Genetic improvement of captive-bred raptors
By Toby Bradshaw
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[*NB*: Quantitative geneticists will recognize that the description below is overly simplified. I have done this deliberately to make the basic genetic principles of selection accessible to the average reader. For those seeking a more detailed understanding, I recommend the books *Introduction to Quantitative Genetics* by Falconer and Mackay and *Principles of Plant Breeding* by Allard.]

For a little more than 50 years raptors have been bred in captivity, primarily for research, reintroduction to the wild, or falconry. Over the past three decades captive breeding has become an increasingly important (and in some countries, exclusive) source of hawks and falcons for falconry. It seems clear that captive propagation will continue to be critical to the future of falconry. Much has been written about the mechanics of captive raptor propagation and training of the hawks and falcons produced by captive breeding, but the genetic principles of long-term captive propagation have received less attention.

Some falconers will insist that "the falconer makes the hawk" – that is, a good falconer can be successful with any hawk, and the differences among hawks are the result of training rather than any inborn qualities. In other words, "nurture" trumps "nature." The truth is more complicated than this, as anyone who has flown a large number of hawks can attest. A trained hawk, like a trained dog or horse, is the product of both its genes and its environment. No hawk, however well-bred, can achieve its full potential without skillful handling. Conversely, no falconer, however skilled, can make a genetically inferior hawk into a great gamehawk, any more than he can train a French bulldog to trail rabbits as well as a beagle does, or turn a plow horse into a winning race horse.

The purpose of this article is to shed light on the genetics of captive-bred raptors for falconry, to help propagators and falconers define and achieve their goals. Fortunately,

we have a long history of plant and animal breeding, as well as a large body of population genetics theory, to guide us.

Goals of captive breeding

Given that falconry was practiced with millions of hawks and falcons for thousands of years before the first raptors were bred in captivity, it follows that captive propagation of raptors must be a difficult and demanding endeavor. Perhaps it should come as no surprise that the chief goal of most raptor breeders has been simply to produce live, healthy young hawks and falcons. Any propagator will remember with crystal clarity the first egg, the first hatchling, and the first kill with a captive-bred hawk or falcon that he or she "made."

But now that reliable methods for establishing natural breeding pairs, artificial insemination, incubating eggs, and rearing young have been developed by a generation of dedicated propagators/falconers, it is time to set more ambitious long-term goals for captive raptor populations that go far beyond just producing just another crop of offspring. Without specific goals for a breeding population, basic principles of population genetics tell us that the quality of captive-bred hawks and falcons will wander around the current average – improvement (by any standard) will just be an accident. Some falconers and breeders may, in fact, subscribe to the idea that no improvement is required, in which case they need read no further.

But for those of us who see the untapped potential in captive-bred hawks and falcons, what sorts of goals might be set by a breeder, or a community of breeders working with the same species? Here are some examples:

Appearance. This has been done already for a few generations of large falcons (and their hybrids) to produce very white or very black progeny, which command the highest prices on the global market. Breeding for appearance is commonplace in domesticated animals, where carefully written breed standards define perfection of form, and show-ring judges decide which animal conforms most closely to the written standard. Variation in physical traits (*e.g.*, color, body size, body shape) often is highly

heritable and easy to measure accurately, and thus responds rapidly to selection by the breeder.

Retaining close connection to wild populations. For many falconers the essence of the sport is working with the "wildness" inherent in a bird of prey. Such falconers always prefer a wild-taken hawk or falcon to its captive-bred counterpart, but for reasons of legality (*e.g.*, in much of the European Union where there is no longer access to wild raptor populations) or convenience will fly a captive-bred bird that matches as closely as possible the genetics and behavior of a wild hawk or falcon. Population genetic theory and many experimental results tell us that ultimately a close genetic connection between captive and wild populations can only be maintained by regular infusions of genes from wild populations. This does not require a large take from the wild – as few as one wild parent added to the captive gene pool every generation will prevent the captive population from diverging from the wild population by more than 20% (except at genes where selection in captivity is strong – *i.e.*, "domestication" genes), and five wild parents added per generation would reduce the possible divergence to less than 5%. [It is an interesting twist of population genetics that the number of wild parents needed to maintain the "connection" is independent of the size of the captive population.] If captive propagation extends across many generations without the influx of "wild" genes, it is inevitable that considerable domestication will occur as the captive population diverges genetically from the wild population. Even if the breeder does not consciously select for "domesticated" traits, those parents better adapted to the captive environment will reproduce at higher rates, leading to the evolution of domestication. Essentially all crop plants and animal breeds were domesticated in this unconscious fashion – selection does not have to be intentional to be effective. I think this is a strong argument for maintaining a modest wild take for propagation purposes even in countries where a falconry take is not allowed.

