Avian genetic diversity: Domesticated species

Genetic diversity is considered crucial to the continued survival of a species, be it wild or domestic. Such within-species diversity has been the raw material of agriculturists over millennia. In response to selective breeding and the differential survival of less fit animals, preferred traits have been accentuated and clustered to produce distinct breeds and varieties of the modern domesticated species (NRC 1993). In more recent times, researchers have deliberately isolated various mutations in specialized stocks, permitting the systematic study of such mutations and promoting a better understanding of the normal function of the affected genes.

The totality of wild and domesticated species form the gene pool or genetic resources base necessary for the survival of the species. The genes and genotypes present in this pool represent genetic resources which are accessible and can be exploited by biologists and breeders. In this report, we emphasize "genetic stocks" which have been bred for specific traits and genes in contrast to breeds in which the individual birds have many traits in common and can generally be maintained with randomly breeding populations. Genetic stocks are typically selected for traits of special interest to breeders and geneticists. Many of them are reproductively, physically, or physiologically compromised, and require special care in breeding and management, even for maintenance or conservation purposes.

Target species

While the AGRTF recognizes the need for conservation of undomesticated avian species, this report primarily addresses the need for conservation of specialty stocks of domesticated species, particularly chicken, turkey, and Japanese quail. A limited number of waterfowl (duck and goose) genetic stocks and semi-domestic game-bird stocks (ring-necked pheasant and bobwhite quail) have been developed and will be noted in this report. Noted below are salient features of the most widely used domesticated species that have the greatest need for conservation of genetic stocks.

Chicken

First domesticated over 6,000 years ago, the chicken (Gallus gallus or G. domesticus) presents by far the greatest amount of genetic diversity of the domesticated avian species, with over 400 identified genetic variations (SOMES 1988). Many are showcased in the more-than 100 recognized chicken breeds and commercial varieties, which variously integrate most of the naturally occurring mutations affecting size, body type, production characteristics, posture, color, feather structure and location, comb shape, and behavior (see Figures 1 and 2 for wild- and domestic-type chickens). Some of the most extreme variants include: the tiny, short-legged Japanese Bantam; the tall, aggressive Old English Game

Figure 1. Red Jungle Fowl rooster from UCD 001 (Photo courtesy of J. Clark, University of California–Davis).
Turkey

The one commercially important avian species originating in North America, the domestic turkey of commerce, is the product of hybridization between two subspecies of turkey: the domesticated *Meleagris gallopavo gallopavo* from Central America and the wild *M. g. sylvestris* from the eastern United States (CRAWFORD 1990). From these hybrids, birds were selected for size, tameness, carcass yield, and rapid growth, resulting in several distinct breeds and varieties (Figure 3). The modern commercial or exhibition turkeys are large, slow-maturing birds with a much lower reproductive potential than chicken or Japanese quail (at one generation per year for the turkey). Although this species is far less popular with researchers or hobbyists than the chicken or the Japanese quail, at least six breeds are still kept for exhibition and a few unique research stocks have been developed (Box 5), including several commercial-type long-term selected and randmbred-control lines kept at Ohio State University (see survey results, Appendix 2, Tables 2.1 and 2.2). Perhaps as a consequence of the few researchers studying the turkey, relatively few mutations (49) have been reported in the turkey compared to the chicken and Japanese quail (SOMES 1988).

Japanese quail

Gaining in popularity as an experimental animal in both research and education, the Japanese quail (*Coturnix japonica*) is a small, early maturing, highly efficient egg and meat producer. Until recently, the Japanese quail was classified as a

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Box 5. Parthenogenetic turkeys

Perhaps the most spectacular use of turkeys in experimental biology was the study of meiosis, fertilization, and early embryonic development with a strain of parthenogenetic turkeys. In the 1960s and 1970s, M.W. Olsen of the United States Department of Agriculture Agricultural Research Center at Beltsville developed a line of turkeys in which an embryo would form in 30 to 50% of the unfertilized eggs (parthenogenesis). Most of these embryos die, but a small proportion of them (about 0.5%) continue to develop, hatch, and grow into fully functional males (OLSEN 1965). The existence of this line has given rise to the notion that genetic imprinting does not exist in birds, although this conclusion must be tentative in the absence of any formal investigation of imprinting in the unique parthenogenetic stock. However, this parthenogenetic stock exists precariously at only two research stations in the world (the University of Guelph (Ontario, Canada) and the University of Oman).

