IV. POLYMORPHISM

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The term polymorphism has a long and interesting history in biology. Darwin used it of genera and species which presented "an inordinate amount of variation." At a later date the term came to be used particularly of those biological entities which assume markedly different forms at different stages of development, e.g., the various species of caterpillar/butterfly. Today's usage is more carefully circumscribed, and the word now refers to one particular class of biological phenomena, found throughout the animal and plant worlds. I shall begin by discussing the essential elements of the present-day definition:

1. Polymorphism always refers to variation within a single population of interbreeding individuals. Species that present several different forms or varieties at different geographical locations are said to be polytypic, and we divide them into two or more subspecies or races, one for each such clearly differentiated "type." Polymorphism, by contrast, always refers to the occurrence of two or more varieties or morphs at one and the same place.

The amount of polymorphism present in a species may well vary from race to race. A well-known example of this is the Bananaquit (Coereba flaveola). This highly variable species consists of 41 separate subspecies, 22 of which are restricted to one or more islands in the Caribbean. ([9], pp. 87-93) One morph (with a white, instead of a gray, throat) occurs only on Isla Cozumel. Black-morph individuals predominate on Grenada and St. Vincent, and they also occur on Los Roques and Los Testigos; i.e., this morph is present in different proportions in 4 races and toally absent from 37.

2. Polymorphism is a form of genotypic variation, by which two points are meant:

   a. Polymorphism refers to an inherited condition, and

   b. Different morphs result from the expression of different "genes" which replace each other on the chromosome. (In technical language, we say they are different alleles of a single gene.)

The reddish pigment of the Purple Finch and Crossbill group often disappears in caged birds, new plumages being more greenish-yellow in coloration. However, this change is environmentally induced, and not inherited. ([2]), p. 270) Greenish-yellow Purple Finches do not, therefore, constitute a separate morph for this species.

Again, first-year birds of the Little Blue Heron (Florida caerulea) are all-white; mature birds are completely dark. Since these color stages occur in one and the same individual, it is obvious that the different forms cannot be attributed to the action of distinct alleles. Modern ornithologists refer to this phenomenon as polyphenism, not as polymorphism. (Illustrations of the two phena can be found in [18], p. 95, and in [16], Plate 20.)

3. Polymorphism is a form of discontinuous variation.

Individuals from a local population of a given species ordinarily differ from each other only in slight ways. Most frequently, each single varying character intergrades, presenting a completely continuous spectrum of variation between two extremes. In certain species, however, individuals may be grouped into two or more discrete classes, defined by the presence or absence of certain fairly conspicuous attributes. Polymorphism is properly used only of these latter species.

Curiously, continuous variation (even when the range of variation is small) is thought to be due to the composite effects of many interacting genes, each of which is presumed to be responsible for only a minute amount of the total variation. It is usually adaptive in nature, correlating well with certain changes in the environment and contributing thereby to the over-all fitness of the individual to survive amidst these altered surroundings.

By contrast, polymorphism is generally non-adaptive in nature. Though frequently dramatic in its expression, it is thought to be controlled by a limited number of genes, often by a single gene, operating according to the classic principles of Mendelian inheritance.

4. Polymorphism refers to forms of variation which are not sex-associated, i.e., two or more morphs must occur within one or the other of the two sexes. (In Massachusetts, all instances of polymorphism are based on characters which are exhibited by both sexes.)

The one situation firmly excluded by this principle is the very common case in which one morph is confined to the male, and the other morph is characteristic of the female. This phenomenon is referred to as sexual dimorphism, not as polymorphism.

Polymorph Characters

Any character--anatomical, morphological, physiological or behavioral--may form the basis for an application of the term polymorphism, provided that character fulfils the conditions enumerated above. Historically, the vast majority of instances of polymorphism have been cases of conspicuous dichromatism, i.e., the occurrence of two or more color phases within one species. Usually, it is possible to describe all but one of the morphs as having an "excess" of some certain color pigment. The remaining morph is then taken to be the "normal" or "wild-phase" morph. In the table below are the technical names commonly used to describe certain of the "abnormal" morphs:

