Usually, an organ is permanently present and hence only its inter-individual variation can be measured. A few structures such as, for example, feathers that are renewed permit one to observe intra-individual variation. This advantage accrues on a much larger scale to all behaviour patterns that occur more often than once; they may vary from total absence to maximal strength or completeness, even under the same external conditions. Having more degrees of freedom, therefore, behaviour patterns would be expected to be more variable than structures. Secondly, behaviour patterns involve temporal in addition to spatial characteristics and hence become susceptible to influences that gain in weight as time goes by. This also leads to a larger variation of behaviour in contrast to structures. This prediction seems to be borne out by a study of structural and behavioural variation in the middle European pied flycatcher *Ficedula h. hypoleuca* (Fig. 1). Wing length, as measured by V, varies substantially more than mobbing at a redbacked shrike *(Lanius collurio)* ♂. Note that the frequency distribution permits the possibility that each single individual uses the entire range of the whole population. In order to test this idea, mobbing responses of individuals were correlated intraindividually. τ_{Kmax} represents the intraindividual correlation of responses recorded in the same year and the same breeding stage. As can be seen this value exceeds τ_{Kmin} resulting from responses recorded in different years and all breeding stages. Yet both correlations are significant, although effects resulting from aging and from changes in other conditions clearly lead to a deterioration of intaindividual response correlation. The latter, however, permits one to reject unequivocally the above-mentioned possibility; individuals are restricted to only part of the overall spectrum of the whole population sampled and thereby reflect a certain degree of individual behavioural stability, as sketched by the individual curves in Fig. 1 b (see also THIELCKE 1964, TSCHANZ 1968, BEER 1970 for birds; JENSSEN 1971 for *Anolis nebulosus*). For the sake of simplicity wing length has been assumed to remain individually almost constant ($\tau_K \sim 1$) although this is clearly not yet proved.

The above prediction is not borne out by studies of stereotyped displays. The strut display of the sage grouse *(Centrocercus urophasianus)* ♂ varies interindividually very little. The interval between two comparable peaks of the display lasts 1.55 ± 0.01 (M±s), with V = 0.07%; a second