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Figure 2. White Leghorn rooster from UCD 003 (Photo courtesy of J. Clark, University of California–Davis).

Figure 3. Flock with different turkey breeds (Photo courtesy of F.A. Bradley, University of California–Davis).
subspecies of the common European quail (C. coturnix). It is now classified as a distinct species because of the nonhybridization of the two in the wild or in captivity (CHENG and KIMURA 1990). According to all available documentation, the domestic Japanese quail strains used in meat and egg production (even in Europe) are descended from C. japonica, which is still found in small wild populations in Japan. While gaining popularity as a food animal in the US, its small size has limited its use as a meat- or egg-producing animal to specialty markets. However, the Japanese quail has other qualities that make it ideally suited for research. Usually reaching sexual maturity by six weeks of age, the females often lay an egg a day for several months. The males are aggressive breeders and maintain high fertility even when housed with four or more hens. The early maturity and short incubation interval (16 to 17 days) permit as many as five generations in a single year, in contrast to the slower-maturing chicken (one to two generations per year) or the even slower maturing and less productive turkey (one generation per year). The quail is sometimes called the mouse of the bird world, since it has become extremely popular as a model species for biological research in several fields, including toxicology, cell biology, nutrition, and selective animal breeding. Although most researchers use unselected or randombred birds, over 100 mutations are known in this species, including many affecting feather color and shape (Figures 4 and 5), and several causing embryo-lethal deformities (SOMES 1988; CHENG and KIMURA 1990). At present, most of these mutant strains are only maintained at the University of British Columbia or by hobbyists. Two drawbacks with this species are that the usual productive life of an individual bird is quite short, frequently less than one year, and, unlike the chicken, close inbreeding is not tolerated. Thus, only one moderately inbred line exists (at the University of British Columbia).

Duck

Almost all of the 15 or so domestic duck breeds recognized today are descended from the wild mallard duck (Anas platyrhynchos platyrhynchos), the exception being the Muscovy duck (Cairina moschata) (LANCASTER 1990). In addition to the different plumage patterns and colors, a variety of body types and behavioral traits are found among the duck breeds, ranging from the boat-shaped, vocal Call ducks to the cane-shaped Indian Runner ducks. Only 22 mutations have been described in the domestic duck, most involving feather color or pattern (LANCASTER 1990). As such, these traits have been used in defining breed and variety standards, especially among the more ornamental duck breeds, such as the Call, Indian Runner, Crested, Cayuga, and Swedish. While such breeds are usually only kept by hobbyists, a few are important in commercial meat production, particularly White Pekins, Rouens, and, in some areas, Muscovy or Muscovy-domestic duck hybrids.

Goose

Six recognized domestic goose breeds were derived from the western Greylag goose of Europe (Anser anser anser). Several other breeds are thought to have descended from the smaller Swan goose of central Asia (A. cygnoides). The African breed is believed to be derived from a
hybrid between these two species (Hawes 1990). Strict herbivores, geese have a long history of domestication, but their delayed maturity (two years) and low egg production rate make them less attractive as an experimental animal or as a commercially viable species (Box 6). However, due to the increasingly diverse consumer groups in the US and Canada, formerly noncommercial species are becoming popular on a small scale for specialty markets. One example is the demand from the Asian markets for a smaller, less fatty meat goose. Until now, Europeans and North Americans have traditionally raised Embden geese for market purposes. This large-bodied, fatty bird is not well suited to the method of cooking employed by Asian chefs. Therefore, waterfowl suppliers are now starting to grow the smaller Chinese geese for this market.

**Gamebirds**

Several species of game birds are commonly bred commercially or by hobbyists, including many subspecies of the Ring-necked pheasant (*Phasianus colchicus*) and the Bobwhite quail (*Colinus virginianus*). Nine color mutations have been identified in the pheasant, along with several affecting skin color and feather structure, and 11 that produce biochemical polymorphisms (Somès 1990). For most populations, very little selective breeding or inbreeding is deliberately practiced, and the development of gamebird stocks for genetic research is unusual. Exceptions include the now-extinct inbred pheasant lines developed at the University of California–Davis (Woodard et al. 1983) and the Bobwhite and pheasant blood-type variants currently kept at Northern Illinois University (Jarvi et al. 1996).