Managing genetic diversity. The long-term survival of a captive population (*i.e.*, a closed, finite gene pool) depends upon having adequate genetic diversity in the founding population, and maintaining that diversity across generations. A rule of

thumb in conservation genetics is that long-term persistence in captivity requires a founding population of approximately 500 individuals (as unrelated as possible). Few (if any) captive raptor populations have at least 500 unrelated founders. Small, isolated populations, typical of captive raptor species, are particularly vulnerable to extinction by "genetic decay." Careful management of genetic diversity through pedigree analysis (sometimes assisted with DNA-based methods for determining relatedness) can preserve genetic variation and reduce the rate of inbreeding if those are the program goals.

Improvement for falconry purposes. Although falconry bears some resemblance to a hawk's hunting in the wild, clearly there are enough differences to prevent the "perfect falconry hawk" from also being the "perfect wild hawk." For instance, nearly all hawks and falcons flown in falconry routinely catch much larger prey than they would in the wild. Larger-than-average body size, or behavioral willingness to tackle large quarry, therefore might be an advantage in falconry, but not in the wild. Similarly, a suspicious, nervous disposition can have survival value in the wild, but is detrimental to falconry performance. Large muscles for exceptionally fast flight might be desirable in a falconry bird, but too costly to maintain for a wild hawk uncertain of its next meal. One need only observe the difference in musculature and speed between a racing homing pigeon and its feral cousin to see the contrast in outcome between artificial selection and natural selection. There is the potential to breed hawks and falcons that are superior for falconry in the same way that racing homing pigeons (and countless other pigeon breeds) have been produced from rock doves by selective breeding. The fundamental basis of artificial selection is outlined below.

The "Breeder's Equation"

Current captive raptor populations are at most a few generations removed from the wild, and (with a very few exceptions) no effective selection for improved falconry

performance has yet been applied. For simplicity's sake, we can consider that today's captive raptor populations are a random sample of the wild populations – the average captive-bred hawk has roughly the same genetic potential for falconry as the average wild-taken hawk.

Assuming that the goal of captive propagation is to produce hawks and falcons better suited to falconry than the current average (*i.e.,* better than the average wild hawk or falcon), we can apply the breeder's equation, which describes the change in a trait within a population as a result of selective breeding (artificial selection, in this case):

Change in average trait value = Selection differential x Heritability

From this equation two things are immediately apparent. To make the most rapid progress possible in selective breeding (*i.e.,* greatest *change in average trait value* within the population), both the *selection differential* and the *heritability* should be large numbers.

The *selection differential* depends strongly upon the size of the starting population from which selected parents are drawn – the larger the population, the greater the selection differential possible, and the more rapid progress will be under selection. In agriculture, it is common to select a small number of parents from a population of thousands, or even millions, of potential breeders. Choosing a tiny number of elite parents from a very large starting population maximizes the selection differential. Intense, deliberate selection of a few parents from a large sample of potential parents has almost never been done in raptor propagation. Now is the time to start.

Heritability depends upon the relative contribution of genetics and environment to the variation in a trait. If trait variation is largely under genetic control, and is relatively insensitive to environmental influences such as diet, temperature, or training during the

growth and development of the hawk or falcon, the numerical value of heritability can approach its maximum value of one. Feather pigmentation is a good example of a trait with high heritability. When we see an exceptionally darkly pigmented adult hawk or


falcon, there is good reason to believe that its offspring will be darker than average as adults. I don't know of any formal studies of feather pigmentation heritability in captive-bred raptors, but based on studies in other animals I would expect feather pigmentation to have a heritability in the range of 0.7-0.9. Highly heritable traits respond rapidly to selection.

Unfortunately, many traits of great interest for genetic improvement (such as tameness, flight speed, footing, willingness to attack large quarry, or propensity to wait on) are strongly affected by environmental variables as well as by genetics. A trait whose variation was entirely the result of environmental influences, with no genetic contribution, would have a heritability of zero and would not respond at all to selection.