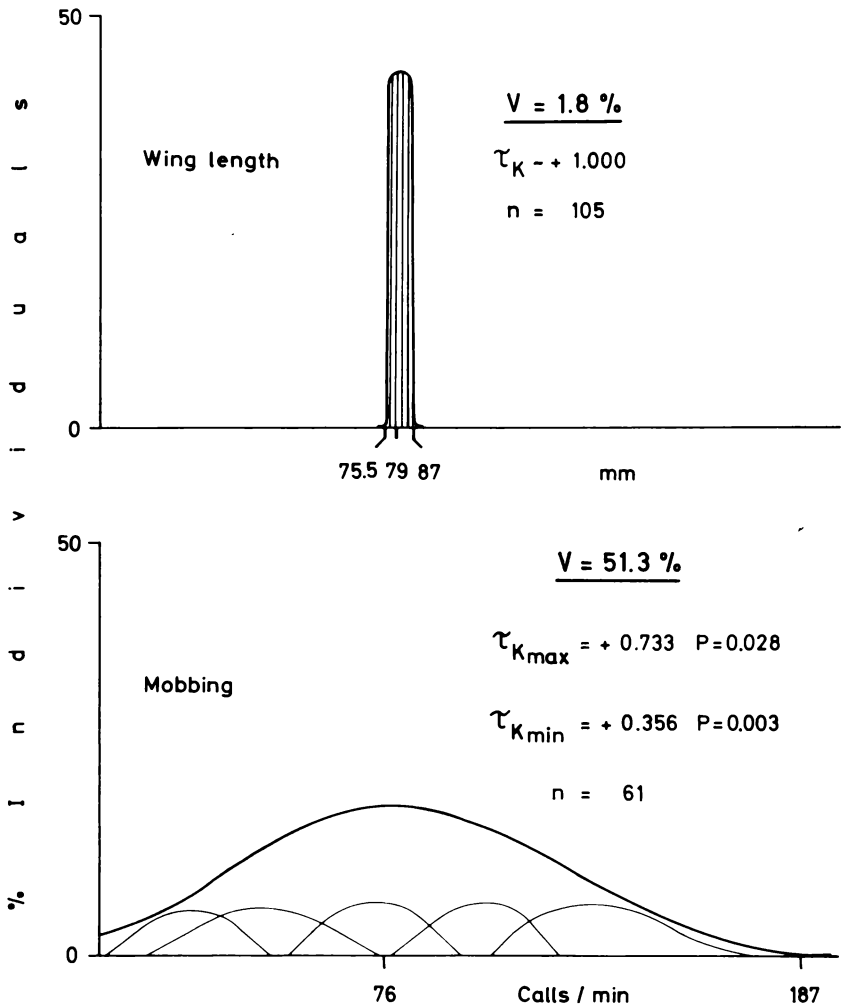

Fig. 1. Diagrammatic representation of individual variation as measured by V = s. 100/M in middle European pied flycatchers *Ficedula h. hypoleuca.* a: wing length (from data in CURIO, 1960); b: mobbing (calls/min) at ♂ redbacked shrike by territorial birds (from CURIO 1975); n = number of individuals recorded. τ_K = KENDALL's rank correlation coefficient. For further explanantion see the text.

method yielded 1.1<V<4.3%. Likewise, strut duration differs only between some ♂♂ but not others. It appears then that intraindividual variation is scarcely less than that of the population (WILEY 1973). Similary, goldeneye *(Bucephala clangula)* ♂ vary little in the duration of their two most stereotyped displays with V = 5.1 and 6.1%, respectively. As in the pied flycatcher, the resticted ranges of the measurements on individual goldeneyes in comparison to the population range suggest that intraindividual variation is smaller than interindividual variation (DANE *et al.* 1959, DANE & van der KLOOT 1964). Temporal patterning of a species song may exhibit as much precision as the strut display mentioned above. The intervals between the onset of successive syllables of two ♂ chipping sparrows *(Spizella passerina)* had V's. of 1.3 and 1.7%, respectively (MARLER & ISAAC 1960). These studies suggest that the patterning of stereotyped displays varies much less than a frequency measure such as the strength of mobbing at a constant stimulus (Fig. 1). This is underlined by two more frequency measures of the pied flycatcher

varying with a similar amplitude. ♂ differ in courtship feeding by a factor of 13 (0.3—3.9/h, 4 ♂ on 13 days of observation), and in greeting the ♀ near the nest hole by a factor of ≥ 100 (o [2 ♂], 0.02, 0.2 and 2.0 times/h, during 101 hs. of observation). Similarly two ♀ differed in the latter respect by a factor of 40. There is an indication that the more a ♂ feeds its mate the more the ♂ will feed its young (CURIO 1959; see also NISBET 1973). There is, of course, the danger that displays directed toward a social companion may be influenced by its individual characteristics. There is no easy way out of this dilemma but for behaviours like feeding the mate or young there should be a maximum demand from those receiving the benefit. Hence constraints of a maximum feeding rate should reside in the provider itself.

The evidence presented so far could be taken to mean that *repetition rates* of *„fixed" action patterns* fluctuate much more dramatically within populations than their *internal temporal patternings.* Since, however, the stereotyped displays mentioned occur prior to or during pair formation or copulation, selection against hybridisation may have led to the precision of their patterning. The question could be settled by looking at species where the repetition rate of a behaviour is of importance in pair formation. According to NISBET (1973) the rate of courtship feeding during pair formation in the common tern *(Sterna hirundo)* ♂ varies a great deal (from which the ♀ could extrapolate on his abilities in feeding her young; the two performances covary). Hence repetition rate *per se* seems more likely to vary individually. Another means of settling this question would be to look at the individual variation of „fixed" action patterns that take place *after* pair formation.