	Name	Description
1.	flavistic, or xanthochroistic	with an excess of yellow pigmentation
2.	erythristic	showing an excess of reddish pigmentation
3.	melanistic	displaying an excess of black or brown pigmentation
4.	leucistic	having a pure white plumage, OR manifesting the wild-phase coloration pattern with extreme paleness
5.	schizochromatic	exhibiting abnormal patches of color (usually white) in the plumage

(NOTE: Until very recently, leucism was referred to as albinism, but this latter term is now reserved for individuals that are totally devoid of any pigmentation. Albinos, therefore, are completely white with pink soft parts and pink eyes. In birds, true albinism is a "freak" condition, never a color phase. The same is usually true of partial albinism (i.e., schizochromism). (But cf. no. 5 in the list below.) (Leucistic morphs, on the other hand, are extremely common.)

Polymorphism is not confined to plumage characteristics. The honey-eater Melidectes belfordi displays epidermal polymorphism: some individuals have cheek wattles, some have throat wattles, and some have both. Other examples of polymorphism involve tooth structures (in mammals), winding pattern (in snail shells), and wing-vein patterns (in insects). ([12], p. 153) Parrots are behaviorally polymorphic, each individual being predominantly left-footed or right-footed. ([6], p. 29)

In all of the above examples, the various polymorph classes are more or less conspicuously differentiated. Defining characteristics are immediately perceivable by the unaided human senses. Anatomical or physiological polymorphism, on the other hand, is detectable only by means of laboratory analyses; it is consequently said to be cryptic (hidden). Birds, like humans, belong to different blood groups. ([12], p. 153) Among the lower animals, other instances of physiological polymorphism have to do with tolerance of heat, need for water, transplant tissue tolerance, etc.

Confusing aspects of polymorphism

In a classic case of polymorphism only two morphs appear, each form being characteristic of one member of a pair of gene alleles. One allele, say A, will be completely dominant over the other, a. By this statement we mean that heterozygotes (i.e., individuals of mixed genetic background which carry both alleles, A and a) will appear identical to "pure-bred" individuals carrying duplicate A-alleles.

Genes, however, are seldom so decorous. Here are some of the irregularities that may be manifested in certain cases of polymorphism:

1. Heterozygotes (Aa) may appear as intermediates, presenting certain characteristics of each of the two basic types. There will then be three distinct morphs instead of the expected two.

2. Certain dominant genes suffer from incomplete penetrance, i.e., they do not always express themselves completely, even when they occur in "pure-bred" (homozygous) individuals. The condition results from genetic interactions. Some other gene, not an allele of A, presumably creates a chemical product which interferes with the gene product which A elaborates; and this in turn results in the modification or total suppression of the characters normally attributable to A. (Cf. nos. 3 and 9 in the list below.)

3. Although a polytypic species often displays apparently the same set of color phases in each of its subspecies, the genetic bases for this polymorphism may vary geographically. Thus, polymorphism often breaks down completely along subspecific boundaries, where individuals of separate races meet and hybridize. A baffling array of "intermediates" results. (Cf. no. 10 in the list below.)

4. Certain cases of polymorphism are due to the simultaneous action of two or more independently operating sets of gene alleles. It is as if there were two or more separate forms of polymorphism superimposed upon each other. The Asiatic bulbul (Microscelis leucocephalus) displays this situation at its worst, with six basic types and a medley of intermediate combinations derived from these types. (Cf. [13], pp. 83-84.)

5. Finally, a few cases of "polymorphism" exhibit essentially continuous variation. (Cf. nos. 2 and 13 below.) It seems likely that the term is, in fact, inappropriately applied to these species, but the usage is sanctified by tradition.

Why does the ornithologist study polymorphism?

Polymorphic variants (morphs) often differ strikingly from the "normal" or wild-phase type of a population, so much so that over 100 of these forms were originally described as separate species. The ornithologist must understand polymorphism if he is to classify his specimens correctly according to species.

In the recent Check-List Supplement ([20]), three "species pairs" were lumped as polymorphic forms of a single species. A similar fate may well await three more "species pairs," currently under investigation:

1. Brant (Branta bernicla)
   Black Brant (Branta nigricans)

2. Eurasian Oystercatcher (Haematopus ostralegus)
   Black Oystercatcher (Haematopus bachmani)

3. Ringed Plover (Charadrius hiaticula)
   Semipalmated Plover (Charadrius semipalmatus)

(Cf. [14], pp. 88-89.)