The only way to tease apart the effects of genes and environment is to rear the offspring from many pairs of parents in a common environment (*i.e.*, without environmental variation), so that any differences among the offspring must be due to genetics. Despite the lack of formal estimates of heritability for these behavioral/performance traits in captive-bred raptors, every hawk or falcon breeder who has more than a few breeding pairs will have observed that there is tremendous variation in traits of interest for

falconry among the offspring of different pairs, even though all of the offspring have been reared and trained in a very similar environment. There is vast potential for genetic improvement of behavioral traits in hawks and falcons, perhaps with the same far-reaching effects on falconry that the domestication of the wolf to produce the hunting dog breeds has had.

Selection differential is the difference between the trait value in the whole population, and the trait value in the subset of individuals selected for breeding. Suppose that the primary goal of a breeder is to produce peregrines with higher flying weights, under the assumption that a heavier tiercel will be more capable on mallards than the average tiercel, and that a heavier falcon will be more capable on sage grouse than the average falcon. If we graph the flying weights of a hypothetical sample of captive peregrines (multiplying the weight of each tiercel by a factor of 1.4, to adjust for body size dimorphism so that both sexes can be placed on the same graph) we would expect a bell-shaped curve (*i.e.*, a normal distribution; Fig. 1).

Fig. 1. Peregrine flying weight distribution
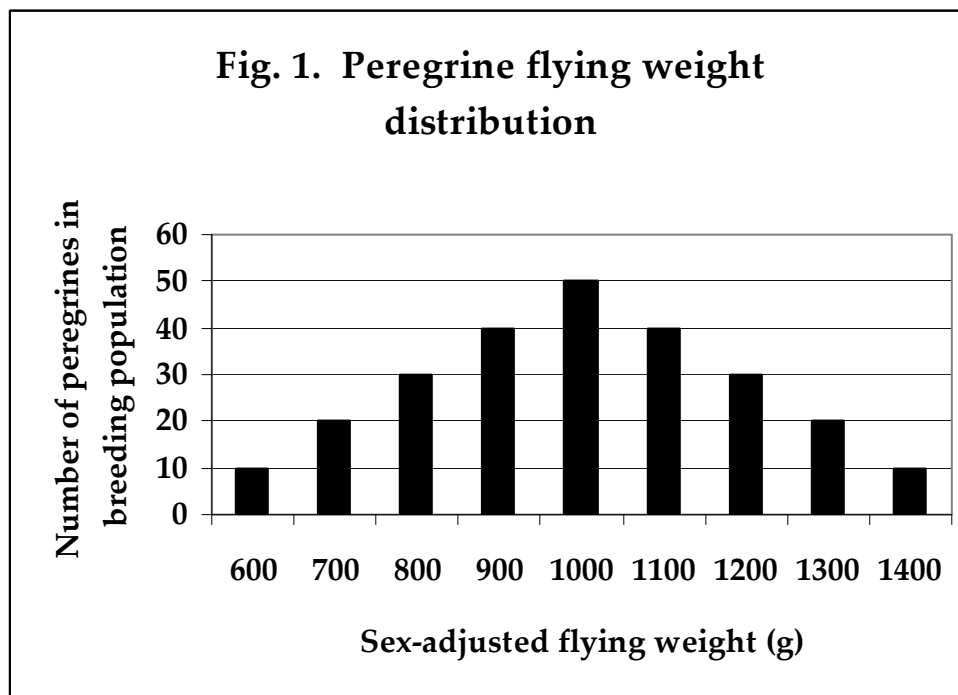
In the left-hand tail of the bell curve we have a few very small peregrines, in the right-hand tail of the curve we have a few very large peregrines, and in the middle of the curve we have many peregrines at intermediate weights. The peak of the curve (1000g) – the most commonly observed weight – is also the average flying weight of the whole population of falcons (and divided by 1.4 would give the average flying weight for tiercels, 714g).   Of course, we expect that the right-hand tail of the bell curve

(containing the heaviest peregrines) will be dominated by individuals from the larger subspecies (*e.g.*, Peale's peregrines), but the same principles could be applied within a subspecies of peregrine if desired by excluding all other subspecies from consideration.