**Types of genetic stocks**

For the purposes of this report, genetic stocks are classified into four categories that reflect the genetic composition and type and the breeding system used to maintain them.

- **Randombred**
- **Highly inbred**
- **Long-term selected**
- **Mutant (including cytogenetic variants and transgenics)**

We are primarily concerned in this report with conservation of genetic stocks developed for research purposes, which include all of these categories. Conservation of genetic stocks in the different categories present different challenges for successful conservation, including: high embryonic mortality, low viability, poor reproductive traits, pronounced susceptibility to one or more diseases, large and deleterious genetic load, poor response to specific environmental stressors, poor recovery of cryopreserved semen, and need for a very large gene pool (more than 100 birds per generation).

**Randombred lines** are maintained as relatively large populations of birds (usually over 100) in which little, if any, selection of breeding stock is done by the curator. Quite simply, the number of progeny from each male or female depends on the reproductive success of that bird at the time the eggs are collected to reproduce the population. Such randombred stocks are generally kept as closed flocks, although new bloodlines may be introduced to the population to improve the vigor of the flock, particularly if inbreeding depression is observed. The birds may be reared and bred in a single large enclosure, with all males having access to all females. This is a common for pheasants, ducks, geese, some chickens, and naturally breeding turkey stocks. Alternatively, the birds may be randomly segregated into smaller floor pens or randomly paired or grouped in cages, as is common with

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**Box 6. Research with goose breeds in Canada**

While geese are not commonly used for experimental purposes, a relatively large experimental population of geese was maintained at the Center for Food Animal Research (CFAR) in Ottawa. Several distinct stocks of Chinese, Embden, and Chinese X Pilgrim hybrid geese were developed in Ottawa to study production traits and DNA fingerprinting patterns (Grunder et al. 1994). The stocks included standard breed control strains, stocks selected for multiple traits, and the unselected reference strains (Somès 1988). As with chicken and turkey research in the early part of this century, most studies with the relatively undeveloped pure and crossed goose varieties have been related to agricultural objectives, including methods of rearing broiler geese and improving egg production with controlled lighting and trapnesting. Early studies with Pilgrim geese (the only goose breed that shows strong sexual dimorphism) included a demonstration of increased egg production with selection (Merritt 1962), and use of light control to increase egg production. More recently, artificial insemination techniques have been improved (Grunder and Pawluczuk 1991) and geese have been shown to lack endogenous viruses (i.e., viral DNA integrated into the host bird chromosomes) of the avian leukosis type (Grunder et al. 1993). Unfortunately, with the loss of funding from the Canadian government in April of 1997, these stocks were either eliminated or dispersed.
Japanese quail. A minimum of 25 pairs, usually more than 150 birds, is needed to keep inbreeding at a minimum. These stocks are often kept as a source of "normal" control birds, and also function as a resource stock, from which inbred or selected stocks can be derived or qualitative mutations isolated.

**Inbred lines** are produced by breeding together close relatives for many generations, resulting in increasingly homozygous and homogeneous progenies. Different types of mating schemes are used, depending on how rapidly the researcher is attempting to approach complete homozygosity. Disregarding parthenogenesis, the most rapid inbreeding is produced by father-daughter, mother-son, or brother-sister (full-sib) matings. These breeding schemes can also be used to expose deleterious recessive traits or to fix preferred or beneficial single-gene traits in a population. Unfortunately, even in the absence of major genetic defects, the fertility and viability of the inbred offspring are almost always lower than the more outbred parent strain, a characteristic called inbreeding depression. If selection and breeding strategies do not compensate for this decline, inbreeding depression can result in the extinction of the line within a few generations. This is a particular concern in lines propagated by full-sib matings which also have large genetic loads (many deleterious alleles). However, once the lethal and sub-vital alleles have been purged from the inbred strain, it can theoretically be bred to essentially complete homozygosity while maintaining reasonable reproductive performance traits (fertility, egg hatchability, egg production rates, viability, etc.). Such genetically uniform stocks can then be used as a standard genetic background in the study of individual genes and gene complexes. Particularly useful inbred lines are those which have been bred for contrasting phenotypes due to allelic differences at single loci. These lines, having the same genetic background for practically all loci except for the alleles of interest, are called congenic lines. They are used to study single-gene effects on productivity, for molecular characterization of genes affecting developmental traits or disease resistance, and many other uses in basic biological and biomedical research (ABPLANALP 1992).