Because of the scarcity and the diversity of data any generalization as to whether behaviour patterns tend to show more individual variation than structures appears premature. V values of metric morphological characters range from ca 1% (MAYNARD SMITH 1960, MAYR 1963) to almost 10% (e. g. van VALEN 1963) and would thus tend to resemble the variation of stereotyped displays referred to above, but not that of behaviour repetition rates with their enormous fluctuation.

3. Allozyme variation

Hardly anything is known in birds about individual variability of allozymes. Their analysis leads to a direct assessment of individual heterozygosity and has, in this respect, become a powerful tool of population genetics applicable to plants and animals alike (review LEWONTIN 1974). It permits glimpses at the genetics of a population without the tedious and often impossible task of conducting breeding experiments. The method is based on the assumption that each structural gene gives rise to an enzyme the variants of which (allozymes) reflect corresponding changes of the underlying genes. As an example, MILNE & ROBERTSON (1965) have analysed the egg albumen of eider ducks *(Somateria mollissima)* in a British breeding area. They found one locus to vary with respect to three alleles a, b und c (Fig. 2). Most remarkably, they found one of two adjacent populations to have a higher frequency of allele b (o. 27) than the other (o. 14), with the former being partially migratory *(Teilzieher)* and the latter being entirely sedentary. The difference in allele frequency indicates some degree of reproductive isolation between both populations, but it need not be causally linked to the difference in their migratory habits.

In several reptiles *(Uta, Anolis, Lacerta)* and in oats *(Avena)* average individual heterozygosity has been found to correlate well with morphological variation (SOULÉ & YANG 1973, SOULÉ *et al.* 1973, GORMAN *et al.* 1975; MARSHALL & ALLARD 1970). Because of this relationship and because of the ubiquitous action of polygenic inheritance of traits, SOULÉ (1972) suggests that measures of morphological individual variation reflect the underlying genotypic variation. If this were true, morphological variation could be used as a convenient indicator of genic variability. Yet it is to be noted first, that the relationship between the two sorts of variation has scarcely been studied in birds, which clearly provides a challenge for future research. Second, we hardly know how within-population genetic diversity expresses itself in behaviour and physiological activities. In a pioneering attempt BAKER (1975; see also NOTTEBOHM & SELANDER 1972) found in populations of white-crowned sparrows *(Zonotrichia leucophrys)* that allozyme variation changed slightly over an altitudinal gradient in a continuous Colorado breeding habitat. The birds displayed no dialects in their territorial song. In California, however, song dialects appear to correspond to populations with some reproductive isolation. The cause-and-effect relationships underlying these findings could be interpreted to mean that dialects arise from colonization and subsequently restrict gene flow between populations. This