Clearly, the larger the starting population, and the more variation present in that population, the greater the selection differential that can be achieved by choosing the very few parents with the most desirable traits to produce the next generation of offspring. **Large, highly variable starting populations are the key to making genetic gains by selection. Genetics and breeding are numbers games, and it is the small number of hawks and falcons kept by most breeders that has limited progress thus far.**

The *selection differential* is calculated in this way:

(Average weight of birds selected as parents) – (Average weight of current population)

If the breeder chooses the ten heaviest parents (the rightmost bar in the graph) from the whole population of 250 peregrines, the average sex-adjusted flying weight of the *selected* parents is 1400g (remembering that the heaviest tiercels would actually weigh 1400g/1.4 = 1000g on average). Since the starting population of 250 peregrines has an average sex-adjusted flying weight of 1000g, the selection differential is:

$$1400g – 1000g = 400g$$

So, if we breed the highly selected parents with an average sex-adjusted flying weight of 1400g, can we expect their female offspring to have an average flying weight of 1400g and their male offspring to fly at 1000g? The short answer is, "No." By examining the Breeder's Equation above it is clear that the change in trait value (flying weight, in this case) *is equal to the full value of the selection differential **only** if the heritability is one.* In practice, trait heritability will almost always be less than one, so the genetic gain in the next generation will almost always be less than the selection differential. For instance, the heritability of body weight in chickens is about 0.55 (*i.e.*, about 55% of the variation in chicken body weight is due to genetic variation, while 45% of the body weight variation is due to environmental variation, such as diet). If we assume for the moment that flying weight in peregrines also has a heritability of 0.55, then we can estimate the

flying weight of the female offspring from our highly selected parents using the Breeder's Equation:

Change in average trait value = Selection differential x Heritability
= 400g x 0.55
= 220g

The Breeder's Equation predicts that after just one generation of selection the female offspring of our selected parents should fly at an average of 1220g; that is, 220g heavier than the 1000g average flying weight of the starting population, with tiercels flying at an average of 871g. Selection for flying weight has been effective, moving the whole population flying weight distribution to the right of the distribution shown in Fig. 1, and producing 30 (out of 250) offspring larger than any of the peregrines observed in the starting population (Fig. 2).

Fig. 2. Response to selection for increased flying weight in peregrines
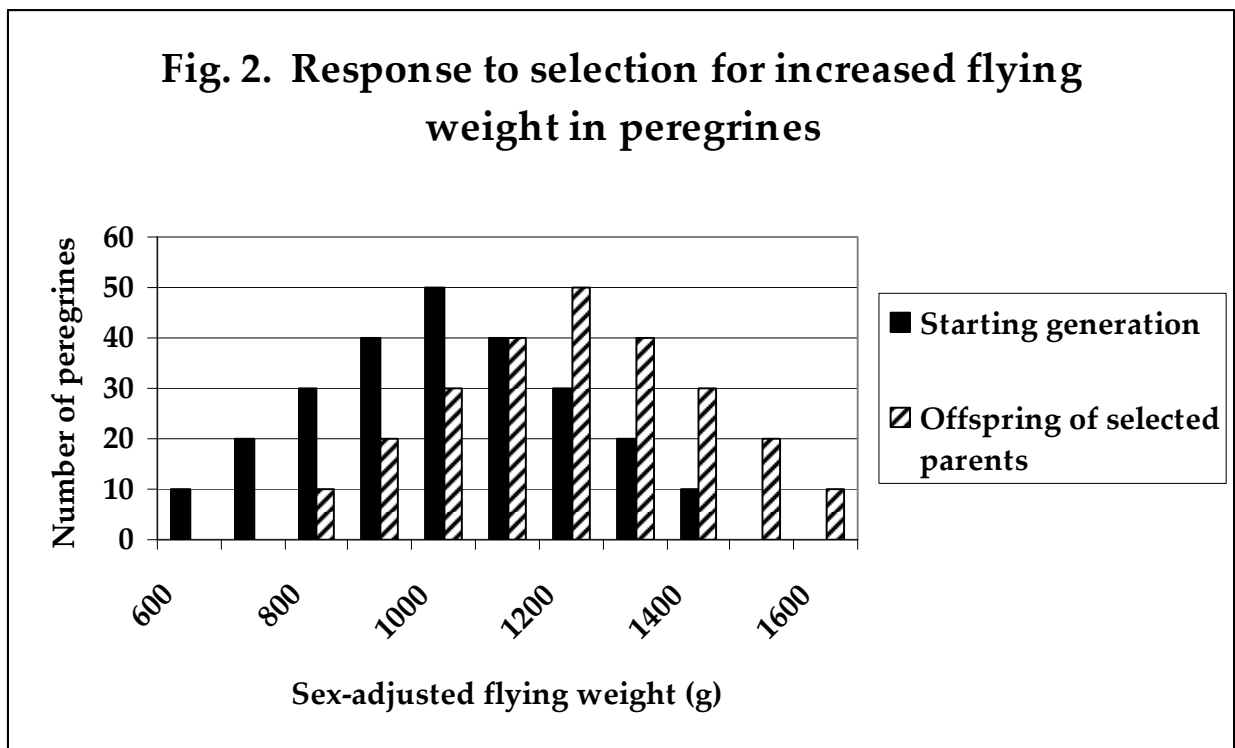
I chose flying weight as an example because it is an easy trait to measure precisely and unambiguously, as all falconers know from daily experience. At first blush, it may seem that weighing a peregrine gives us a direct estimate of the underlying genetic contribution to body size, and that the heritability of flying weight might be considerably higher than the 0.55 we used in the example above. A higher heritability