Highly inbred genetic stocks are invaluable in a wide range of research fields, particularly genomics (gene mapping) and immunogenetics (Box 7). A good example of the usefulness of inbred strains in genomics is the mapping of classical mutations. While over 80 classically identified genetic mutations have been assigned to the chicken linkage map, only a few have been located on the molecular map. This is due to the lack of genetic characterization of the exhibition breeds and lines in which most of these mutations are found. Such nonuniform genetic backgrounds make them difficult to use in matings designed to integrate the maps. In contrast, congenic lines, mentioned above, are uniquely useful for such genetic mapping. The integration of genes in exhibition breeds into defined inbred lines would provide the necessary uniformity for molecular mapping of these traits.

**Long-term selected stocks** are the result of many generations of testing and selective breeding for traits governed by multiple genes (the so-called quantitative or polygenic traits). Many valued heritable characteristics in the poultry breeds belong in this category. These include egg production rate, egg size, feed efficiency, fertility, hatchability, viability, disease resistance, body size and shape, and behavioral characteristics. To change the population mean for one or more of these quantitative traits requires rigorous testing and ranking of the individuals and family groups for the traits-of-interest each generation, followed by selective breeding of the higher-ranked individuals and families to produce the next generation. Many factors can affect the rate of improvement in response to selection including 1) degree of heritability of the trait or traits involved, 2) selection stringency, 3) level of inbreeding depression, and 4) genetic load due to deleterious recessive traits or to fix preexisting deleterious recessive traits. These breeding schemes can also be used to expose deleterious recessive traits or to fix preferred or beneficial single-gene traits in populations. Unfortunately, even in the absence of major genetic defects, the fertility and viability of the inbred offspring are almost always lower than the more outbred parent strain, a characteristic called inbreeding depression. If selection and breeding strategies do not compensate for this decline, inbreeding depression can result in the extinction of the line within a few generations. This is a particular concern in lines propagated by full-sib matings which also have large genetic loads (many deleterious alleles). However, once the lethal and sub-vital alleles have been purged from the inbred strain, it can theoretically be bred to essentially complete homozygosity while maintaining reasonable reproductive performance traits (fertility, egg hatchability, egg production rates, viability, etc.). Such genetically uniform stocks can then be used as a standard genetic background in the study of individual genes and gene complexes. Particularly useful inbred lines are those which have been bred for contrasting phenotypes due to allelic differences at single loci. These lines, having the same genetic background for practically all loci except for the alleles of interest, are called congenic lines. They are used to study single-gene effects on productivity, for molecular characterization of genes affecting developmental traits or disease resistance, and many other uses in basic biological and biomedical research (ABPLANALP 1992).

**Box 7. Highly inbred stocks in immunogenetics**

*Basic information about factors controlling disease resistance in the chicken has been gathered largely from studies with congenic strains of chickens (birds with identical, highly inbred backgrounds but different major histocompatibility complex (MHC) haplotypes; ABPLANALP 1992). A number of these congenic strains have been developed at the University of California–Davis, the USDA Avian Disease and Oncology Laboratory in East Lansing, MI, the University of New Hampshire, and Iowa State University. Researchers have shown how each MHC-haplotype could directly affect the resistance of a bird to a variety of different diseases, including coccidiosis, Newcastle’s disease, and the tumor-inducing viruses that cause Marek’s disease and lymphoid leukosis. The congenic MHC strains, most requiring at least ten generations of back-crossing and blood-testing to develop, are key resources required for furthering our understanding of the way the MHC genes function. Studies with these stocks have already given the primary poultry breeders vital information to use in determining the best of several alternative breeding strategies to enhance disease resistance potential of their production stocks.*
breeding, and 4) genetic variation in the original source population. Selected stocks usually require several generations to develop, tend to revert towards the original stock values if the selection pressure is lifted (i.e., if random or non-selected pedigree reproduction is used), and usually need to be reproduced in large numbers (several hundred birds) each generation for the best selection differential with minimized in-breeding.

