

THE SUPER HENS (Part I): DIFFERENCES AMONG DUCKS

By Mickey Heitmeyer

Editor's Note: This is the first of a critically important and alarming four-part series examining in detail the broad scope of problems facing ducks, duck hunters and waterfowl managers. The author, Mickey Heitmeyer, one of the world's leading authorities on mallards, provides unique and extraordinarily perceptive insights and solutions. We highly commend it to your attention. Because of its semi-technical nature, it is recommended that you first print the article, then read from the printed page. The remaining parts of this series will follow in weekly installments.

Variation among individuals is a basic fact of biological life. Biologists refer to this variation as heterogeneity, and it takes many forms - from obvious differences between species, sex and age-groups to more subtle, yet highly important, individual differences in genetic makeup, morphology (physical characteristics), behavior, and physiology. These variable traits influence whether an individual duck (or any living organism) survives, reproduces, adds offspring to the population and transfers genes to subsequent generations. Over time, natural selection causes traits of successful individuals to be retained, while discarding or reducing the frequency of those traits that are not. Consequently, how a duck looks, its behavior and food habits, and where it lives and moves throughout the year represents the accumulated adaptations of both a species and an individual to a changing environment.

If heterogeneity is so basic to our understanding of biology and ecology, why is it seldom incorporated into waterfowl management (with obvious exceptions such as variable bag limits for some species and hen restrictions for mallards)? Do waterfowl biologists not understand it? Is it difficult to incorporate into management programs? Do biologists simply disregard it? Does it really matter?

This four-part series asks these simple, yet hard, questions as they relate to contemporary waterfowl management. Specifically, questions are asked (and perspectives offered) about how changes in habitat type and availability, regional and continental land uses, and hunting regulations have changed the "playing field" for waterfowl. Do these basic adaptations and genetic makeup of birds still protect them from environmental and anthropogenic (man-made) factors? Or, are they potentially jeopardizing the future of species and populations?

Part I introduces the basic considerations of heterogeneity. Part II discusses how heterogeneity influences reproduction - the additions to the population. Part III discusses how heterogeneity affects variation in mortality and survival rates - the subtractions from

a population. Finally, Part IV addresses issues related to effects, both intended and unintended, of current harvest regulations, including sources and directions of biases in population analyses, additive vs. compensatory mortality, and the thorny issues of spinning-wing decoys and expanded season lengths.

This series is deeply rooted in science. Despite heterogeneity's relative lack of attention in contemporary waterfowl harvest and management programs, the subject is richly and widely represented in the scientific literature. Many of the descriptions of waterfowl heterogeneity in this series are simplified for sake of space and many exceptions to the generalizations exist. At the end of each part, I offer a few examples of scientific references to the reader who wishes to learn more about, or challenge, the scientific foundation of this series or my conclusions. Despite the semi-technical nature of these articles, I hope the average duck hunter will be able to relate to numerous examples from his or her own hunting experiences. Hopefully they will never look at another dead duck "in-the-pile" in the same way. Every hunter knows that not all ducks are the same - from the obvious differences in species, sex, and age to varying size and fatness, plumages and, importantly, their response (or lack thereof) to calls, decoys, and setups in various locations.

Species

Waterfowl are a wonderfully diverse group of species. Contemporary taxonomy recognizes 43 species that are native breeders in North America and another five-to-six species that are irregular visitors from Eurasia. These species have remarkable variation in morphology, behavior and social structure, physiology, and distribution - each trait an adaptation to the dynamic and widely distributed wetland resources they exploit. At the highest separating taxonomic level (subfamily) geese and swans have many obvious and distinct differences from most ducks. Geese and swans are large, slow to mature (first breeding typically does not occur until two to four years of age), mate for life, lay small clutches, do not reneest, provide extended parental care, and have long life-spans. Geese and swans also are highly philopatric, i.e., they have strong traditions of use to specific geographical areas throughout the annual cycle. Generally, geese and swans can be considered "slow species" with more of what biologists call "K" reproduction strategies. This "slowness" to mature and reproduce, etc., is overcome by strategies designed to increase survival and production of young (e.g., strong philopatry, laying fewer eggs annually but over a greater number of years, producing larger eggs that result from large body sizes and stored nutrients, high incubation constancy, strong defense of nests and young, and extended parental care by both parents. Clearly, for these species, long-term stability and growth of populations requires high survival rates. By living a long time, geese and swans can "hedge-their-bets" against poor breeding success in any given year caused by bad weather, habitat changes and/or man-induced disturbance conditions.

Ducks in North America have an especially wide diversity of morphology, behavior, and life history strategies that range from species with many K-strategy traits similar to geese (e.g., Mergini, the sea ducks, have delayed maturity, large body size, reliance on stored nutrient reserves, low clutch sizes) to "fast species" that have what biologists call "R" reproductive strategies. These R-strategy species, such as blue-winged teal, have small body size, short life span, weak pair bonds, large clutch sizes,

and tendencies to reneest (sometimes many times). However, even within the common dabbling duck tribe (Anatini) huge differences exist among species in timing of pairing, migration, and reproduction (e.g., early for mallards vs. late for shovelers); propensity to reneest and overall reproductive potential (e.g., high in mallard, low in pintail); nutrient reserve storage; and many other behavioral and physiological attributes.

Like a financial balance sheet, additions (recruitment of young) must equal, or exceed, subtractions (mortality) for the account (population) to remain in the “black.”

Consequently, variations in life history among waterfowl species affect their ability to accommodate different annual rates of mortality. In North America, management of geese generally has incorporated species differences better than for ducks, partly because there are fewer species and also because populations are better defined (see next section). Many species-specific regulations (e.g., variable bag limits) and some habitat management programs exist for ducks. However, management often generalizes among species and is highly influenced by trends in mid-continent mallard numbers, including current Adaptive Harvest Management (AHM) models. Certainly, there is value in simplifying regulations, but we have somewhat limited information for some species. The assumption that many duck species respond similarly to mallards in regard to management decisions is largely untested and probably incorrect.

Subspecies, Populations, and Genetic Variation

All waterfowl species are comprised of individuals of different genetic makeup. In some species, such as Canada geese, genetic differences are manifested as geographically distinct subspecies (e.g., the small Cackling Goose group of Dusky, Aleutian, Richardson, and Cackling subspecies). In other species, such as common eider, “races” are recognized (i.e., American, Northern, Hudson Bay and Pacific). Still others have defined “morphs”, [e.g., the mallard complex (see below)]. Finally, most species have at least some distinct “local populations” that share a single “gene pool” and have somewhat defined geographic ranges throughout their annual life cycle. In geese and swans (and probably some sea duck species) the identity of the “population” is maintained over time because young accompany parents to migration and wintering grounds and “learn” the routes and destinations, which become embedded traditions of use. Where these populations can be identified, they allow managers to implement specific habitat and harvest management actions. Examples of individually managed populations include the mid-sized Canada goose flocks – the Atlantic, Southern James Bay, Mississippi Valley, Eastern Prairie, Rocky Mountain, Hi-Line, and Pacific. For these populations, surveys are scheduled for known breeding, migration, and wintering locations and trends in recruitment and survival can be monitored annually.

In contrast to geese and swans, many ducks are more panmictic (mingled, with somewhat random mating) breeders and are not as segregated into distinct populations. Breeding philopatry (returning to the same area to nest in subsequent years) is female-based in ducks. That is, females determine the ultimate location of, and migration routes to, nesting areas and the male mate follows the female to the breeding site. Most ducks form new pair bonds each year. As an example, a male mallard pairs with a female mallard in December 2003 (say in central Arkansas) and follows her to a breeding area in

Saskatchewan in the spring of 2004. The following year that same male returns to central Arkansas and pairs with a different female that eventually will nest in Wisconsin in 2005. Further, females typically abandon ducklings late in brood rearing (hens of some species such as pintails abandon the young much earlier than the norm), and juveniles separated from parents intermix with ducks from many clutches and breeding locations during fall. Juveniles then follow adults with varying traditional migration and wintering patterns to nonbreeding areas. It is common for brood-mates to have different migration and wintering locations depending on who they intermix with, and follow, during migration. Consequently, traditions of use are “learned” differently in ducks than in geese.