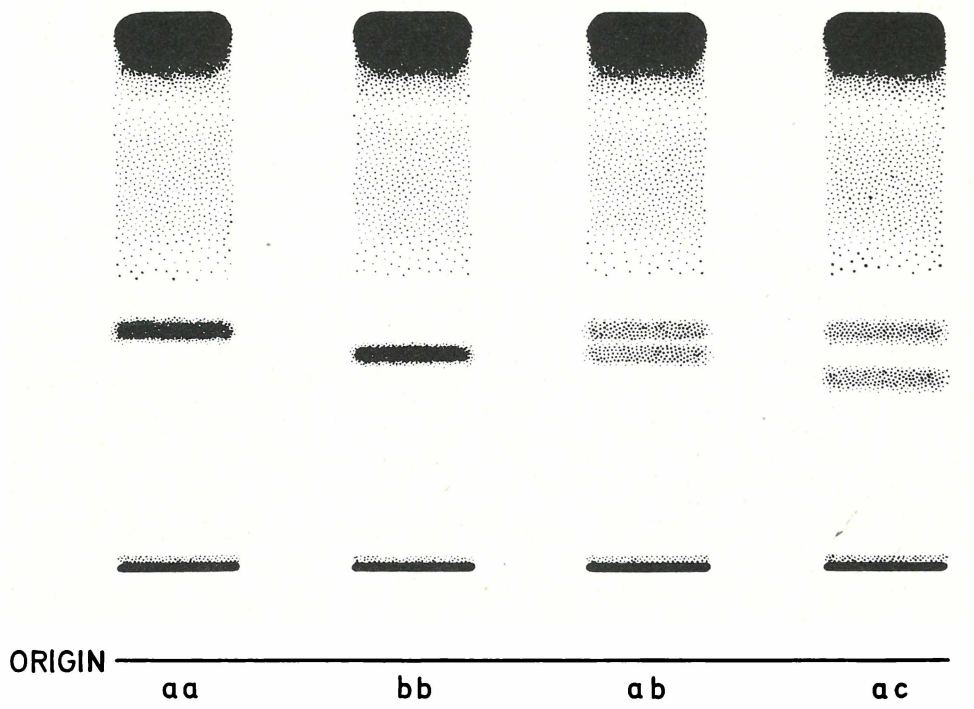

Fig. 2. The appearance of eider duck albumen produced by four different genotypes after starch-gel electrophoresis, stained with amido-black. a, b and c are alleles of the same structural gene (redrawn from MILNE & ROBERTSON 1965).

idea would work if song were acquired by tradition, which is likely the case. Viewed in this way, song variation would not be a consequence but a *cause* of genic diversity. Therefore, songs may not be the best trait to look at when studying behavioural variation as a consequence of genotypic variability.

Another finding of BAKER (*l. c.*) cautions against SOULÉ's suggestion to take structural variation as an indicator of the amount of heterozygosity: Despite a fair degree of allozyme variation, four metric traits were quite uniform across the four populations studied.

Behavioural variation may arise directly as an expression of the underlying genic variability. It could also be due, however, to an intervening morphological variation and not to the genes directly. For example, HINDE (1958) suggested that animals while growing up learn to take those foods which their „repertoire of behaviour patterns and structure permit to exploit most efficiently". Against the generality of this hypothesis a number of criticisms have been leveled (CURIO 1976). Here another will be added. Although the idea may well apply to relationships between sexual dimorphism in beak and tongue morphology in some woodpeckers *(Centurus spec.)* and a corresponding dimorphism of their foraging techniques (SELANDER 1966), it is clearly disproved by LIGON's (1968) work on the cockaded woodpecker *(Dendrocopus borealis)*; here the sexes differ markedly in their foraging behaviour but not at all in their feeding apparatus. Hence sexual variation of feeding behaviour should have some more deeply rooted cause than the postulated variation of structure. Behaviour patterns that are resistant to environmental modification would best lend themselves to an investigation of how genic variability affects behaviour.

4. The variation — niche breadth hypothesis

Is individual variation adaptive or is it an undesirable genetic load? Following LUDWIG (1950), LEVENE (1953), MAYR (1963) and others, van VALEN (1965) devised a model that accounts for morphological variation in terms of niche breadth. Accordingly a species can be a

generalist in one or both of two ways; either each phenotype uses a smaller range of resources than the overall population and/or each individual can itself be relatively flexible and generalized with the resources utilized by any individual being similar to those exploited by the entire population. In addition, individual differences must be in part genetic. Given a minimal heterogeneity of the niche, specialist phenotypes will leave more offspring than generalist phenotypes because their efficiency of exploitation is thought to be higher. Moreover, by reducing niche overlap among the members of a population phenotype-specific niche expansion might be expected to reduce average competition between phenotypes. As theoretically shown by LEVENE (1953) specialization for a segment of the species' niche could be advantageous even if dispersal of individuals were random over all segments with the advantage increasing if individuals actively were to select the optimal segment.