Secondly, polymorphism is of interest to ornithologists because, by definition, it represents a conspicuous and elementary case of genetic variation. In other words, polymorphism represents the most convenient and accessible way to study the genetics of populations. Much current interest centers on research into the manifold effects of single-gene alterations. Very little is known in this area concerning birds; much more has been established for humans. Did you know that humans of blood-type A are more susceptible to stomach carcinoma (by 10%), to pernicious anemia, diabetes, fatal infantile broncho-pneumonia, portal cirrhosis and to hip fractures? ([12], p. 161) Detailed correlations of this sort are not as yet established for any avian morph, but ornithologists are convinced that they exist. Is the Blue Goose more tolerant of heat than the Snow Goose? Can it fly faster? Can the Great White Heron digest certain toads which the Great Blue most avoid? These or similar questions may soon be answered by ornithologists researching the different varieties of polymorphic species.

The Massachusetts "Check-List"

To complete this article, I have assembled a list of those polymorphic species which are known to have occurred in Massachusetts. I have included even those species for which it

is known that alternate morphs do not occur here. In all too many cases I was unable to ascertain exactly which morphs are on record for this state. Hopefully, future reports will be more complete.

References are given to commonly available field guides, whenever these books contain appropriate illustrations. Short descriptions supplement the field guide information where necessary

1. Western Grebe (Aechmophorus occidentalis)

Two color phases:
1) Black of crown extends below eye; bill is dusky to yellow-buff.
2) Black of crown extends down to eye or terminates above eye; bill is yellow.

Illustrations: 1) in [15], p. 99; 2) in [18], p. 21 or [16], Pl. 1. Polymorphism in this species is discussed by Storer [19].

2. Northern Fulmar (Fulmarus glacialis)

Four morphs are recognized: 1) double light, 2) light, 3) dark and 4) double dark. All four are portrayed in Palmer ([15], plate facing p. 60). Illustrations of morphs 1) and 4) can be found in [18], p. 23, and [16], Pl. 4. Palmer says (p. 60) that individual variation is actually fairly continuous from lightest to darkest. Dark birds predominate in the far north; lighter individuals are more likely in Massachusetts waters. There are no "dark-phase" specimens from this state, according to Griscom and Snyder ([7], p. 25).

3. Great Blue Heron (Ardea herodias)

Two or more color phases in the South Florida population:
1) normal blue phase
2) leucistic (white) phase, formerly known as the Great White Heron ("A. occidentalis")
3) dilutants, i.e., pale birds having the color pattern of the normal blue morph. In some of the literature, these individuals are referred to as "Ward's Heron." The name seems inappropriate: A. h. wardi is the subspecies breeding throughout the southeastern states; dilutants are localized in Florida, particularly in the outer keys.
4) Würdemann's Heron, resembling a pale, blue-phase bird, but with an all-white head.

Ornithologists are just beginning to understand the genetics of this species properly. Categories 3) and 4) above may represent true and distinct color phases, or they may consist entirely of heterozygotes. The most likely explanation, however, is that these two categories represent instances of incomplete penetrance. Morphs 1) and 2) are illustrated in [18], pp. 93 and 95, and in [16], Plate 20. Morphs 1), 2) and 4) are illustrated in [15], plate facing p. 278. White-phase birds have occurred as far north as Pennsylvania. Griscom reported a "Ward's Heron" from Monomoy in 1946. ([1], p. 41.)

4. Green Heron (Butorides virescens)

There is a dark reddish (erythristic) phase, individuals of which have been found in Cuba and the Isle of Pines. ([15], p. 416) This phase has never occurred within the A.O.U. Checklist area.

5. Reddish Egret (Dichromanassa rufescens)

Two color phases: 1) red (erythristic) and 2) white (leucistic).

A rare species in that the two morphs are apparent even in the natal down at hatching! There are also occasional dark birds with patches of white scattered throughout the plumage (schizochromism). (Illustrations: [18], p. 95; [16], Pl. 20.) Bailey ([1], p. 42) reports one sight record for this species from Monomoy in 1953. Presumably this was a red-phase bird.