**Mutant stocks** incorporate one or more of the many single-gene mutations that have a major effect on specific morphological or physiological traits. These include variants (alleles) that affect eggshell color, feather color or shape, skin color, comb shape, metabolic function, major histo-compatibility complex (MHC) haplotype identity, and pattern formation in the developing embryo. The wide array of mutations affecting feather color and shape are important for distinguishing between breeds and varieties within breeds. In the poultry industry, eggshell color, skin color, feather color, and feathering rate mutations, and, more recently, MHC types, have all played important roles in the development of commercial strains and varieties. Of particular interest to biomedical researchers are those mutations that cause disease conditions that mimic human genetic disorders, including muscular dystrophy, scoliosis, scleroderma, and a variety of developmental mutations (usually lethal) that affect the development of the face, limbs, integument, and internal organs.

Cytogenetic variants are birds that have chromosomal abnormalities, such as aneuploidy, polyploidy, translocations, and large insertions or deletions. A small number have been established in the chicken, and these have provided useful model systems for the study of meiosis, inheritance, recombination, linkage, transcriptional regulation, and gene dosage effects. Such stocks include: aneuploidy for the chromosome encoding the MHC and nucleolar organizer region (NOR), complete triploidy (three copies, instead of two, of all chromosomes), large deletions (the mPNU line, in which there is segregation of an MHC/NOR chromosome with a deleted NOR), and various stocks carrying translocations between macrochromosomes (Box 8).

Transgenic stocks are formed by inserting foreign DNA, usually containing a gene of interest, into one of the chromosomes of germline or somatic cells. While some transgenic chickens have been produced in the past few years (Salter et al. 1986; 1987; Salter and Crittenden 1989), the creation of transgenics is still very much experimental in chickens and other avian species. However, a number of research groups continue to develop and refine transgenic methodologies, and report promising advances in the production of transgenic birds (Salter et al. 1987; Love et al. 1994; Thoraval et al. 1995; Maruyama et al. 1998).

**Research genetic stocks**

Genetic stocks are used in three areas of research: agricultural, biomedical, and basic or fundamental biological research.

Agriculturally important avian genetic stocks primarily include those selected for various production-related characteristics (egg production, body shape, feed-use efficiency, leg strength, disease resistance). Another use for such stocks is to provide a flexible, rapidly responding model system for testing breeding techniques and systems that might also be useful with large livestock species (e.g., pigs, sheep, and cattle). These stocks are particularly vulnerable to funding cuts due to the long development period needed for most selected stocks, and the relatively large numbers that must be produced and monitored annually to produce the selected population.

Biomedical research specifically uses animal models for the study of various human diseases. Avian models, mostly in the chicken, exist for the autoimmune forms of vitiligo, scleroderma, and thyroiditis, as well as for various developmental defects, such as polydactyly, scoliosis, and cleft palate. Genetic stocks are also used in avian health research for studying the nature of

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**Box 8. Chicken chromosome rearrangement stocks**

**FROM THE MID-1960S TO THE 1980s, animal genetics laboratories at Ohio State University, the University of Minnesota, and New Mexico State University developed about 40 different chromosome rearrangement strains in the chicken (Zartman 1971; Wooster et al. 1977; Wang et al. 1982). A number of studies by these laboratories made important contributions to our understanding of chromosome behavior in avian species (including recombination, chromosome segregation, identification of pseudoautosomal regions on the sex chromosomes, and sources of aneuploids). Unfortunately, with the lack of support by various agencies over the last ten years, over thirty of these unique genetic resources were irretrievably lost. The seven still in existence, along with a recently isolated spontaneous translocation, are currently being maintained at the University of Wisconsin. However, with departmental reorganizations and budgetary difficulties, these stocks are also threatened.**
disease resistance and effects of specific genes on productivity under disease stresses.

Most of the genetic stocks are of value for studying questions in basic biology that may lead to more applied biomedical or agricultural research, or by simply contributing to the knowledge of how different biological systems function in a wide variety of studies in the life sciences.

Some of the specialized stocks have been derived directly from commercial chicken, turkey, or Japanese quail lines, while others were developed from special breeds, landraces, or wild-types.

**Commercial stocks**

The commercial poultry stocks have made remarkable genetic progress in the last 50 years (Boxes 9, 10, and 11). At this time, selected stocks used in commercial egg or meat production must fit very specialized production criteria. To develop these criteria, each breeding company has identified particular commercial goals (egg production, weight gain, feed conversion, carcass characteristics, etc.) and seeks to meet them in the shortest possible time (EMSLEY 1993). In this way, the fundamental difference between basic and applied research is highlighted. While a researcher may have a preferred outcome for an experiment, any result can provide useful information to that researcher or others in the research community. For the commercial breeder, the only outcome that is acceptable is one that improves the commercial product for the consumer, and increases final profitability for the producer (HUNTON 1990).

From a commercial production point of view, the loss of unique avian germplasm has a number of negative repercussions. To start with, production objectives and economic standards are constantly changing, particularly for meat production birds. This means that agronomic industries will continue to need access to genetic diversity to meet future market demands, to adapt to adverse environmental conditions, to fight new diseases, and to meet the demands for different nutritional values. Thus, an effort must be made to identify and conserve all useful genetic resources that could have commercial importance, such as the sex-linked gene controlling the rate of feather growth that has been heavily utilized by modern chicken breeders (Box 9).

In marked contrast to the general perception that commercial poultry stocks all have a relatively small and diminishing genetic base, some researchers have reported the opposite. Specifically, DUNNINGTON et al. (1994) used DNA fingerprinting to measure variability among commercial chicken breeding populations and concluded that a considerable reservoir of genetic diversity yet remained. IRAQI et al. (1991) reported a great degree of polymorphism for endogenous viral (ev) genes in five egg-type populations maintained by an Israeli commercial breeder. AARTS et al. (1991) also found variation for ev genes among and within six WL and four medium-heavy brown eggshell lines. While none of these methods specifically reflects the variation remaining in genes associated with economically important traits, the recent substantial progress in the development of the genetic map of the chicken (CHENG et al. 1995; CHENG 1997) should soon lead to more thorough and realistic assessment of the amount of economic trait variability remaining in commercial poultry populations.

**Fancy breeds and mid-level production stocks**

For at least 50 years, poultry fanciers have been the main conservators of the majority of the

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**Box 9. Economics of sex-linked genes and chicken genetics**

In 1908, SPILLMAN reported that the female was the heterogametic sex in chickens (now described as ZW, as compared to mammals where the male is heterogametic, XY). This was based on the finding that the barring gene was inherited as a sex-linked gene, being passed from the dam to her sons. This early finding has played an important role in commercial poultry breeding, as many lines are now sexed at hatch time using the sex-linked rate-of-feathering gene. This gene influences development of the early wing feathers in the chick. If the dam carries the slow feathering mutation, K, she passes this on to all her sons, and her W chromosome to her daughters. If the sire is pure for the wild type gene, K+, all the daughters receive the wild type fast-feathering gene. The male chicks are all slow feathering and the female chicks are all fast feathering. Such chicks can be easily sexed at hatch time by the relative feather growth by anyone with a minimum of training. Previously chicks were sexed using the vent sexing method, whereby rudimentary copulatory organs were examined to determine sex. This was a costly procedure, and at $0.03 per chick would cost a hatchery $3,000 for every 100,000 chicks hatched. Over 600 million egg-type chicks are hatched annually in the US. If only half of these are sexed by feather sexing, the chicken industry saves over $9 million per year. Broiler breeders are incorporating this gene also, as sex-separate rearing becomes more prevalent. With over 9 billion broilers hatched in the US each year, this also will have an economic advantage to the industry.
poultry breeds and varieties in North America, particularly the old dual-purpose or mid-level production breeds (Box 12). As the Leghorn chicken, Rock-Cornish cross chicken, and broad-breasted Large White turkey became the dominant commercial birds, commercial breeders could see no economic benefit to maintaining other standard breeds and varieties of poultry recognized by the American Poultry Association (APA 1998). Today, without fanciers, it would be very hard to find an Ancona or Silkie chicken or a Royal Palm turkey. The Lamona chicken breed, developed by the USDA, is a notable American example of a once-useful old-fashioned production strain now fallen from favor.

In some cases, access to mid-level stocks can help small-scale producers stay in business. While they cannot compete with the Rock-Cornish meat cross or Leghorn egg-layer in the highly commercial marketplaces, they can become financially successful by raising some of these heirloom birds to supply specialized niche markets (Box 12). There are many other positive aspects to this practice: small parcels of land can remain agriculturally productive; open space is maintained, family farmers are aided; and moneys go into the local economy.

Biomedical researchers are starting to become aware of the genetic reservoir available in the fancy breeds. They usually seek specific standard breeds or feather patterns that can be used in exploring biological questions (see Chapter 3) or problems related to human medical disorders, e.g., a form of vitiligo in barred chickens (Bowers et al. 1994). The Silkie breed (Figure 9) is particularly useful, with six dominant mutations: crest (Cr), rosecomb (R), muffs-and-beard (Mb), polydactyly (Po), ptilopody (Pt), fibromelanosana (Fm); and one recessive mutation, hookless (h). These mutant alleles produce: elongated feathers on the crown of the head (Cr) and on the face and chin (Mb), a broad, flattened comb that is covered with small, fleshy nodules (R), extra toes (Po), feathered legs and feet (Pt), dark skin, bones, and viscera (Fm), and loose, exceptionally fluffy body feathers (h). Not only have

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**Box 10. Development of egg-laying stocks**

Commercial egg-laying chickens (Figure 6) have shown a substantial increase in productivity in the past 60 years. Some of this improvement has been due to developments in the areas of management, nutrition, and disease control, but the effect of genetic improvement is clear (Arthur 1986). Between 1940 and 1955, the number of eggs laid per hen in the United States increased from 134 to 192 (USDA-NASS 1998). By 1994, eggs per hen had increased to 254. The change in the 1940s and 1950s was primarily due to the introduction of hybrid stock, utilizing pure breeds which had been under development by numerous small breeders participating in the National Poultry Improvement Plan (NPIP). The more recent increase has been primarily due to selection for increased egg numbers. However, it should be remembered that the work of the small breeders and the formal testing parameters set by NPIP shaped the foundation stocks, paving the way for the phenomenal performance in the modern commercial birds.

Today, only a few large international poultry breeding companies produce most of the world’s commercial egg-type chickens. Just 40 years ago, the 1958-59 summary of US random-sample-egg-production tests (ARS 1960) listed 132 breeding firms. In the most recent egg-layer test still conducted in North America, (North Carolina Cooperative Extension Service 1996) only five breeding companies were listed. These were actually owned by just three international firms. These three firms breed over 90% of all the egg-type chickens in North America, and probably well over half of the commercial egg-type chickens worldwide.

Crosses among lines of the White Leghorn (WL) breed produce nearly all the commercially marketed white-shell chicken eggs in North America. The WL lines in use today stem from the pure-bred stocks sold in the 1930s and 1940s. Though there has been intercrossing in many cases to develop new strains, many of the currently used stocks appear to have been selected without intermixing for 30 years or more. Of particular note is the common use of the Mount Hope strain, which is distinguishable by its large egg size and the B-19 and B-21 major histocompatibility complex blood types which it carries (for an explanation of the major histocompatibility complex (MHC) and B-blood types, see the section on Immunogenetics in Chapter 3).

In response to regional consumer preferences, several commercial brown-eggshell chicken lines have also been developed. Typically less efficient than the White Leghorn strains, commercial brown-eggshell chicken lines are usually produced by crossing Rhode Island Red males with high production White Leghorn females. Alternatively, some high egg production strains of Rhode Island Red or Barred Plymouth Rock may be used.

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**Figure 6.** White Leghorn hen (Photo courtesy of U.K. Abbott, University of California–Davis).
the hobby breeders helped in supplying such research birds for one-time projects, but some of them have participated in long-term breeding programs for researchers.

Although the majority of exhibition and mid-level production poultry breeds have continued to exist under the rather informal stewardship of the hobby breeders and the different breed organizations, a number of problems are associated with their conservation: 1) most of the amateur conservators often only keep their stocks for a short period of time (typically just five years); 2) small-scale hobby breeders who get breeding stock from a central clearing house of poultry

**Box 11. Development of meat-producing stocks**

In 1950, a commercial broiler took 84 days to grow to 1800 grams; by 1970, this was cut to 59 days, and by 1988, it was down to 43 days (from Hunton 1990). As with the egg-type chickens, a large proportion of the improved performance of meat birds can be attributed to developments in the areas of management, nutrition, and disease control. But choice of foundation breeding stock and early use of breed crosses were also important in the development of the broiler industry.

More so than the egg market, the broiler market is strongly consumer-driven (Pollock 1999). Early consumer input (chicken of tomorrow competitions between 1946 and 1948) gave the broiler-breeders and growers a good picture of consumer preferences: compact, well-fleshed carcasses at affordable prices. In other words, the scrawny, angular cockerels (Figure 7) available in large numbers from egg-selected Single-comb White Leghorn lines did not even approach the consumer ideal. The broiler-breeders were fortunate to have available the Cornish breed (derived from fighting stock imported from India), which had many of the desired carcass characteristics. The breeders also found that the production characteristics (body type, rate of gain, feed conversion) improved rapidly in response to selection. Unfortunately, improvement in these areas had a strong negative effect on the already poor reproduction characteristics of the Cornish lines (low egg production, low fertility, poor hatchability, reduced chick viability), and seriously impaired disease resistance (see section on immunogenetics, Chapter 3). The early breeders found that crossing the Cornish roosters with hens from improved dual purpose breeds solved many of these problems. These “female” line breeds, including the Plymouth Rock and New Hampshire, have better body type than Single-comb White Leghorns, yet lay eggs at a relatively high rate compared to the Cornish “male” lines. Today, the commercial sire is often a cross between two predominantly Cornish strains, and the commercial dam is a cross between two strains descended from one or more of the dual-purpose breeds. The outbred or crossbred parents have better reproductive traits and general vigor than parents from the pure-lines, and their offspring, a three- or four-way cross, exhibit even more hybrid vigor. Unfortunately, despite careful evaluation of the breeding stock, some serious structural and physiological problems have surfaced that appear to be the result of the intense selection for desirable production characteristics. These include: leg weakness, cardio-pulmonary insufficiency, breast blisters, increased fat deposition, and muscle anomalies.

While the turkey industry is considerably smaller than the broiler chicken industry, many of the same breeding methods have been used, and many of the same problems have been encountered (Hunton 1990). With a smaller genetic base, and a much larger bird to start with (Figure 8), the structural and physiological problems found in chickens are often magnified in turkeys. Considering the small number of primary breeders (three) and the scarcity of exhibition or research turkey breeding stock, it is imperative to safeguard the remaining genetic diversity of this domestic species.

**Figure 7.** Traditional broiler-type chicken carcass of the 1940s (Photo courtesy of F.A. Bradley, University of California–Davis).

**Figure 8.** Commercial Large White turkey tom (Photo courtesy of R.A. Ernst, University of California–Davis).
stocks may never know their egg source or the
degree of relationship of their foundation stock;
3) breeding populations are often very small,
particularly for the rarer breeds, and pedigree
information is frequently limited or not available;
4) some hobbyists deliberately inter-cross differ-
ent breeds or varieties in attempts to improve or
modify exhibition traits; 5) selection for produc-
tion characteristics (e.g., fertility, viability, egg
production, or disease resistance) may be largely
ignored in these small-scale breeding programs,
although de facto natural selection will tend to
eliminate the infertile, disease-susceptible, or
least-viable individuals; and 6) backyard breed-
ers tend to have problems in controlling diseases
and may have serious endemic diseases. If there
were a formal conservation pro-
gram for avian genetic resour-
ces, it would be logical for it to
provide technical services to
these hobbyists who are a very
important component of avian
genetic resources conservation.

Figure 9. Silkie rooster from UCD Silkie (Photo cour-
tesy of J. Clark, University of California–Davis).

Box 12. Small renaissance of old-style chicken breeds

With the increasing cultural diversity
of our population, the white-feathered, highly selected meat- or egg-produc-
ing bird no longer meets the needs of
all consumers. In response to a great
demand by ethnic markets and the
many upscale restaurants searching for
the “chicken of yesterday”, more and
more small producers are starting to
raise “old fashioned” mid-level produc-
tion or dual purpose breeds (those that
are reasonably efficient at producing
both meat and eggs). These produc-
ers are getting their stocks from the
few people who still maintain popula-
tions of true Rhode Island Reds, Speck-
led Sussex, New Hampshires, and so
on. Those supplying the specialty egg
markets are also looking for different
breeds to produce a colored egg that
will be distinctive (brown, tan, green,
or blue), such as Orpington, Rhode Is-
land Red, and Ameraucana. Unfortu-
nately, most of these so-called mid-
level production breeds have all but
disappeared from American farms.