The hypothesis predicts individuals to be more variable in environments freed from some interspecific competition. For various reasons islands with their impoverished fauna are thought to belong to such environments, provided they are sufficiently heterogeneous (GRANT 1971). By comparing bill dimensions of six songbirds on both various island habitats and a mainland habitat, van VALEN (1965) found individuals to be about twice as variable on an island as on the mainland. The chaffinch *(Fringilla coelebs)* permitted one to test the objection of whether the finding was due to an island effect *per se* rather than to a reduction in interspecific competition. The species proved to be least variable on two of the Canaries, where it presumably suffers most from competition with the endemic Teyde finch *(Fringilla teydea)* that excludes the chaffinch from the pine forests, a stronghold of the chaffinch on the mainland. All other species with no or fewer competing congeners on islands were, according to the prediction, more variable in the broader island niche.

The variation — niche breadth hypothesis has been criticized by SOULÉ & STEWART (1970) who could not find „euryphagous" bird species like crows to be more variable in bill size than „stenophagic" species like flycatchers. Similarly, WILLSON (1969) found that the bill dimensions of some tropical birds are at least as variable as those of some North Temperate species. If one considers that tropical species are often considered to be more spezialized than temperate species, one would have expected a larger variation in the latter. As van VALEN & GRANT (1970) rightly commented, the critique of SOULÉ & STEWART would perhaps be acceptable had the europhagous species been composed of different specialist phenotypes. The contrary might be true with all individuals flexibly exploiting the entire food spectrum of the species. A similar qualification applies to WILLSON's expectation. Although I concur with van VALEN & GRANT

Table 1. Mean genic heterozygosity of animals with different mobility as assessed by their allozyme variation (review SELANDER & KAUFMAN 1973).

Organism	No. of species	No. of loci	Heterozygosity Mean	Heterozygosity Range
Invertebrates				
Drosophila spec.	19	11—33	0.145	0.05—0.22
Gryllus integer	1	20	0.145	—
Pulmonata	3	17	0.207	0.14—0.25
Limulus polyphemus	1	25	0.097	—
Total	24		*0.1507*	
Vertebrates				
Astyanax mexicanus	1	17	0.112	—
Iguanidae	4	15—29	0.058	0.05—0.07
Zonotrichia capensis	1	15	0.059	—
Rodentia	14	18—41	0.056	0.01—0.09
Mirounga leonina	1	19	0.030	—
Homo sapiens (European)	1	70	0.067	—
Total	22		*0.0584*	