6. Black-crowned Night Heron (Nycticorax nycticorax)

In South America, this species occurs in two phases (light and dark), with

intermediates also present. The subspecies in our area consists entirely of light-phase birds.

7. Least Bittern (Ixobrychus exilis)

There is a rare, dark phase of this species, known as Cory's Least Bittern, which occurs in eastern North America. In this phase, the lighter areas of normal-phase birds are deep russet or chocolate. A specimen of this morph was taken in Scituate in 1901, and an additional sight record from 1945 exists. ([7], p. 35) The center of abundance for this phase is apparently near Toronto, Ontario.

8. Brant (Branta bernicla)

Listed in the 1957 A.O.U. Checklist as two species (cf. above). The light morph is the normal form in this state, but there are two specimens and several sight records of the dark morph. ([7], p. 40) Most populations are monomorphic, but both phases apparently occur in the Banks Island area of Canada. Literature supporting the merger of the two species into one species is cited in Mayr and Short ([14], pp. 32-33). Whether the variation involves a case of true polymorphism is still under investigation. (Illustrations: [18], p. 41; [16], Pl. 10 and 11--morph 1) only.)

9. Snow Goose (Chen caerulescens)

Two morphs: 1) White, and 2) wild-phase, formerly known as the Blue Goose. Both forms are illustrated in [18], p. 43, and [16], Pl. 11. Occasionally "intermediates" appear. One is illustrated in [17], Pl. 9.

This particular case of polymorphism is now quite well understood. The two morphs result from the action of two alternative forms (alleles) of a single gene, and this gene is not sex-linked. The blue-morph allele is complete dominant; the white-morph allele, recessive. Both morphs are somewhat variable, and this variability have been ascribed to environmental influences as well as the effects of modifier genes (incomplete penetrance). Every individual, however, belongs definitely to one or the other of the two forms. The picture in [17] is of a variant Blue Goose, not of a "hybrid." (Cf. Cooke and Mirsky, [5].)

The dark morph occurs only in the western race, the Lesser Snow Goose (C. c. caerulescens). It is apparently due to a recent mutation and is at present spreading rapidly throughout the race. Massachusetts birds are primarily from the eastern subspecies, which explains the relative scarcity of blue-phase birds. "Blue Geese" are, however, almost regular in the state.

(NOTE: General remarks on the Falconiformes.

A great many hawks are polymorphic, often exhibiting more than the usual two morphs per species. Field guides are, in general, fairly exemplary in their treatment of this problem. For example, Robbins [18] illustrates 15 forms in 6 species. However, polymorphism in hawks is extremely complicated, with the number of forms varying from race to race and many examples of "boundary break-up" along subspecific borders. Cf. [8], for flight silhouettes and detailed morph descriptions.)

10. Red-tailed Hawk (Buteo jamaicensis)

Three phases in the West (light, red and dark); eastern birds are of the light phase. In the Northwest, the subspecies formerly known as Harlan's Hawk (now B. j. harlani) shows light and dark phases, but no red. Frequent instances of "boundary break-up" along the Mississippi River and in the Prairie States.

11. Swainson's Hawk (Buteo swainsoni)

Light and dark phases, with intermediates. Immature plumages are uniform, and it takes 3-4 years for the "adult" polymorphic plumages to develop fully. Most New England specimens are dark-phase birds! (Cf. [7], p. 70.)

12. Broad-winged Hawk (Buteo platypterus)

The rare dark phase is "virtually indistinguishable in the field from the dark phase of the Short-tailed Hawk (Buteo brachyurus) in tropical climates." ([8], p. 274;

with illustration of the latter, p. 272. Cf. also, [18], p. 75.) The dark phase seems not to be on record for this state.

13. Rough-legged Hawk (Buteo lagopus)

Two morphs (light and dark) are usually named; but, in fact, the variation is more or less continuous. Certain of the morph characteristics are more or less sex-linked. Females have the highest incidence of dark coloration (belly band and broad tail band); in males the melanism is much more restricted.

14. Gyrfalcon (Falco rusticolus)

Three phases (white, gray and dark gray), strongly geographically oriented. The white morph is most common in the high artic, especially in Greenland; dark-phase birds are typical of western Canada, but they also predominate in northern Labrador. Most of the Massachusetts records are of dark-morph birds, but several authors (e.g., Bailey [1], p. 77) have questioned the validity of these records. All three forms have been recorded.