Despite the generalized panmictic nature of duck breeding, recent studies suggest stronger traditions of use patterns, especially during migration and winter, than previously assumed for many duck species. “Homing” to certain geographical migration and wintering areas is common for many ducks. Further, genetic investigations suggest that different population segments of ducks exist, at least for some species and locations. For example, relatively distinct populations occur for mallards that: 1) nest in eastern Canada and winter along the Atlantic Coast; 2) form the larger, mixed group of mallards present in the mid-continent region; and 3) breed in Washington, Oregon, and California and have short migration routes between Pacific Flyway wintering and breeding sites. In another example, recent satellite telemetry and biochemical “marker” information suggests some pintails are predisposed to breed in Alaska, others follow interior routes to prairie Canada, and still others vary migration and breeding site-selection depending on weather and habitat conditions. Other genetic and banding data suggest population segments for wigeon, green-winged teal, wood duck, canvasback, and lesser scaup (and probably many others). New technologies undoubtedly will refine information on “population” segments of each waterfowl species. With this information, managers can, and should, monitor and devise specific management programs for identifiable population segments.

An especially contentious management debate in North America concerns the mallard-mottled-Mexican-black duck species complex. Most likely, this group of “mallard-like” ducks was in varying stages of geographical and genetic isolation when European settlers arrived in North America. In a Holarctic species such as the mallard, considerable “polymorphism” (phenotypic variation within an interbreeding population) exists and genetic variation apparently was advancing at the time of settlement toward a separation of the various morphs (mallard, black duck, Florida duck, mottled duck, Mexican duck) both in form (i.e., lack of sexual dimorphism in all except the mallard) and geography. Despite the apparent advancing divergence, the current genetic makeup of these morphs is very similar and probably is not deserving of species designation. In fact, more genetic variation exists within some populations of mallards (see above) than exists between mallards and black ducks. Black ducks and mallards interbreed freely and there may be more “hybrids” than “pure” black ducks in many locations. Controversy exists over the causes of increased hybridization of mallards and black ducks (and also between mottled, Florida, and Mexican ducks) and the capability, or willingness, to manage these morphs separately. It appears both high harvest rates and long-term habitat changes are to blame for declines in black ducks. In this extreme case of intra-specific heterogeneity, data on cause-and-effect are clouded and many critical management issues must be carefully addressed if the objective is to sustain the black duck morph.

Sex and Age

Probably the most recognizable groups (cohorts) within a waterfowl population are the sex- and age-classes of individuals. Demographic studies and management of any organism (whether mallard or mongoose) depends on understanding the differences between males and females, and also among age classes (at least juveniles vs. adults). In all waterfowl populations that have been studied for a long time, females have a higher annual mortality rate than males. Consequently more males exist in a population than females. This male-biased sex ratio causes females to be the limiting factor (as potential mates) of a population and increases competition among males for mates. Mate selection in waterfowl is “assortative” whereby females test (and make mate choices from) the potential fitness of males through assessment of their size, courtship displays, stamina, dominance, plumage, etc. These competitive forces have “selected” for the bright coloration of males (for showing off traits in courtship) vs. the complex relatively dull “browns” of females (for camouflage during nesting). Later parts of this series will discuss why the “quality” of the mate (either male or female) is so important to maximizing survival and reproduction, but for now we must acknowledge that not all females (or males) are of equal quality or have equal quality mates. These inequalities greatly impact reproductive potential and ultimate effects of differential mortality on one segment of the population vs. another. Further, and of obvious importance, managing (i.e., reducing) mortality factors for females is much more important than for males.

Investment of time and energy in annual events (e.g., incubation, egg-laying, brood rearing) varies among sexes and species of waterfowl. In geese, where extended parental care is the norm, both sexes contribute to rearing young, and timing of annual events such as migration are synchronized. In contrast, male ducks contribute less to recruitment and typically abandon female mates late in incubation. This separation causes asynchronous timing of subsequent events for male and female ducks and the sexes often become geographically separated for extended periods. As an example, male pintails leave females in mid-late incubation, depart prairie breeding grounds early in summer, and move to molting areas. Here, they complete wing and body molt and begin southern movements as early as August. In contrast, successfully nesting female pintails remain with broods into mid-late summer, and usually molt on, or near, breeding areas. Females and juveniles often leave breeding areas together in fall. Consequently, the first pintails arriving on wintering areas in the Central Valley of California are predominantly male; females and young do not begin arriving until one-to-two months later. In this case, depending on hunting season dates at various locations, harvest could potentially, and perhaps unknowingly, be differentially directed at a particular sex or age cohort.

As shown in the above example, different age cohorts (within and between sexes) may have different distribution, timing, and behavioral patterns. As with most animals, waterfowl young of the year [known to biologists as hatch-year (HY) birds] typically are smaller, have delayed and less defined coloration, unrefined courtship displays, slower succession of annual events, higher mortality, and lower recruitment rates than adult after-hatch-year (AHY) birds. A further age complication occurs for species with delayed maturation such as geese, where the “adolescent” or “subadult” period may last two-to-three years before pairing and first breeding occurs. Plumage characteristics (including feather patterns on the wing) often enable biologists to determine whether a bird is HY,

subadult, or AHY. Many population analyses attempt to determine differences in survival/harvest rates of these age classes. Other species have additional unique morphological features that allow age determination for several years (e.g., eye color of lesser scaup is different from age one to age five or six). Finally, banding and color marking (including neck collars, nasal saddles, and patagial or wing markers) have been employed to determine exact ages of birds in some species and populations. Despite the obvious differences in age classes of waterfowl, the significant efforts to determine age-classes of species, and the differential contribution to changes in population size and distribution, it is disappointing to find them lumped together in certain population analyses such as Adaptive Harvest Management and in studies of distribution dynamics.

It is important to recognize that certain traits of waterfowl, whether they be population-, sex-, or age-related, are inherent (nature) and genetically programmed. Others are a product of the environment, a duck's experiences and its ability to "learn" successful survival and reproductive tactics (nurture). Collectively, these factors create heterogeneity - and they create inequality or differential success in reproduction and survival among individuals. The key to enlightened and progressive management of waterfowl is understanding which individuals are the most reproductively successful ("super hens") and which hens are less consequential to population changes. In the second part of this series I will discuss characteristics of the "super hens," explain why they produce most of the young each year, and why management actions are needed to enlarge this population segment.

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If we take care of the ducks, the ducks will take care of us.

THE SUPER HENS (Part II): VARIATION AND RECRUITMENT

By Mickey Heitmeyer

Editor's Note: This is the second of our four-part series examining in detail the broad scope of problems facing ducks, duck hunters and waterfowl managers. The author, Mickey Heitmeyer, one of the world's leading authorities on mallards, provides unique and extraordinarily perceptive insights and solutions. We highly commend it to your attention. Because of its semi-technical nature, it is recommended that you first print the article, then read from the printed page. The remaining parts of this series will follow in weekly installments.

Many factors influence the reproductive output (recruitment) of waterfowl, both for an individual and a population. These include: 1) the number of potential breeding birds, 2) the proportion of individuals that actually attempt to breed, 3) location and timing of nesting, 4) clutch size and nest success (survival of the egg), and 5) survival of young produced. These components of reproduction are influenced by many things, some "nature" and some "nurture." True to the theme of this series, it is critically important to understand and appreciate the tremendous variation (heterogeneity) that exists in each of these components.

Number of Potential Breeding Birds

The primary determinant of the potential number of birds that can breed in a given year is the survival of females in a population. Much of the discussion of survival will be covered in Part III of this series, but we must identify a few survival issues now to fully understand recruitment. First, survival of all waterfowl species varies among species, sex, age, condition of bird, geographical location, climate, and habitat condition. A conclusion of Part II (see below) is that variation in survival is the most important factor determining "lifetime reproductive success" (the total number of breeding-age offspring produced by a female during her lifetime). Second, the number of waterfowl breeding in an area is determined by "homing" or philopatry of females to natal (the area where they were hatched) or previously successful breeding sites; "pioneering" or "immigration" of birds into non-natal areas; and "emigration" of adults that may have bred in the area in the previous year but chose a different area to settle in subsequent years.

"Homing" is measured as a "return rate" to a location, whether it be a breeding, migration, or wintering site. Return to an area is a reflection of: 1) survival of the bird that allows it to return to that site, and 2) the relative success of the bird in that site that encourages it to return. In a simple analogy, if we visit a restaurant and the food is poor, in short supply, or costly we are unlikely to return. No wonder we all have our favorite "diners." Ducks are no different. Return rates to habitats, especially breeding locations,

are higher for adults than for juveniles. This is no surprise, in part because juveniles have lower survival rates than adults. Further, adults have the benefit of previous breeding and nesting “experience.” The experience of the breeder is affected by habitat conditions, density of co-breeders, and predation or other disturbances. If too many conspecifics occur in a site, resources may be limited both for the adult and the forthcoming brood. Also, too big a “crowd” may attract more predators. Competition and the risk of being eaten (or the eggs destroyed) are not factors likely to encourage return to an area. But what if that area is the only “diner” in town? If this is the case, then the population either produces poorly, or birds seek other locales. If they find suitable habitat elsewhere, they may move or “immigrate” into that area. Long term studies of snow geese, Canada geese, and wood ducks indicate that the most successful females (the “super hens”) have genetic predispositions in their broods for some ducklings/goslings to be “pioneers,” i.e. these young will not return to natal sites regardless of their quality and instead will seek different breeding sites. As in entrepreneurship, it takes only an occasional “hit” to make this strategy work, often in a big way. This is the name of the game in speciation and genetics - to maximize your distribution and contribution - conquer the world if you will.

Proportion of Birds that Attempt to Breed

The percentage of females in waterfowl populations that attempt to breed in any given year is different among species (e.g., some species such as geese, eiders, etc. do not reach maturity until ages two-to-four) and is influenced by weather, age (after maturity), breeding experience(s), timing, body condition, wetland and habitat condition, and maybe population density. Certain of these factors are innate, others are directly influenced by abiotic factors on breeding grounds, and still others are the product of “cross-seasonal” effects (factors occurring on migration and wintering grounds that influence reproductive potential many months later). Most, perhaps all, of these factors are interrelated. None are completely independent from each other. Also, most events that lead to eventual breeding attempts depend on the timing and success of preceding events. For example, body condition of a female is influenced by age, prior experience, and habitat conditions on migration and wintering areas. This affects the timing of pairing, quality of mate obtained, progression of prebasic molt of females, spring migration departure time, storage of nutrient reserves used in migration, time of arrival on breeding grounds, egg production and incubation, probability of encountering and surviving inclement weather, predation, competition with others, capability to renest if needed, and so on. Understandably, ducks, geese, and swans are impacted by a succession of habitat conditions (including anthropogenic or “man-related” influences) throughout the year. Success or failure in each area has consequences on the next event and area used, from the simple factor of surviving to the next event to the condition of the bird when the next event begins. For these reasons alone, management of waterfowl in North America must address habitats used throughout the annual cycle. Some disproportionate conservation effort may be deserved for specific times and areas, but not at the expense (or exclusion) of the integrity of the entire range of a species.

Studying the percentage of “nonbreeders” in waterfowl species is difficult because of their mobility, extensive areas used during the annual cycle, and limited number of marked birds in most populations. The best data are from long term studies of geese, swans, and brant although some long-term data also exist for wood duck,

canvasback, and mallard. Also, many techniques used to track individual birds over long periods have potentially severe biases (e.g., radio transmitters placed on birds may impede their ability, or willingness, to attempt breeding because of constraints on energetics, mating, egg production, etc). Despite limitations of current technology and methods, data suggest the incidence of nonbreeding may approach 20-30 percent for geese, brant, and swans; 10-20 percent for diving ducks, and 5-15 percent for dabbling ducks. If any of the above factors increase the incidence of nonbreeding, the impacts on size of fall flights could be substantial. And, if some females (a “super hen,” for example) almost always attempt to nest (and re-nest multiple times if necessary) while others seldom or never nest, then impacts of factors affecting the “super hen” are much more important than those affecting nonbreeding hens.

Location and timing of Nesting and Clutch Size

It should be apparent by now that both environmental (nurture) and intrinsic (nature) factors influence all aspects of waterfowl life histories, including reproduction. Location and timing of nesting, re-nesting (if it occurs in a species), and clutch size are not exceptions. The usual factors apply - age, experience, body condition, mate quality, habitat condition, and climate. Certain individuals seem to be able to nest at opportune times and in good locations and some do not. Here, I submit that success begets success and failure usually begets failure. Studies of geese have been most instructive (because of the ability to mark individual birds and follow them through successive years). The cycle begins with a successful nesting attempt - success being defined as producing a breeding-age offspring. Likely, this success was attained because the breeding female was older, had a good quality mate, and was in good body condition. This combination of traits allowed the female to arrive on breeding grounds earlier, enabling them to select better habitats and territories, have dominance over resources and reduce competition, nest in a more secure location (general habitat or within a colony), produce a larger clutch (up to some species-specific pre-programmed point), be more vigilant in incubation, hatch young at times that coincided with optimum food availability for broods, guide broods to better and safer foraging areas, etc. This sequence of success ultimately creates higher recruitment for that female. Furthermore, having experienced this success, the female is more likely to repeat this pattern in subsequent years if she survives, and the young are given the advantage of earlier maturation and positive learning experiences. These female offspring of the “super hens” then become the next generation of “super hens.” Recent long term studies of geese, brant, wood ducks, hooded mergansers, shovelers, tufted ducks, common pochards, and goldeneye confirm the long suspected phenomena that some familial lineages are more successful than others.

Nest Success

Recently, much contemporary waterfowl management in North America, at least for prairie-nesting ducks, has advocated a need to increase “nest success.” Obviously, a nest must hatch before young can be produced. Data suggest that nest success in at least part of the traditional breeding area in the prairie pothole region is lower than in past times because of higher predation rates and poor quality upland and wetland habitats. However, one must understand that predation on nesting females and their eggs always has been a dominant force in the evolution of waterfowl traits and life history strategies,

and that high predation rates typically occurred in many breeding areas and for many (perhaps most) species, perhaps especially for the prairie-nesters. So, low nest success historically was the norm, not the exception. The key to successful management is to understand “how much” nest success is needed to sustain populations given contemporary changes in land uses, disturbance, predator populations, harvest, etc.

Some studies in the prairies during the 1970s and 1980s suggested 15 percent nest success was the magic point needed to obtain stability in duck populations. This level is an over-generalization for species/populations and locations, and has been misused by many biologists, agencies, non-governmental groups, and the popular press seeking to promote certain agendas. This number might be an average annual “rate” that is needed for stability of some populations, but it is doubtful this figure represents the evolutionary norm. Moreover, it does not reflect the average “life-time” nest success need of an individual. For true population stability, a female only has to produce one breeding age female offspring during her lifetime to replace herself. Theoretically, if all females eventually produce one female recruit, it doesn’t matter how good or poor nest success is in an individual year. Likewise, theoretically it wouldn’t matter whether a female dies or not after she produces a breeding age female offspring. Unfortunately, not all females ultimately produce one breeding age female. The population must rely on the “super hen” to make up the difference for those that do not live or do not produce recruits. Here, we begin to appreciate the problems of averaged “size-of-the-pile” statistics used in analyses of “population dynamics.” They fail to appreciate and incorporate individual heterogeneity.

Realistically, the critical questions about nest success become: 1) are contemporary landscapes capable of supporting population sizes that ultimately can replace themselves given current nest success rates, 2) can landscapes be improved (via whatever means) to increase recruitment, and/or 3) can individuals (birds and species) learn (ala Canada geese and mallards nesting on buildings in cities) new strategies to nest successfully? These questions are not confined solely to breeding ground habitat condition either. As already stated, the succession of events leading up to breeding are not independent. Nest success is no exception because it depends on timing and location of nesting, experience and condition of female, mate quality, vigilance, and many other factors that are influenced by habitat conditions, disturbance, energetics, etc. on migration and wintering areas.

Brood and Subadult Survival

At this point, perhaps little more needs to be said about the factors that cause variation in waterfowl recruitment, including the need for young to survive to breeding age. The importance of survival of young after hatch has been overshadowed by the “press” surrounding nest success issues. However, recruitment is not achieved upon hatching of a nest or when the young reach flight stage. True recruitment is when offspring reach breeding age. The importance of first-year (and subadult) survival will be expanded in Part III of this series. It varies among species, locations, and parentage. It may be especially critical for geese and swans that have extended parental care and for the “super hen” that gives her offspring the advantage in time, space, and resources.

Lifetime Reproductive Success

In a generalized form, what matters evolutionarily is not so much how the “population” does, but rather how the “individual” does. Even concepts of altruistic “group-“ and “kin-selection” have the ultimate common currency of passing genes to future generations. Perhaps hunters (or others with vested interests in the number of hunters) care only about total numbers (the “size of the pile”) and not the individual (“who is in the pile”). But, they should. The ultimate future of waterfowl (and hunting opportunity) depends on sustaining the genetic integrity of populations - which means sustaining the “super hen” component.

“Super hens” are *the females that produce the most female recruits over their lifetimes*, not necessarily in an individual year. The few long-term studies of waterfowl that have documented lifetime reproductive success (LRS) conclude that the number of breeding attempts in a female’s lifetime (i.e. longevity and high annual survival) is the strongest correlate of LRS. Also, early nesting females generally fare better than late nesters and those with greater body mass (fatter hens) ultimately produce more young than leaner birds. These two attributes are related. This tells us that annual nest success is important for LRS, but much less so than survival, age, and physical condition of the hen. The study with the largest, most comprehensive data set for ducks (see Blums *et al.* in the Selected References) exemplifies this conclusion. This study for the first time simultaneously considered both direct (i.e., factors on breeding areas) and indirect (body condition and survival on nonbreeding areas) effects of potentially interacting variables on estimates of LRS. A remarkable, yet disturbing, result of this study was that 59-74 percent of all females in the populations studied never produced breeding age offspring. Maybe the 80:20 (or 60:40) rule applies for ducks. Other long-term data from wood ducks, hooded mergansers, geese, and swans suggest it does. If indeed 20 to 40 percent of the females in a population produce 60 to 80 percent of future breeders, then the implications for management are staggering.

If only 20 to 40 percent of female waterfowl produce most recruits, then these females must average three-to-four females recruited to the next generation to achieve population stability. Current waterfowl management is based on averages. It does not recognize variation in individual performance. Obviously, the death of one of these “super hens” is three-to-four times more costly than the death of a dud (unless the super hen has already done her job at that point). Hunters should ask themselves: Is that hen mallard I just shot a “super hen,” a member of the valuable 20 percent? Or is it the dud, the compensatory duck, the remaining 80 percent? In Part III of this series, we will delve into the issues affecting survival of waterfowl and discuss the potential problems and biases of survival and life-model analyses that do not incorporate heterogeneity.

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If we take care of the ducks, the ducks will take care of us.

THE SUPER HENS (Part III): SURVIVAL AND LIFE CYCLE

By Mickey Heitmeyer

Editor's Note: This is the third of our four-part series examining in detail the problems facing ducks, duck hunters and waterfowl managers. The author, Mickey Heitmeyer, one of the world's leading authorities on mallards, provides unique and extraordinarily perceptive insights and solutions. We highly commend it to your attention. Because of its semi-technical nature, it is recommended that you first print the article, then read from the printed page.

Many things kill waterfowl. However, survival of a duck, goose, or swan is mostly related to a bird's ability to avoid being eaten by something, whether it be fox, man or microbe. Consequently, understanding a duck's life is in large part understanding what kills (or seeks to kill) it, and when it gets killed. Generally, the killing (mortality) agents take two forms: 1) natural and 2) human-caused (this also is natural, but for sake of this discussion and the changing and controlling nature of it, waterfowl managers treat it separately).

Natural Mortality

The big three natural mortality agents for waterfowl are 1) predation, 2) weather, and 3) disease. A fourth agent, starvation, generally is not considered a major factor causing mortality in waterfowl (however, the recent overpopulation of snow geese has depleted certain "goose pastures" in the Arctic and essentially starved young goslings). In many cases, the natural mortality agents are related. For example, extended cold and ice may increase incidence of certain diseases or predation during winter.

Most natural mortality agents have at least some "selectivity" in who gets killed, and when they are killed, especially if the agent is predation. Television nature shows and many stories of natural selection usually imply "survival of the fittest" being manifested as predators catching the "weak" individuals in a population. Predation of waterfowl (or any living organism) can occur at any time and place, and typically happens when an individual is placed in a compromised position. The compromise may be caused by weakness or poor physical condition (e.g., an inability to escape), poor visibility or inattention (e.g., bad weather, dense cover, distraction), exposure (e.g., poor habitat that causes a female and her brood to forage in more risky areas or on degraded sites with inadequate food or cover), and/or a physiological event (e.g., confinement of a female on the nest during incubation).

Enter heterogeneity (the differences between individuals) again! Age, physical condition, accumulated experience, and so forth all affect whether a bird is in a

compromised position, and for how long. This may be especially true during breeding. By far the greatest mortality agent on breeding grounds is predation on nesting females and pre-fledged young. Many studies of mammal (e.g., red and arctic fox, raccoons, mink), avian (e.g., raptors, gulls, crows, ravens), and even fish and reptile (e.g., bass, bullfrogs) predation indicate that waterfowl mortality is greatest in areas of poor habitat, crowded conditions, or simply within the range of a skilled predator. To no surprise, a female's (and her broods) chances of survival are better if she is older; has a good quality, vigilant mate (or attentive parent); good body condition; and experience (including, perhaps, experienced parents). These individual qualities generally increase the probability that a female will nest early and hatch young successfully (at least historically). Further, if an early nest hatches it means the female will not have to re-nest (for those species that are inclined to do so, like most dabbling ducks), which would increase the time she is exposed to predators while sitting on a nest. The greatest mortality on ducklings/goslings occurs in the first few days following hatching. Consequently if a female hatches a brood early in the spring when wetlands are coming alive following ice-out, many alternate foods are available for predators to seek and eat besides ducklings. Moreover, food, cover, and water are plentiful because wetlands haven't started drying.

Less is known about natural predation on migration and wintering areas, and it appears to be less common or important than on breeding areas. Nonetheless, the few studies that have documented predation (primarily raptors and falcons) on nonbreeding areas indicate mortality is greatest for individuals in poor body condition, and that are isolated from or on the edges of flocks, unpaired, and in open habitats. Further, while actual death from predation may be infrequent on migration or wintering areas, its potential presence has been an important evolutionary force dictating behavior and habitat use of birds during migration and winter. This also holds true for such factors as pair formation and nutrient reserve storage.

Disease, weather, and starvation are lesser mortality agents than predation, especially on breeding grounds. However, they can be significant at certain times and locations. To a degree some disease outbreaks and weather events are non-selective and essentially kill everything in their path. However, limited data again suggests older (up to a certain point of senescence) and better condition birds may be less susceptible.

Human-Caused Mortality

The two primary human-caused mortality agents for waterfowl are: 1) harvest, both sport and subsistence; and 2) contaminants. Other human activities also cause mortality in waterfowl such as collisions (wires, roads, farm machinery such as hay mowers, etc.), but they are relatively unimportant events in most areas. Clearly, the largest human-caused mortality agent is sport hunting and it is confined to fall and winter. In contrast, predation, the major natural mortality agent, operates mostly in spring and summer. I do not discount subsistence harvest as being inconsequential, because it is substantial for some species that nest in far northern latitudes such as goose, brant, and eider colonies on the Yukon-Kuskokwim Delta in Alaska, along Hudson Bay, and in other Arctic sites. Subsistence harvest occurs mostly in spring, but some substantial harvest also occurs in key staging areas in fall.

Sport hunting (and probably subsistence harvest also) is not a random mortality agent. Every hunter knows that some birds respond better to calls and decoys than others. Why? The vulnerability of birds varies with time (during the day as well as over the season), location, climate and habitat conditions, species, sex, age, body condition, annual cycle event, social status, flock size, color phase, and hunting technique. Some discrimination in harvest is intentional and is related to regulations including shooting hours, season dates, zones, species and sex restrictions, etc. Other variation is caused by inherent differences in vulnerability of individual birds. It is easy to understand why some birds might be harvested at higher rates. Young birds and those in poor condition may be less wary in approaching decoys and responding to calling because they have less experience or they simply are hungry or seek company.

It is no surprise that the age-ratio (the number of juveniles per adult) of waterfowl shot by hunters is much higher in northern states and Canada in early fall compared to later seasons in the south. Hunters in northern areas enjoy the benefits of many recently hatched, inexperienced young birds, and harvest them at a high rate, as shown below.

Mallard Age Ratios

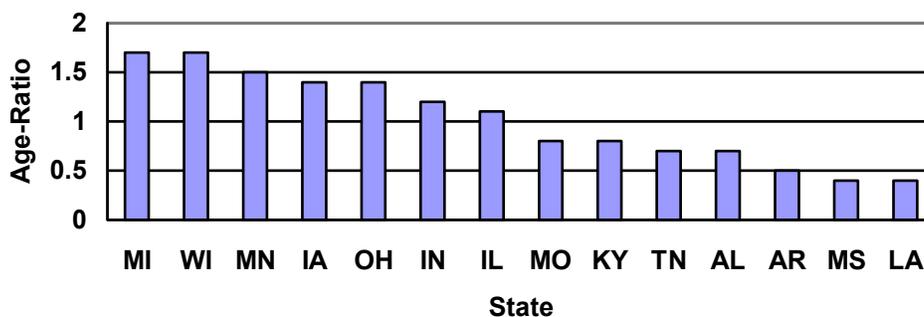


Figure 1. The number of juveniles per adult in the hunter’s bag is highest in northern states and lowest in southern states, as you can see from this graph of age-ratios of mallards killed in the Mississippi Flyway in 2002. Source: USFWS.

By the time birds migrate to mid-latitude and southern states, many young are already dead, and hunters are dealing with more educated, older and wiser birds. In Louisiana and Arkansas, age-ratios of harvested mallards may be as low as 0.4-0.6:1. It stands to reason that the later and longer hunting seasons run in winter, the proportion of adults harvested will be higher. Not only is harvesting a high proportion of adults potentially harmful to populations, most adults shot in late winter are already paired. Adults form pair bonds earlier than juveniles and typically pair with another adult (the better mate selection). If a member of a pair dies (from hunting or another cause), the surviving pair member must find another mate. By late winter, most of the better quality adults are already paired and the unpaired bird is left with the dilemma – “Are there any good mates left?”

Very early hunting seasons also “prey” on a nonrandom segment of duck populations. If hunting seasons start early in the north, some late-hatched young can

barely fly, if they can fly at all, and hunting on natal marshes is devastating to them. Further, many adult females that nest and hatch a brood late (perhaps because earlier nests were destroyed, forcing them to re-nest) remain on natal marshes well into fall because they are accompanying the late-hatched broods and undergoing their annual wing molt (when they cannot fly for six-to-eight weeks). Consequently, these “successful,” but late, females also are harvested at a high rate in natal marshes.

Understanding the types and degrees of these differences in sport harvest is essential to understanding the potential effects of various harvest regulations. The process of setting harvest regulations *must* seek to: 1) understand what proportions of “super hens” are killed each year, 2) document where and when “super hen” mortality is greatest, and 3) attempt to minimize deaths within this group.

Much remains unknown about contaminants, a second human-caused mortality agent. Some contaminants are differentially lethal to certain population segments, (e.g., agricultural chemicals used near prairie potholes affect nesting females and young broods). Since Rachel Carson wrote the book “Silent Spring,” we now appreciate the potentially devastating consequences of certain chemicals in our environment. Fortunately, the most potent organochlorines now are banned from use. However, many other highly toxic chemicals and naturally occurring heavy metals remain in use (or are present in the environment), including herbicides, pesticides, petroleum products, solvents, etc. Some of these chemicals may not directly kill a duck, but they can become “biomagnified” in body tissues of birds and reduce their reproductive capacity, or immunity to disease, or less favorable environmental conditions. Lead was one natural element that was widely distributed in hunted wetlands and exacerbated exposure to waterfowl. Lead shot is now banned from use in waterfowl hunting because of its lethal effects. It is our obligation to reduce or eliminate exposure of the other contaminants as well.

Life-cycle Models

Biologists have attempted to model the life cycle, along with annual and long-term changes, of waterfowl populations using a combination of recruitment (Part II of this series) and survival (Part III) estimates. Unfortunately, most models use average rates for the population in question rather than subdividing the population into segments based on heterogeneous recruitment and survival rates. If heterogeneity is not identified or accounted for, the estimates of survival and recruitment of the population that are based on “averages” can be highly biased and misleading. Doug Johnson and colleagues (see Selected References) provided an excellent example of the potential impacts of ignoring heterogeneity in such models.

Using a modification of Johnson et al’s example, consider a hypothetical mallard population of 1000 females with two groups – the “super hens” and the “duds.” Group 1, the super hens, comprises 20 percent of the population (200 birds), has an average annual survival of 80 percent (160 of the 200 survive in a given year), and an average annual recruitment of two young per breeding female. Consequently, the 160 surviving females produce 320 young for a total of 480 females the next year. Group 2, the duds, comprises 80 percent of the population (800 birds), has 50 percent survival (400 of the 800 survive),

and an annual recruitment rate of 0.5 young per female. This group of 400 surviving females produces 200 young the following year for a total of 600 females. Combined (480 super hens + 600 duds), the population now has 1080 females, or an 8 percent growth rate. Further, the proportion of super hens in the population now has increased from 20 percent to 44 percent of the population. Waterfowl managers like to be in this position (as would an investor in a stock portfolio) because contributions of the better quality females should be compounded (like interest) in future years.

Conversely, if averages are used for the above population, instead of separating the groups, then this population has 56 percent survival and 0.8 young/female recruitment and a total population size of 1008 females, an 0.08 percent increase. In this example, the super hen dominated population is actually growing nicely (8 percent), but the averaged statistics do not recognize the differential productivity of the super hens, and suggests the population essentially is stable (0.08 percent) with little growth. It also demonstrates why duck management should not overemphasize average nest success rates. In this example, 80 percent of breeding females had very poor (0.5 young/female) recruitment (only partly affected by nest success), yet the population grew well (8 percent) when it contained a modest (20 percent) amount of super hens that survived well.

Now, let's say some factor such as changed harvest regulations are capable of increasing by two to three times the annual harvest rate (such as liberal vs. restrictive AHM regulations or spinning-winged decoys that will be discussed in Part Four of this series). This alters the survival rate of the super hen group from 80 percent to 50 percent. In this case the duds still produce 200 young and have a total size of 600, but the super hen group has only 100 survivors that produce 2 young/each for a total size of 300. Combined the population now has only 900 individuals, a 10 percent annual *decrease* in population size, and a 17 percent reduction in recruitment compared to the prior year. Here, the decline in recruitment was solely caused by increasing mortality rate of super hens, not from any change in nest success, brood survival, etc. Stated another way, *only 60 more dead ducks (from an initial population of 1000) caused the population to go from growing eight percent annually to declining 10 percent annually.* A potential irony exists here: greater survival of a certain population segment may be more important to recruiting young than actual breeding success of the entire population. This begs the question: which is easier and less risky to achieve - changing hunting regulations to increase survival or changing habitat conditions across extensive breeding areas?

Johnson and colleagues further noted that "heterogeneity also can lend the appearance of compensation between hunting and natural mortality." Consider, for example, two subpopulations in equal numbers. In year one, birds in group A survive natural mortality at a rate of 80 percent and hunting mortality at a rate of 90 percent. Without compensation, annual survival is 72 percent (0.8×0.9). Birds in group B have corresponding survival rates of 60 percent and 80 percent, for an annual rate of 48 percent. The annual survival for the combined groups is 60 percent. If rates of hunting and annual survival were known precisely, survival from natural mortality would be estimated as annual survival divided by hunting survival ($.6/.85$) = 70.6 percent. Suppose now that hunting mortality rates are doubled for each group the following year. Hunting survival rates then drop to 80 percent and 60 percent, and annual survival rates decrease to 64 percent and 36 percent; the averaged annual survival rate is 50 percent. Survival

from natural mortality is now 71.4 percent. Thus, the natural mortality rate appears to decline as hunting rate goes up. Consequently, without considering heterogeneity, the natural and hunting mortality forces appear compensatory, *when in fact they are not*.

I apologize for the above math exercise, but mathematics are a necessary part of understanding how mallards are doing these days, and to comprehending the effects of current management activities, especially hunting regulations. Further, it is essential to recognize all of the factors in the equation to achieve the correct answer. In the above simplified examples, it should be clear that potentially huge mistakes could be made if heterogeneity is ignored. Part IV will take a detailed look at some “big” issues in the regulations debates and offer thoughts on how to avoid analytical mistakes and protect the “super hen.”

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THE SUPER HENS (Part IV): HUNTING REGULATIONS

By Mickey Heitmeyer

(Editor's Note: This is the final installment of our four-part series examining the broad scope of problems facing ducks, duck hunters and waterfowl managers. The author, Mickey Heitmeyer, one of the world's leading authorities on mallards, offers his conclusions and recommendations. Because of its semi-technical nature, it is recommended that you first print the article, then read from the printed page.)

* * *

***“Survival, particularly in the first year of life, is the major source of variance in reproductive success. Yet the major source of mortality is the North American hunter, an instrument of selection for only the past hundred generations of snow geese. He (or she) may be a relatively indiscriminating selective agent in terms of phenotypic characteristics that were important during most of the bird's evolutionary history”
(Cooke and Rockwell 1988)***

Waterfowl are among the most successful groups of birds in the world. The diversity of species, their mobility and awe-inspiring migrations, the amazing architecture of morphology and physiology, and an uncanny timing of annual cycle events that coincide with periods of increased resource availability and reduced mortality agents across the North American continent are mind-boggling. But the gnawing question remains: Have we so altered their environment; the timing, sequence, and successful completion of annual events, and their exposure to mortality agents that by default we have jeopardized their resiliency and capability to sustain populations? Like it or not, one of the factors that contributes to this dilemma is sport hunting. We, as hunters, must demand that the best scientific information be used to design, implement, and regulate waterfowl hunting seasons. Further, we must evaluate both science and regulations to see if our old friend (or foe) heterogeneity and the “super hen” are included.

Adaptive Harvest Management

In 1995, the U.S. Fish and Wildlife Service adopted the concept of Adaptive Harvest Management (AHM) to regulate duck harvests in the United States. Most waterfowl biologists initially embraced this “new” approach because it explicitly admitted that the consequences of hunting regulations could not be predicted with certainty, and it provided a framework for learning and making decisions in the face of

uncertainty. It also incorporated the virtue of “adapting” or changing decisions as new information is learned.

AHM was developed with the intent of dealing with uncertainties by: 1) offering a limited number of regulatory options (liberal, moderate, restrictive), 2) incorporating statistical models that would test hypotheses about harvest and environmental factors, 3) using an objective function that seeks to optimize the balance between maximizing harvest and maintaining a “viable” population over the long term, and 4) monitoring changes in population size to determine if regulatory changes are needed. AHM specifically sought to answer questions about whether harvest was “compensatory” or “additive” and whether density of birds had any effect on annual recruitment and survival.

All well and good, except for a few fundamental issues. First, the models did not initially define a “viable” population. Second, AHM regulatory options were based only on population changes of mid-continent mallards. Third, the only environmental variable used in models was the number of May “ponds” counted in the prairie-pothole breeding region of Canada. Further it assumed that duck production remains highly correlated with prairie pond numbers as historically was the case (at least since breeding surveys began in 1955) despite the fact that prairie ponds at the end of the 20th century have become highly degraded and are within modified landscapes where ecosystem processes have been highly compromised. Fourth, only four hypotheses (the various combinations of compensatory/additive and density dependence/independence) were deemed important and testable. Fifth, the objective function, which sought maximum harvest, was assumed to be the desire of the American duck hunter. And, finally, as you might suspect, analyses were based on “average” population parameters and did not incorporate heterogeneity (differences) within or among species.

Since initial implementation of AHM, some attempts have been made to address these problems. First, population viability now is assumed to be the species goals set by the North American Waterfowl Management Plan (NAWMP). The question is: Do these NAWMP goals actually represent true population viability in today’s modified landscapes? NAWMP goals are specifically stated to be numbers present under “average” long-term environmental conditions. Breeding mallard numbers have been at or above NAWMP goals in some recent years, but they certainly were not achieved under average environmental conditions (the late 1990s had nearly unprecedented “wet” conditions and high May pond numbers on U.S. breeding grounds). Second, some attempts have been made to include “other” mallard stocks such as those breeding in eastern areas, but, to date, inclusion of other stocks and species is limited. Third, biologists have repeatedly argued for inclusion of more comprehensive, and contemporary, measures of habitat conditions throughout breeding, migration, and wintering areas, rather than the singular Canadian “May pond” numbers used in predictive equations. But to date inclusion of other habitat measures and geographical regions has not been incorporated. Fourth, in a related issue, no changes in hypothesis testing has occurred, despite increasing evidence of other important population phenomena. For example, effects of density dependence/independence are not functions solely related to breeding habitat conditions.

Lastly, heterogeneity in population parameters (such as identified in life cycle models in Part III of this series) has not been recognized. Unfortunately, AHM is still too “simple.”

For many obvious reasons, simplifying harvest regulations is important both for the science of learning and for compliance by hunters. However, when simplicity trumps extensively documented knowledge of the multiple biological factors affecting population dynamics, it is unacceptable. The potential risk of making long-term mistakes with hunting regulations simply is too great. Mathematicians call these errors “Type I” and “Type II.” A Type I error rejects the null hypothesis (e.g. hunting is additive) when it is in fact true. Conversely, Type II errors accept the null hypotheses (e.g., density dependence) when it is in fact false. Either error type is dangerous for waterfowl management, and the failure to incorporate heterogeneity in population analyses increases the probability of both.

Additive vs. Compensatory Mortality

The question of whether duck hunting harvest is “compensatory” or “additive” (or both) to natural mortality from non-hunting causes (see Part III of this series) has been widely debated among waterfowl managers for nearly 30 years, yet we still are uncertain about it. Simply put, and as defined by Williams 2002 et al. (see reference list), the “compensatory” mortality hypothesis states that hunting harvest reduces density of ducks and thereby reduces natural mortality. In essence, if compensation occurs, harvest (at least up to some point) does not cause higher total annual mortality of populations. The alternative “additive” mortality hypothesis states that annual mortality from hunting adds to mortality from non-hunting causes and creates higher total mortality in populations. Based on the preceding discussions of heterogeneity, I submit that both additivity and compensation exist. In fairness, the first authors writing on this subject also believed both “compensation” and “additivity” existed. They hypothesized that harvest was compensatory up to some unknown “threshold” point, and then harvest exceeding that threshold became additive. This undoubtedly is true. At some point, if we kill too many ducks the population is going to decline no matter what (if any) compensation exists.

But the compensatory/additive concept is more complicated than a “size of the pile” threshold. It includes a “who is in the pile” factor. The preceding parts of this series have identified the substantial individual variation in populations, both in recruitment and survival. If a female that produces no or few recruits (for many reasons, including age, body condition, genetics, etc.) is killed, her mortality may be relatively unimportant to subsequent population changes and thus likely is compensatory (at least in part). In contrast, if a “super hen” is killed, it invariably will be an additive death (regardless of the number of other ducks killed) unless the bird is at the end of its lifespan and reproductive capability. Many other factors are involved also. For example, a bird that has consumed lead shot, one that is diseased, or one that has some morphological and physiological defect probably will die, and not produce recruits, so killing this bird probably is compensatory. Further, to a degree, harvesting a juvenile may be more compensatory than killing an adult. However, additivity is exacerbated if too many juveniles are killed (the source of the next generation) and if the juvenile is a progeny of the “super hen” genetic stock.

Obviously, much more information is needed before we completely accept, or dismiss, either compensation or additivity. But, heterogeneity of different species and population segments must be acknowledged and considered in analyses.

Early and Late Season Frameworks

The problems of early and late hunting seasons have already been discussed in this series. Much of the debate on this issue involves mallards because of their abundance and hunter preference for them. Early seasons kill a higher proportion of juveniles and late-nesting females. Late seasons kill a higher proportion of adults and paired birds. Both consequences can be detrimental to the reproductive potential of mallard populations depending on the extent that early and late seasons kill more successful “super hens.” Extended seasons likely are detrimental to other species also, especially early seasons on breeding areas where the multiple species collections of “brown” juvenile birds and females makes hunting more indiscriminate among species and sexes.

The “tit-for-tat” politics that caused the current extended beginning and ending dates for duck season frameworks are disgusting. Initially spawned by insolence from certain Mississippi politicians about the need for late January seasons, the pendulum swung to reciprocation demands for early seasons in northern states (and Canada). If, by default, either early or late seasons increases the mortality of “super hens,” then changes must be made.

I know this conclusion will not make hunters in either the north or south happy. It speaks of inequality in opportunity by geography. But who said the duck pie must be divided equally? God certainly didn't. Ducks are not distributed equally or randomly, nor should hunting be so. Further, in my opinion, the continuation of the contemporary lengthy season frameworks (both early and late) runs the high risk of changing waterfowl distribution in the future (e.g., next section on spinning-wing decoys).

Obviously, we need increased support for wetland and waterfowl conservation throughout North America from all segments (and geographies) of society. We also need stronger conservation leadership. Politicians and administrators fear the controversy of inequality lest a minority group cry oppression and seek to boot them out of office. But the reverse is true also. If the majority need is not met, then all suffer. Who has, or is willing to accept, the fiduciary responsibility for waterfowl in North America? For years duck hunters throughout North America have supported habitat programs in northern breeding areas (sometimes at the expense of their own local habitat programs) because they understood the need to produce ducks that would eventually migrate to areas where they could be harvested. Also, some northern hunters have contributed to habitat programs on wintering and migration areas because they understood that if nonbreeding habitat wasn't present there would be no ducks to return to breeding areas. Some geographical priority must be given to habitat conservation programs in both breeding and nonbreeding areas. Likewise, some geographical priority (that requires different regulations) must be included in harvest regulations. If that means changing the framework system, so be it.

Spinning-wing decoys

Another major issue that must be addressed involves the effects of spinning-wing decoys on duck populations. Many other hunting issues deserve discussion also [e.g., refuges, zones and splits, species-specific regulations (or the lack thereof), etc.], but space is limited and the reader may be tired of this by now. Perhaps later.

The use of electronic duck decoys, especially spinning-wing decoys (SWDs), became widespread across North America during the late 1990s. Today, more than 70% of duck hunters use them, at least occasionally, across the U.S. (percentages are higher in some states and locations). Why? Because they work. The greatest test tube in the world is a duck hunter. Duck hunters are relentless in the pursuit of things that will help them be more successful. The immediate and continued acceptance of, and massive expenditures for, SWDs by duck hunters have shown that their use increases the vulnerability of ducks to being killed. No further statistics or scientific studies are needed to believe this. If you don't accept this, then you haven't spent much time in a duck blind.

The scientific community believes this also. A California study showed that in paired tests (one group using, and one group not using SWDs) harvest rates of hunters using SWDs was six times higher in early season, four times higher in mid-season, and two times higher in late season. A Manitoba study showed mallard harvest was five times higher for hunters using SWDs in marshes and *24 times* higher in agricultural fields. A Missouri study found daily success for hunters using SWDs increased 13-19 percent, and in paired tests, harvest was 1.5 times higher for hunters using SWDs early and late season and three times higher in mid season. A Nebraska study using paired tests showed that hunters using SWDs harvested twice as many ducks in marshes and the mallard harvest was three to four times higher in late season. A Minnesota study found mallard flocks were 2.9 times more likely to respond to hunters, and sizes of flocks were 1.25 times bigger when SWDs were used. Mallard kill/hour/hunter was 4.7 times higher when SWDs were used. Juveniles were especially susceptible to SWDs. It was estimated that if 47 percent and 79 percent of Minnesota hunters (actual percentages now are above that) had used SWDs in 2000 and 2002, the mallard harvest in the state would have doubled.

Interestingly (and I don't think coincidentally), the distribution of mallard harvest has changed in the last six years since use of SWDs has become widespread. For example, in the combined Central and Mississippi Flyways, distribution of mallard harvest was 22.6 percent, 22.4 percent, and 55.1 percent in northern, mid-latitude, and southern states, respectively in the 1990s (pre-SWD). Since 2000, distribution of mallard harvest is closer to 30 percent, 25 percent, and 45 percent in northern, mid-latitude, and southern states, respectively. Additionally, the age-ratios (young per adult) of mallards harvested in these states changed. Pre-SWDs age ratios of mallards were 2.5:1, 2:1, and 1:1 in northern, mid-latitude, and southern states, but since 2000 the age ratios have averaged nearly 3:1, 1.5:1, and 0.5:1 in these same areas. The bottom line is that more birds, and more young birds, are being shot in northern states than ever before. Another interesting coincidence (maybe cause-and-effect?) is that hunter numbers and their

reported number of days hunted per year have increased dramatically in many northern states (e.g., North Dakota) in the Central and Mississippi Flyways since SWDs emerged.

Certain reviews of mallard harvest rates in the United States in the last two decades have indicated that total harvest rates have not changed since SWDs have been in existence. There seems to be a paradox here. How can numerous studies, and the hunter “test-tube” of high use of SWDs (greater than 70 percent) and increased number of hunters and days spent afield, all indicate major increases in vulnerability and total harvest of ducks, yet total harvest estimated from banding analyses and surveys of hunters remain the same? Is there some problem with the adequacy of banding analyses, sampling protocols, and surveys? I don’t know. Some suspect a problem in estimating band recovery rates that occurred after the inscription on bands was changed to include a 1-800 phone number in the 1990s. Reward bands have been placed on mallards and wood ducks over the past few years to identify the “new” reporting rates of bands associated with the 1-800 number and these data should provide more confidence in the precision and stability of recovery rates (that are used to calculate harvest and annual survival rates). Biologists typically assume that biases in sampling, banding, and analyses remain consistent among years/areas and therefore, even if the precision of estimates are “off,” that the trends in data remain useful. This may be true for some analyses, but if substantial heterogeneity exists among species, years, methods, etc., then the biases may be significant. This may be especially true for an estimate such as harvest rate, because even a slight deviation from “true” mortality rates of “super hens” can cause large variance in modeling population estimates (see Part III of this series).

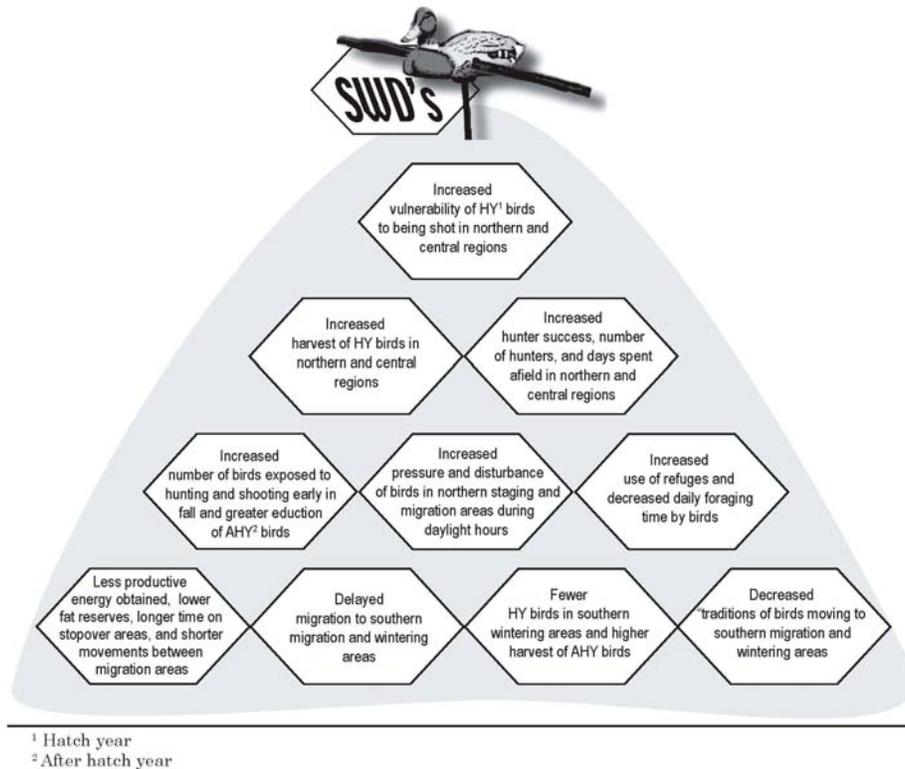
Even if total harvest rate of mallards in the U.S. (or within flyways) has not increased (unlikely from my point of view), the changed vulnerability of birds, and the changed distribution of harvest across latitudes after SWDs came on the hunting scene can still have demonstrable negative effects on populations. I offer an example that this time includes “heterogeneity”, instead of “size of pile” statistics. Consider a somewhat hypothetical (much data are real, however) harvest scenario for midcontinent mallards pre- and post-SWDs (Table 1 in Addendum). In this population, we have 10,000 female mallards (5,000 adults and 5,000 juveniles) present at the beginning of duck season. One-thousand subsequently are shot by hunters (a 10 percent harvest rate). Distribution of harvest pre-SWDs is 22.6 percent in northern states, 22.4 percent in mid-latitude states, and 55.1 percent in southern states. This leads to 585 juveniles and 416 adults being killed (a population average of 1.4:1 age ratio). Post-SWDs, we assume no change in total harvest rate (still 1000 total mallards shot), but we acknowledge the changed distribution of harvest and increased vulnerability of juveniles in various latitudes (Table 1). Now, post-SWD, 540 juveniles and 459 adults are shot. Consequently, even though total number of mallards shot (harvest rate) was the same pre- and post-SWD, the harvest of adults increased 10 percent. Simple math tells us more adults were shot in southern states post-SWDs because the population that migrated to the south contained more adults (i.e., a high proportion of young were shot in northern states and Canada).

A 10 percent increase in harvest of adult females may not seem significant to some, but if one follows the simple life model examples used in Part III of this series, this

10 percent increase probably includes many super hens (adult pairs that have lived to reach southern wintering areas) and their death could substantially decrease subsequent recruitment. Also, by simple math, more dead adults in the south (caused by higher harvest of young up north) could quickly decrease traditions of use by birds migrating to more southern areas and compound changes in both future bird and harvest distribution. Messing with evolutionary patterns of waterfowl migration and distribution, particularly in today's highly modified landscapes, is scary, often latent, stuff.

The problem with ignoring heterogeneity in waterfowl management decisions raises its ugly head again in this SWD example. In addition to making fundamental mistakes about population consequences, it also demonstrates the potential for many unintended consequences to occur. A flow-chart (Figure 1) shows the sequence of effects of using SWDs, some social, some biological, and all interrelated.

Figure 1. Flow diagram of effects of widespread use of spinning-winged decoys on mallard populations in the mid-continent U.S.



Furthermore, use of SWDs raises many issues related to the ethics of fair chase. Many of these ethical issues are similar to those dealt with years ago (and with much less biological data involved) when decisions were made to ban live decoys, baiting, electronic callers, and night hunting. I won't discuss this ethical dilemma here, but leave it to say, that in my opinion, this time we have both ethical and biological concerns with continued use of SWDs.

Conclusion

The objective of this series was to identify the importance of understanding, and incorporating, heterogeneity into future waterfowl population and habitat management programs. Specifically, I believe we must seek to better understand and protect the “super hen” component of all species and populations.

Heterogeneity is not new to waterfowl biologists and it has been incorporated into some programs (e.g., different harvest regulations for mallard stocks and sexes). I respect the ongoing efforts to improve management capability. Increasing the complexity of analyses and understanding is difficult, but I think possible. Having worked in the waterfowl business for nearly 30 years, I appreciate some of the difficulties in doing so, especially in today’s social and politically-oriented environment. Unfortunately: 1) waterfowl and wetland ecology curricula and research at universities are declining, highly fragmented, and less applied; 2) state, provincial, and federal resource agency biologists have less time, money, and motivation to work on waterfowl; 3) agendas of most non-governmental groups mainly are focused on raising money and seldom invest in science or improved understanding and application of complex or controversial issues; 4) the “farm-system” of developing future waterfowl biologists that are passionate and hunter-oriented is sparse; and 5) waterfowl hunters are increasingly disengaged from regulation and management programs.

Collectively, the waterfowl community of hunters, biologists, administrators, and policy-makers can help correct some of the declining emphasis on waterfowl/wetland programs and improve current waterfowl management by including heterogeneity concerns. Many needs have been identified in this series; and at the very least, I believe we should:

- Continue to expand long-term studies of key waterfowl species that attempt to understand lifetime reproductive success (LRS) and identify heterogeneity in population segments.
- Clarify reasonable indicators (e.g., early paired adults, better body condition, advanced plumage development, etc.) of “super hens” among species and populations.
- Develop monitoring programs to determine seasonal, annual, and geographical variances in “super hen” indicators.
- Develop population dynamics models that include multiple population segments based on known or potential varying reproductive and survival probabilities, including analyses of LRS for key species and populations.
- Support habitat and harvest management programs for multiple species and populations and not assume all duck species respond to programs like mid-continent mallards.

- Conduct specific analyses of harvest age-ratios and other “super hen” indicators related to temporal, spatial, and harvest regulations variables (such as SWD effects).
- Update AHM models to reduce problems outlined earlier in this Part IV AHM section.
- Improve education of, and communication between, hunters, biologists, and administrators on waterfowl management issues.

Obviously, hunters play a critical role in the future of waterfowl management. If changes in hunting regulations are warranted, and can reduce excessive mortality of “super hens,” then they offer a quick, less expensive, and probably a hunter-acceptable option compared to the longer term, expensive, and politically challenging work of changing habitat and predator populations over widespread geographical areas throughout breeding, migration, and wintering areas. Certainly, we must continue to invest for the long term in habitat programs, but we should not dismiss the contributions (short- and long-term) related to harvest regulations. At the very least, if one believes that heterogeneity is an important consideration in waterfowl management, then shortening season length frameworks, reducing hen bag limits and banning SWDs are “no brainers.”

We owe it to our wonderful waterfowl to use every tool and every piece of information possible to make better, more informed, decisions. May more “super hens” fly each year.

Addendum

Table 1. Effects of a changed distribution of harvest (total and young, adult) caused by use of spinning-wing decoys (SWD) on the percentage of adults killed in a hypothetical mallard population.

State Area	Harvest Distribution	# Birds Killed	Age-ratio of Harvest	Juveniles Harvested	Adults Harvested
<u>Pre-SWD</u>					
Northern	22.6	226	2.5:1	160	65
Mid-latitude	22.4	224	2.0:1	149	75
<u>Southern</u>	<u>55.1</u>	<u>551</u>	<u>1.0:1</u>	<u>276</u>	<u>276</u>
Total	100.0	1000	1.4:1	585	416
<u>Post-SWD</u>					
Northern	30.0	300	3.0:1	225	75
Mid-latitude	25.0	250	1.5:1	167	83
<u>Southern</u>	<u>45.0</u>	<u>450</u>	<u>0.5:1</u>	<u>148</u>	<u>301</u>
Total	100.0	1000	1.2:1	540	459

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If we take care of the ducks, the ducks will take care of us.