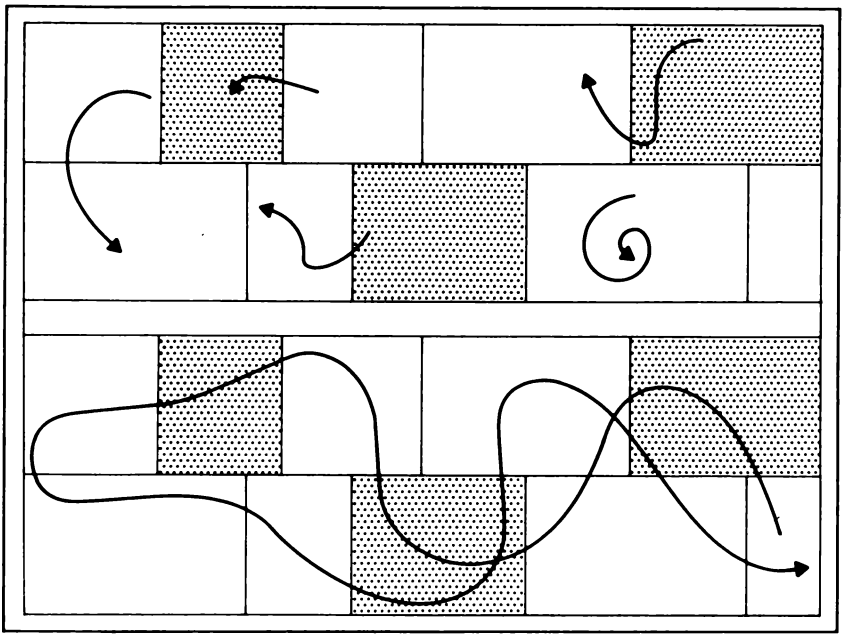

Fig. 3. Schematic representation of „coarse-grained" (above) versus „fine-grained"use of the same environment by a species with little mobility (above) and with high mobility, respectively. The environment offers two ecologically different types of habitat, e. g. forest and meadow, over which animals move during their lifetime (arrows).

in rejecting this particular critique, I would like to point out that on *a priori* grounds euryphagy offers the *opportunity* for an animal to undergo individual diversification of food exploitation, whereas stenophagy does not. Whether such an opportunity is made use of depends on a number of constraints. In order to verify van VALEN's hypothesis one ought, therefore, to compare the variability of animals with a broad niche with that of narrow-niched species. This is what SOULÉ & STEWART (1970) possibly began to do, but they neglected to look directly at specialization versus flexibility of individuals. Thus a verification of the hypothesis would have to entail a study of the exploitation of the niche by the individual phenotypes. The hypothesis receives further support from two pieces of indirect evidence:

1) If it is accepted that invertebrates, on the average, are less mobile than vertebrates, one would expect the former to be more heterozygous. As SELANDER & KAUFMAN (1973) have shown (Table 1), invertebrate individual heterozygosity is about three times greater than that of vertebrates, including a bird *(Zonotrichia capensis).* The inference is that the less mobile species use their habitat in a „coarse-grained" way (LEVINS 1968), since they have no choice, whereas the more mobile species use it in a „fine-grained" fashion (Fig. 3). Note that a mobile species like a bird could use its environment „coarse-grained" if it elected to exploit its resources in proportions other than offered by the environment. That this, in fact, occurs is indicated by a heterozygosity above zero in all highly mobile species.

2) A Darwin's finch *(Geospiza fortis)* exhibits larger variation in bill dimensions on Indefatigable Island with an extremely rich flora than on small Daphne Major Island with a poor and barren habitat. This correlation may be due, in part, to the hypothesis discussed here: Individuals with different bill sizes occur in different vegetation zones on Indefatigable Island. As shown by GRANT *et al.* (1976) in field experiments, different-sized individuals consume rice grains at different rates, but the relationship is a complicated one. One may speculate that the coarse-grained use by *G. fortis* of Indefatigable Island is due to different phenotypes handling seeds with different efficiency. Since the species of seeds vary with the vegetation, individuals might elect to stay where they are most efficient in feeding. — The species varies interindividually with

respect to lactate dehydrogenase, but almost not at all in terms of certain esterases (FORD *et al.* 1974).

If van VALEN's hypothesis is to have some generality, the following predictions are worth testing:

1) Tropical sedentary bird species should vary less than (partly) migratory species that experience a larger diversity of climate, food, predators, competitors, etc. A study of the ecology of the species selected should precede the actual test to make sure the premise of the prediction is correct.

2) Tropical sedentary species should vary less than temperate sedentary species because of differences in environmental predictability (see GRANT *et al.* 1976).

3) Flightless species should vary more than flying relatives because of the probably more „coarse-grained" use of their habitats.

4) Juveniles should vary more than adults because of their more „coarse-grained" use of the species habitat.

In accordance with prediction 4) arctic tern *(Sterna paradisaea)* chicks have dimorphic juvenile plumages with the proportion of the morphs nicely adjusted to the concealing background of different strips of coast (LEMMETYINEN *et al.* 1974).

Finally it should be remembered that not all variation is due to natural selection. Even after extended inbreeding and selection against any variance, there remains residual phenotypic variation ($V > 1\%$), probably due to random processes during ontogeny (Refs. in MAYNARD SMITH 1960).

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5. Summary

The generally observed correlation between the mean of a sample and its variance is a challenge to the developmental physiologist. Meristic traits below a certain number of units may fail to vary individually, which can be accounted for by a number of quantitative models (MAYNARD SMITH). These models do not yet account for behavioural variation, especially since it is not clear what those units should be.

There seems to be no gross difference in the variation of some stereotyped displays and organs in birds ($1\% < V < 10\%$), but repetition rates of behaviour patterns vary tremendously. Despite this, intra-individual variation seems to be generally smaller than inter-individual variation.

Little is known about allozyme variation in birds. Whereas in several reptiles and in oats this type of variation mirrors morphological variation, the only study in a bird fails to demonstrate such a relationship. Individual variation in behaviour need not be accompanied by a corresponding structural variation.

According to van VALEN's variation niche-breadth hypothesis, individuals of a species are adapted to certain segments of an ecologically heterogeneous niche. Accordingly such species should be more variable than others in a more homogeneous habitat, provided individuals are not generalists. The prediction has been fulfilled in six songbirds (a); in that invertebrates exhibit a higher degree of mean heterozygosity than more mobile vertebrates including a bird (b); in that *Geospiza fortis* has different beak sizes in different vegetation zones of an island (c). The hypothesis leads to a number of testable predictions about individual variation in relation to mobility and migratory behaviour in birds.

6. Zusammenfassung

Einige Seiten individueller Variation bei Vögeln

Die allgemein beobachtete positive Korrelation zwischen dem Mittel einer Stichprobe von Tieren und der zugehörigen individuellen Streuung bürdet dem Entwicklungsphysiologen ein noch ungelöstes Problem auf. Meristische Merkmale, deren Elementanzahl unter einer bestimmten Größe bleibt, brauchen überhaupt nicht zu variieren. Oberhalb dieser Grenzzahl aber nimmt ihre individuelle Streuung mit der Anzahl der Elemente allgemein zu.Dieser Zusammenhang kann durch formal verschiedene Modelle erklärt werden (MAYNARD SMITH). Sie können die genannte Korrelation im Bereich des Verhaltens aber noch nicht erklären, weil nicht klar ist, was hier den meristischen Einheiten der Morphologie entspricht.

Die individuelle Variation der Form einiger Ausdrucksbewegungen von Vögeln scheint genauso groß zu sein wie die ihrer Organe ($1\% < V < 10\%$), doch schwankt die Wiederholungsrate bestimmter Verhaltensweisen individuell ungemein. Dennoch scheint die intra-individuelle Variation allgemein kleiner zu sein als die (inter-)individuelle.

Über die individuelle Streuung von Allozymen ist bei Vögeln wenig bekannt. Während bei verschiedenen Reptilien und beim Hafer diese Variation die morphologische widerspiegelt, läßt die einzige diesbezügliche Arbeit an einem Vogel eine solche Beziehung vermissen. Ferner braucht individuelle Variation des Verhaltens nicht mit einer entsprechenden morphologischen Streuung verknüpft zu sein.

Nach VAN VALEN's Nischenbreiten-Variations-Hypothese sind verschiedene Individuen einer Art an jeweils abweichende Unternischen einer heterogenen Artnische angepaßt. Demnach sollten solche Arten individuell mehr streuen als andere in einem homogeneren Biotop, doch nur dann, wenn jene Individuen fein eingenischte Spezialisten, nicht Generalisten, sind. Die Vorhersage gilt bisher für morphologische Streuung und Nischenheterogenität von sechs Singvogelarten (a); weiter haben Wirbellose einen höheren Grad mittlerer Heterozygotie als die ortsbeweglicheren Wirbeltiere einschließlich eines Vogels (b); und schließlich hat *Geospiza fortis* einen verschieden großen Schnabel je nach der Vegetationszone der betreffenden Insel (c). Die Nischenbreiten-Variations-Hypothese führt zu einer Reihe prüfbarer Voraussagen über individuelle Variation in bezug auf Ortsbeweglichkeit und Wanderverhalten von Vögeln.

7. References

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Intraspezifische Selektion und die Wechselbeziehungen zwischen natürlicher Auslese und geschlechtlicher Zuchtwahl

Von Jürgen Nicolai

Die so selbstverständlich erscheinende Tatsache, daß Angehörige einer Tierart sich untereinander besser verstehen, als mit Vertretern jeder anderen Art, daß zwischen ihnen ein Kommunikationssystem besteht,das allen Verständigungsmöglichkeiten mit anderen Arten überlegen ist, hat in der Evolution eine Vorgeschichte, die nicht weniger dramatisch verlaufen ist, als die anderer Entwicklungsvorgänge. Die soziale Kommunikation wird zwischen Artgenossen durch eine Vielzahl von optischen, akustischen und häufig auch olfaktorischen, taktilen und elektrischen Signalen aufrecht erhalten. Jedes dieser Signale verdankt seine gegenwärtige Form Selektionsvorgängen, die sich im wesentlichen innerhalb der Arten abgespielt haben, an deren Ergebnis allerdings die Umwelt immer ein entscheidendes Wort mitgesprochen hat. Die Entwicklung neuer Merkmale im Bereich des Sozialverhaltens ist wohl stets so vor sich gegangen, daß eine mutativ entstandene Neuerung oder eine Erfindung vom Artgenossen gegenüber dem bisherigen Merkmal bevorzugt und dadurch mit einem positiven Selektionswert belegt wurde.

In der Klasse der Vögel ist die Kommunikation zwischen Artgenossen auf den Austausch von optischen, akustischen und taktilen Signalen beschränkt. Optische Signale können als Dauersender tätig sein, so bestimmte Gefiederfarben und -strukturen oder sekundäre Geschlechtsmerkmale, wie Kamm- oder Lappenbildungen im männlichen Geschlecht, oder sie können nach Ablauf der Fortpflanzungsperiode durch Gefiederwechsel oder Rückbildung wieder abgeschaltet werden.Fast immer wird die Wirkung auffälliger Gefiederfarben und -strukturen durch auf den Artgenossen orientierte Bewegungsweisen unterstützt, die das Signal dem Adressaten gegenüber voll zur Geltung bringen.

Optische Signale können jedoch auch ohne Unterstützung durch Farben und Strukturen allein in typischen Veränderungen der Körperhaltung bestehen. Farbmerkmale und Gefiederstrukturen erlauben jedoch als Signalsender nur relativ einfache Mitteilungen, so über das Geschlecht ihres Trägers und seine Fortpflanzungsreife. Die Kommunikation durch akustische Signale hat dagegen nahezu unbegrenzte Möglichkeiten, Nachrichten mit differenzierten Aussagen zu ganz verschiedenen sozialen Situationen zu übermitteln. Die explosive Evolution der Passeres, deren Artenzahl mit 58% an der Gesamtzahl der Vogelarten beteiligt ist, und die Besetzung nahezu aller terrestrischen ökologischen Nischen durch Sperlingsvögel ist nach meiner Überzeugung ganz wesentlich durch ihre Fähigkeit zu differenzierter akustischer Kommunikation beeinflußt worden.

Wir wollen hier ein Kommunikationssystem näher betrachten: die Verständigung zwischen den Geschlechtern. Bei der Mehrzahl aller Vogelarten, die Brutpflege betreiben, sind beide Geschlechter in irgendeiner Form an der Brutfürsorge beteiligt. Das bedeutet, daß Männchen und Weibchen für einen kürzeren oder längeren Zeitraum im Jahresablauf zusammenbleiben und kooperieren müssen, um die gemeinsamen Aufgaben der Brutpflege zu bewältigen. Eine sinnvolle Kooperation ist aber nur durchführbar, wenn die Geschlechter sich

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