15. American Kestrel (Falco sparverius)

Caribbean populations are polymorphic (white- vs. ferruginous-chested morphs). In the United States, only a single morph is present.

16. Ruffed Grouse (Bonasa umbellus)

Red-tailed and gray-tailed morphs, geographically oriented. (Cf. [16], pp. 52-53, for comments; [18], p. 85, for illustrations.)

17. Pomarine Jaeger (Stercorarius pomarinus)

Dark and light phases. Watson ([21], p. 43) estimates the ratio of these two morphs to be 1:8.

18. Parasitic Jaeger (Stercorarius parasiticus)

Dark and light phases. Griscom and Snyder ([7], p. 117) consider the dark phase to be "quite frequent." (Illustrations: [18], p. 131, [16], Pl. 4.)

19. Long-tailed Jaeger (Stercorarius longicaudus)

Dark and light phases, both extremely rare. One dark-phase specimen and 4 light-phase specimens were examined by Griscom and Snyder, who consider jaeger specimens representative of Massachusetts transient populations. ([7], p. 118)

20. Common Murre (Uria aalge)

There is an uncommon morph, sometimes called the "Ringed Murre," with a narrow white ring about the eye during the breeding season only. (Illustrated in [18], p.149.) In winter plumage, the entire face is white in both morphs. Almost all Massachusetts records are of winter birds.

21. Barn Owl (Tyto alba)

Two color phases: 1) white-breasted paler individuals, and 2) orange-breasted darker birds. Both morphs are common throughout North America. ([8], p. 140)

22. Screech Owl (Otus asio)

Two well-known morphs (gray and red) with intermediates (brown). In the West, there are two phases (gray and brown, no red), but these birds may well represent a distinct species. The gray allele is recessive (i.e., offspring of a gray pair will all be gray phase). ([18], p. 160; [16], Pl. 38).

23. Great Horned Owl (Bubo virginianus)

According to Grossman and Hamlet ([8], p. 422), there are two color phases, differing as follows:

Character	Leucistic	Flavistic
Facial disc	White to buff-yellow	Tawny
Tarsi and toes	White, sometimes mottled	Tawny
Tail	White to light ochre (barred)	Amber-brown (barred)
Throat locket	White	Tawny

24. Dark-eyed Junco (Junco hyemalis)

This is an extremely variable species, still under active investigation. As a result of the recent Check-list changes ([19], p. 418), the species now consists of 13 subspecies; it may soon be merged with the Gray-headed Junco (J. caniceps) to raise the total number of subspecies to 15. Many of these subspecies hybridize and intergrade with each other, creating an unusual amount of intraspecific variation. According to Mayr and Short ([14], p. 88), there is also polymorphism within the species, but I am unable to locate in the literature any statements identifying the exact nature of this polymorphism. The following statement from Bent [3] is suggestive and may refer, in fact, to this phenomenon:

Oregon Junco (J. h. montanus, shufeldti and thurberi): "White wing spotting is a rare variant." (p. 1059)

25. White-throated Sparrow (Zonotrichia albicollis)

Polymorphism in this species was only recently discovered. (Cf. Lowther, [10] and [11], not consulted by me.) As recounted in Bent ([4], pp. 1374-5, 1381-2, 1367), the two morphs are color variants differing in a variety of small ways from each other. The essential character distinguishing the two morphs is, however, the color of the median crown stripe in the adult bird, this stripe being either white or tan. White-striped adults are illustrated in [18], p. 320, and in [16], Pl. 58. Tan-striped adults cannot be distinguished from immatures of the first winter plumage. The songs of the two types are essentially identical, but the two morphs are behaviorally distinct with reference to the singing of this song.

In a nutshell, white-striped birds display a higher level of intraspecific aggression; and this is evidenced in two ways:

1) A white-striped female will respond to another singing bird by singing the territorial song herself. She "talks back," as it were. Tan-striped females do not sing in the field.
2) White-striped males are most hostile indeed toward any other bird singing the territorial song. In particular, they react aggressively towards singing white-striped females. Tan-striped males that have been sexually aroused by a female's trill-note do not respond to a subsequent delivery of the territorial song.