would result more rapid gains under selection. But is the determination of the *genetic* variation in flying weight among peregrines really as simple as putting 250 different peregrines on a balance? Or is there *non-genetic* ("environmental") variation that also contributes to variation in peregrine flying weight, but which cannot be transmitted to the offspring? Obvious sources of non-genetic variation contributing to variation in flying weights include the age of the falcon, its physical condition, whether it is an imprint or a chamber-reared bird, the degree of control preferred by the falconer, and so on. Such non-genetic variation reduces the heritability even of a seemingly simple trait like flying weight.

As far as I know, we have no reliable, quantitative heritability estimates for *any* trait in captive-bred raptors, making it impossible to predict with confidence the *magnitude* of change in the selected trait. However, as long as at least some of the observed trait variation has a genetic basis (*i.e.*, heritability > 0), selection always will produce change in the desired *direction*.

Selection for behavioral and performance traits

The Breeder's Equation can also be applied to traits that are more complicated than plumage color or flying weight. Behavioral traits (*e.g.*, tameness, sociability, intelligence) and hunting performance traits (*e.g.*, flight speed, willingness to wait on, footing skill, intensity on game) are likely to be more difficult targets for selection because they are hard to quantify, or are strongly affected by non-genetic factors (*e.g.*, rearing, training, conditioning, hunting experience) which reduce heritability.

But it would be a grave mistake to give up and assume that critical (but complex) behavioral and performance traits will not respond to selection in hawks and falcons. We know from the history of animal domestication and breeding that such traits *do* respond to selection. Greyhounds are much faster than wolves, thoroughbreds are much faster than Przewalski's horses, homing pigeons are much faster than rock doves, and Siamese cats are much tamer and more social than African wildcats. Great progress with hawks and falcons is, therefore, possible.

The keys to making progress in selecting hawks and falcons for improvement in behavioral and performance traits are to: 1) devise and implement a quantitative measure for the trait(s) of interest; and, 2) standardize the rearing, training, and hunting environments of all potential breeders as much as possible, so that the measured trait values are truly comparable.

The silver fox experiment. The most compelling and well-documented example of manipulating the behavior of a wild animal by artificial selection is the deliberate domestication of the silver fox (*Vulpes vulpes*) by Dmitry Belyaev, Lyudmila Trut, and their colleagues at the Institute of Cytology and Genetics in Novosibirsk. Beginning in 1959 with 130 fur-farm foxes (essentially the equivalent of most of today's early-generation captive-bred raptors), Belyaev's group applied strong selection for one trait: a positive social response to human contact which they referred to as "tamability." Initial breeding experiments yielded a heritability estimate of 0.35 for tamability, suggesting that genetic improvement for this trait could be quite rapid if strong selection was imposed. Over the next 35 generations more than 45,000 fox pups were scored for their reaction to human contact (feeding, petting), with only 5%-20% of the "friendliest" offspring retained as parents of the next generation (*i.e.*, a high selection intensity). In that 40-year time span, the fox population evolved from predominately Class III behavior (flee from humans, bite when handled) to predominately Class I elite behavior (actively seek out human companionship even when other foxes are present, lick and nuzzle humans affectionately).

Several things about the silver fox domestication experiment are worth noting (and emulating). First, the scientists established clear scoring criteria for "tamability." This standard was applied throughout the experiment. Second, the research team estimated the heritability of tamability, in order to predict the response to selection. Third, strong selection was applied, with only the top-scoring 5% of males and 20% of females retained for breeding in each generation. Fourth, large numbers of offspring (approximately 1000 per year) were reared in standardized conditions and scored for tamability. Finally, the experiment spanned 35 fox generations, ample time to increase the frequency even of rare genes contributing to the desired trait within the fox population.

The Coulsons's Harris's hawks. Are there any hawk or falcon breeding efforts comparable to Belyaev's silver fox experiment? The only one I know of is Tom and Jennifer Coulson's Harris's hawk breeding and selection program, which, like Belyaev's foxes, has focused on tameness as a primary selection criterion (in addition to superior hunting ability once trained). Over the past 26 years and 5 generations, the Coulsons have tested 28 male parents, 31 female parents, and 45 different pairings by scoring their 900+ offspring for tameness and sociability in a standardized rearing and training regime. Tom and Jenn have personally flown more than 100 of the selected offspring to identify parents for each successive generation.

Those of us who fly and breed the advanced-generation progeny from Tom and Jenn can attest to the effectiveness of their selection scheme. These hawks have such dog-like

affinity for humans that they practically train themselves, and are exceptionally capable in the field.

Figure 3. My female Harris's hawk "Q", feeding the 5th generation of line-bred (White Wing) offspring selected for tameness and hunting ability. Obviously, both Q and her young are completely at ease with humans and cameras, since this photo was taken at a range of about 18 inches!

Recommendations for the future

Genetic gains resulting from selection depend on two things: 1) a well-defined goal (*e.g.*, increased flying weight, greater tameness, plumage color, or flight speed); and, 2) a large starting population of parents having genetic variation for the trait(s) under selection. We have at least two examples of demonstrable genetic gain in captive-bred hawks and falcons: plumage color in gyrfalcons (and their hybrids) and tameness in Harris's hawks. The vast majority of raptor propagators have too few pairs or offspring, and too little turnover of generations, to make selection effective, and these have been the most serious impediments to progress.

The role of breeding consortia or cooperatives. Raptor breeding cooperatives have the potential to overcome the limitations of small numbers of breeding pairs by "pooling" pairs and progeny from many small-scale breeders. If a group of propagators could agree on a specific target trait for selection, standardize the measurement of this trait (including making rearing/training environments as similar as possible) in the all of the offspring, and commit to a long-term plan for replacement of breeders with elite, selected offspring, the whole falconry community could benefit.

Record keeping and public pedigree/performance databases. In the U.S., raptor propagators are required to keep pedigree records on their captive-bred progeny, yet there is no requirement to report this information (even to the U.S. Fish and Wildlife Service). As a consequence, there is no way for current breeders to assess the relatedness of their stock to that of other breeders, nor for a beginning breeder to know whether his/her new pair are unrelated or are brother and sister. Thus there is no effective management of genetic diversity, inbreeding, genetic improvement, or any other aspect of propagation that extends across generations.

The sole exception to this disturbing lack of pedigree information is BaywingDB, a public database for pedigree and hunting performance information for Harris's hawks (http://home.comcast.net/~baywingdb). Even BaywingDB, with more than 1300 Harris's hawks recorded for the past 30 years, is incomplete. Data contribution is entirely voluntary, and most small-scale breeders are unaware of the need for, or value of, such detailed multi-generation information.

Estimating heritability. It would be valuable scientifically, and from a purely practical viewpoint, to estimate the heritability of traits under selection. While such estimates are not necessary to make progress in the right direction, they do give us the ability to predict rates of evolutionary change in response to selection. As long as trait data are entered into pedigree databases, heritabilities could be estimated.

Turnover of generations. Most breeders are reluctant to break up a successful breeding pair, since it takes several years for a pair to reach sexual maturity and being producing offspring. Hawks and falcons are long-lived, with many breeding pairs in full production well into their 20s.

Yet, evolutionary gains in response to artificial selection are maximized by rapid turnover of generations, as in the silver fox experiment where a new cohort of parents was selected every year. If hawk and falcon breeders are really committed to finding the fastest route to genetic improvement, it will require testing the first few offspring

from each breeding pair, assessing the quality of those offspring, and selecting the best of those early offspring as parents for the next generation.

The "demand" side of genetic improvement. No rapid genetic improvement of hawks and falcons for falconry purposes is likely to take place unless and until falconers themselves demand superior eyasses from breeders. At the moment, except for plumage color and body size, the average falconer has shown virtually no interest in paying a premium for eyasses that are the product of effective selection for traits that really matter: tameness, hunting desire, athletic ability (*e.g.*, speed, footing), sociability, or intelligence. If falconers gave half as much thought to the pedigree of their hawks and falcons as they do to their hunting dogs, and were willing to pay up front for genetic superiority that pleasurably manifests itself for the next 10 or 20 years of hunting, the incentive structure for raptor propagators would change dramatically for the better.

Someday soon I hope that falconers realize that it is the genetically inferior hawk, which never fully repays the effort of training and flying it, that costs more in the long run!

Good hawking!

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