The two morphs occur in roughly equal proportions so that the result is a system of assortative mating between opposite morphs, which is unique among birds: white-striped males mate exclusively with tan-striped females, and white-striped females mate almost exclusively with tan-striped males. (A few excess pairs are formed with mates both of the same morph. Almost all of these are pairs of tan-striped birds.)

On the Reporting of Morphs

I can think of few arguments to support field identification of subspecies. In a few species, one or more subspecies will be well-marked, but the opposite is more often the case. For example, the races of the Dark-eyed Junco resemble each other so closely that it has been suggested that not even a bird-bander can classify an individual bird accurately. A correct subspecific determination can only be made for a non-fidgety, i.e., dead, bird.

How different the case of polymorphism! Morphs are, by definition, well-marked and easily categorized into one of a small number of dissimilar classes. They are easily identified in the field under suitable visual conditions by any competent and well-

informed observer. It would seem to be essential in the reporting of any polymorphic species that all individuals be identified as to type. When more than one morph is present, careful counts should be made of each form. Take a little extra time and observe the birds carefully. After all, we should be bird-watchers first and listers second. Are there any significant differences in behavior? any signs of intraspecific aggression? any differences in the food taken?

Remember, in no other science have amateurs played the major role that they have played in ornithology. The observations you make may well become the basis for a major new piece of research.

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TERN CATASTROPHE

by Wayne Hanley, M.A.S.

A sudden wave of death this summer wiped out almost all the young birds in a Common Tern colony on Jeremy's Point in Wellfleet. Dr. I. C. T. Nisbet, who heads field research into tern problems for the Massachusetts Audubon Society, witnessed the unexpected die off.

Dr. Nisbet said, "There were 1500 young terns in the colony. About 100 of them progressed to the point where they could fly. At about the same time, all other young in the colony just sat there on the beach and died.

"Death among young terns is not uncommon. But this is the first time we have witnessed such a die off without any clue as to why it happened. In years when fishing is poor, many young terns die because their parents cannot find enough food for them. But these young birds were fat. We have had pathological examinations made, and no disease was found. The pattern of death did not indicate chemical or pesticide poisoning. The whole thing still is a complete mystery."

There are four species of terns along the New England coast. Three species are doing very badly, while one has begun a slow comeback. Least Terns, the small terns with yellow bills and white foreheads, hit a low ebb about five years ago, but now are recovering. The Massachusetts population of Least Terns is estimated at about 1200 pairs.

Common Terns, which were estimated at 9000 pairs in Massachusetts five years ago, had declined to 6000 pairs this summer. Roseate Terns have dropped about 50% in five years and now are down to 2000 pairs. Part of their decline locally was caused by a major defection of Massachusetts birds to Long Island, N. Y., colonies.

Arctic Terns, which use Massachusetts as the southern rim of their breeding range, seem to be in the worst condition of all the terns here. Their population of 300 to 400 pairs five years ago now has dropped to 50 pairs. Dr. Nisbet said, "Most Arctic Terns along the Massachusetts coast now are old birds. Some are over 20 years old, according to their bands. They seem to lack the deep urge necessary to keep them feeding their young. Perhaps it is something akin to senility."

Part of the four species' difficulty comes from a lack of options. Given a choice, terns prefer to breed on offshore islands where ground predators are few. The recent population explosion among Herring Gulls and Great Black-backed Gulls has forced terns from most of the desirable islands. Gulls nest first and occupy all sites before the terns return from the south. Meanwhile coastal construction and hordes of bathers have evicted the terns from their only alternative breeding grounds, the mainland beaches.

NOUNS OF ASSEMBLAGE

The English language contains a rich variety of words known as nouns of assemblage or nouns of multitude. Each is a term to be used for a group of animals or humans, all of the same type. Some of these words are still in common use: we speak of a gaggle of geese, a kettle of hawks, of a clutch of eggs, or a raft of ducks (raft = a large and motley collection, as in the word riffraff).

The heyday for the formation of these words seems to have been in the fifteenth century, and birds received their full share of attention. James Lipton has collected these terms and published them in his beautifully illustrated book, An Exaltation of Larks (Grossman Publishers, New York, 1968). He gives the following as authentic to the early period: